LIFE ON EARTH

An Encyclopedia of Biodiversity, Ecology, and Evolution

Prepared in collaboration with the
American Museum of Natural History

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An Encyclopedia of Biodiversity, Ecology, and Evolution

VOLUME 1 A–G

Edited by Niles Eldredge

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Introduction

Life has been on Earth for at least three and a half *billion* years—an incomprehensibly long period of time. Earth itself is just over four and a half billion years old. The oldest rocks we know are about 4 billion years old—but they are granites, cooled from a molten melt, so they cannot be expected to contain any remains of ancient, fossilized life. The oldest sedimentary rocks—the very kind of rocks that often *do* have fossils in them—that were formed from grains of silt and sand deposited in ancient seaways are around three and a half billion years old. These most ancient sediments have yielded traces of early bacterial life on earth. If the oldest rocks that could possibly contain fossils *do* have fossils, we can only assume that life inhabited earth more than three and a half billion years ago—in other words, we would expect to find the chemical and fossil evidence of even older bacteria if we were to get lucky and find even older sediments. Life, we can only conclude, has been an integral part of the earth almost since the world began.

It took nearly one and a half billion years before more complex cells evolved: the eukaryotic cells we have in our own bodies, the sort of cell we share with all other animals, as well as plants, fungi, and single-celled, mostly microscopic protoctistans like amoebae. Then it took another one and a half billion years for multicelled animals (and even later for plants) to evolve. Life's evolutionary history is full of long periods where nothing much seems to happen before the next big evolutionary advance (often an increase in complexity). The evidence is increasingly mounting that innovations throughout the evolutionary history of life have been triggered by major, physical environmental events that disrupted older systems and spurred the development of the newer ones.

Consider the major mass extinctions of the past half billion years or so—the ones that disrupted life so much, driving great groups like the terrestrial dinosaurs to extinction. There have been five of these global mass extinctions, and each one has profoundly altered the course of evolutionary history. If dinosaurs had not died out—victims of the explosive collision between the earth and one or more comets 65 million years ago—mammals would not have begun to evolve into the tremendously diverse array of species we have seen on Earth in the last 60 million years. That means that we, human beings of the species *Homo sapiens*, members of the mammalian Order Primates, would not be here.

We cannot understand life—what it is and how it got to be the way we find it today—without also understanding how life fits into the physical dynamics of the earth—its waters (hydrosphere), its gaseous envelope (atmosphere), and its rocks and soils (lithosphere). The history of life and the history of our planet are inseparable. Life on earth continues to exist as an integral part of the physical system, which is its home and its source of sustenance.

Now we find that life is confronted by something not seen for 65 million years: the very real threat of a major mass extinction, a loss of species so rapid and so great that it rivals the five preceding global mass extinctions. The Sixth Extinction. Harvard biologist E. O. Wilson has estimated that the earth is losing species at the rate of three *every hour*—30,000 species a year. Though we are not sure exactly how many species exist on the earth right now, there are at least 10,000,000 of them. Though there is no way that humans will end up removing absolutely all of the earth's species, most will surely be gone during the next 1,000 years if this rate of loss continues unchecked.

This Sixth Extinction is also known as the Biodiversity Crisis. Like the mass extinctions of the past, the Sixth Extinction is the result of the abrupt and devastating loss of habitat for species in nearly all the world's ecosystems. Unlike the five mass extinctions of the geological past, however, this one is not being caused by comets crashing into the earth or by climatic change overwhelming the earth's species—its cause can be traced to the actions of a single species: *Homo sapiens*. We are the ones who are cutting the forests, plowing the prairies, paving the landscape, and building the cities. We are the ones overharvesting the world's fisheries and forests. We are the ones polluting the rivers, lakes, and oceans. We are the ones moving animals, plants, and microbes around the globe—often to the detriment of local species. We are the ones behind this Sixth Extinction—the human equivalents of the comets that came close to destroying life on earth 65 million years ago.

We should ask ourselves: Does it matter? Should we be concerned that we are destroying, faster and faster, so much of the world's remaining wilderness and driving more and more species to extinction? After all, we no longer live within local ecosystems; we have not done so since we invented agriculture 10,000 years ago and took food production into our own hands. So why should we care that we are destroying the rest of the ecosystems and species of the planet?

Well, of course, it *does* matter. We are living, breathing animals, after all. We need clean air. We need water—nearly a third of the 6 billion of us on the planet right now do not have access to safe drinking water! We need those fisheries in the ocean—and those trees in the forest (though it is high time we think about sustainable harvesting so future generations can eat fish and use wood to build houses). We need oxygen—and the many chemical cycles essential for all life (certainly including our own) that are essential functions provided only by healthy, intact ecosystems. And, many of us increasingly think, we need nature around us because it is where we came from—it is an essential part of us, as we are a part of it. It is beautiful, this natural world. We need it for that reason alone.

That's what this encyclopedia is about. Far more than just another reference on natural history, far more than a great source of information on ecology and evolution, this book tells us about the earth, about life, and about how humans fit into the scheme of things. It tells us, too, how we are destroying the very fabric of life, why we should not destroy it, and what we can do about stemming the tide of the Sixth Extinction.

We begin with four expansive essays exploring the four questions: What is biodioversity? Why is biodiversity important? What are humans doing to cause the loss of so many species? And, finally, what can we do to stop the loss?

Then, in familiar A–Z format, we present incisive entries on a surprisingly wide range of topics. We are talking here of humans on the planet—what our history has been, how we fit in it, how we cause major ecosystem disruption and species loss, and why and how we should correct our course as we continue collectively to sail through life. To provide a reference that will meet such demanding needs, we have assembled entries in anthropology, archeology, economics, and sociology; geology is also presented, as we need to understand the physical structure of the earth as well as its history. Paleontology is here, too, as we need to understand the history of life—how it came to be the way it is—before we can understand its present condition.

And, because biodiversity—all the species represented in all the world's ecosystems—is a double-identity subject, we include entries from the two central subjects: ecology and evolutionary biology. We need to become familiar, if not with each of the 10,000,000 species on earth, at least with the major groupings of life—from bacteria to redwood trees—that evolution has produced. These are the players in the game of life. On the other hand, the actual game of life is played in the world's ecosystems—comprised of a mélange of players drawn from the bacterial, protoctistan, fungal, plant, and animal basic divisions of the evolutionary spectrum of life. You cannot understand biodiversity unless you realize it is two-sided: first, there is a spectrum of living organisms, from bacteria to redwood trees to ourselves, produced by evolution, and second, there is a world in which matter and energy flow between organisms—the world of ecosystems. Biodiversity is not a dry summary of the principles of ecology and evolution (though both are in this volume in great detail!); rather, biodiversity is the interplay between these realms and beyond, encompassing the physical earth systems in which life exists. Given the role that humans are playing on Earth, biodiversity encompasses all that is human (and all we know about who humans are), how we have evolved, and how we fit into the world around us.

Our hope is to awaken curiosity and to inspire younger generations to gain the wisdom and courage necessary to confront the complex issues of the twenty-first century. May this encyclopedia help you on your way to learning about the world in which you live—and to discover ways in which humanity might continue to prosper without destroying the earth from which we came and on which we still so deeply depend.

What Is Biodiversity?

The question "What is biodiversity?" lies at the crux of this entire encyclopedia, not to mention efforts to conserve biodiversity. Yet as you will see, the answer to this question is complicated, depending upon who is defining biodiversity and for what purpose. When we choose a strategy for conserving biodiversity, we want to evaluate the success of that strategy. One way we do this is to take initial measurements of biodiversity and monitor how it changes over time. Key to this process is choosing how you define and measure biodiversity.

Definition of Biodiversity

Biodiversity, an abbreviation of the phrase *biological diversity,* is a complex topic, covering many aspects of biological variation. In popular usage, the word *biodiversity* generally refers to all the individuals and species living in a particular area. If we consider this area at its largest scale—the entire world—then biodiversity can be summarized as "life on earth." However, scientists use a broader definition of biodiversity, designed to include not just the organisms themselves but also the interactions between them, and their interactions with the abiotic (nonliving) aspects of their environment. Multiple definitions, emphasizing one aspect or another of this biological variation, can be found throughout the sci-

***A male adult palmate newt,* Triturus helveticus. *Biodiversity refers to all organisms on earth, the interactions between them, and their interactions with their environment.* (George McCarthy/Corbis)**

Figure 1

The Levels of Organization for Biological Diversity

Genetic Diversity: The different forms of a single gene found in an individual and the variation of genes and chromosomes between individuals

Organismal Diversity: Variation in the anatomical, physiological, and behavioral characteristics of individual organisms

Population Diversity: Variation in the quantitative and spatial characteristics of populations, such as the numbers of individuals present and the geographic range of the population

Species Diversity: Variation in the number and phylogenetic diversity (or evolutionary relatedness) of species present in an area

Community Diversity: Variation in the ecological interactions between organisms, populations, and species that share an environment and the different types of communities that are formed

Ecosystem Diversity: Variation in the interdependence of biotic communities and the abiotic (nonliving) aspects of the environments in which the biotic communities are found

Landscape and Seascape Diversity: Variation between landscapes and seascapes, based on the different types of ecosystems they compose

Biogeographic Diversity: Variation of the evolutionary history of the biota of a region (and hence the current species diversity) is related to the geological and geographic history of that region or landscape

entific and lay literature (see Gaston, 1996, Table 1.1). For the purposes of this essay, biodiversity is defined as the variety of life on earth at all its levels, from genes to biogeographic regions, and the ecological and evolutionary processes that sustain it.

A comprehensive definition of biodiversity includes several levels of organization, from genetic through landscape (see Figure 1) and encompasses the "functional" aspects of biodiversity. In addition to spanning organizational levels, biodiversity traverses spatial scales (from local through regional and national to global) and times (from daily to seasonal, annual, and evolutionary). Spatial patterns of biodiversity are affected by climate, geology, and physiography (Redford and Richter, 1999).

There are different views on whether one should include the activities of humans in a definition of biodiversity. Some conservation biologists (for example, ibid.) confine biodiversity to the natural variety and variability excluding biotic patterns and ecosystems that result from human activity. Yet it is difficult to assess the "naturalness" of an ecosystem, because human influence is so pervasive and varied (Hunter, 1996; Angermeier, 2000). Many people consider humans to be a part of nature, and therefore a part of biodiversity. If one takes humans as part of nature, then cultural diversity of human populations and the ways that these populations use or otherwise interact with habitats and other species on earth are components of biodiversity, too. Most conservation biologists make a compromise between totally including or excluding human activities as a part of biodiversity. These biologists do not accept all aspects of human activity and culture as part of biodiversity, but they recognize that the ecological and evolutionary diversity of domestic species and the species composition and ecology of agricultural ecosystems are part of biodiversity.

A Short History of the Study of Biodiversity

The term *biodiversity* (as the contracted form of *biological diversity*) was first used at a planning meeting of the National Forum on BioDiversity (Wilson and Peters, 1988). The word now frequently appears in current newspaper articles and other mass media and has focused public awareness in some countries on the importance of conservation. A poll of U.S. residents in 2002 showed that biodiversity is "not just for scientists anymore"; 30 percent had heard of biological diversity, compared with only 19 percent in 1996 (Biodiversity Project, 2002). However, many who have heard of the term still do not understand what it means. Part of the confusion is that the term *biodiversity* applies to different aspects of biological variation and, therefore, has become a catchphrase that has multiple meanings. Even though the term *biodiversity* is relatively new, for thousands of years philosophers and scientists have studied aspects of biodiversity.

Aristotle (384–322 B.C.) was the earliest Western philosopher who attempted to place biodiversity in some formal order or classification. He analyzed variation in the appearance and biology of organisms, and searched for similar patterns by which to group organisms together. This is the science of taxonomy, an essential tool for describing the biological diversity of organisms.

Traditionally, biologists described the diversity of organisms by comparing their anatomy and physiology. Since the 1960s, biologists have developed increasingly sophisticated techniques to study biological variation at the cellular and molecular levels. Scientists now examine chromosomes and genes with more precision, gathering more details about the extent of genetic variation between individuals, populations, and species.

Today, scientists who study population dynamics in biodiversity still turn to studies undertaken by scientists more than two centuries ago. Malthus (1798) provided one of the earliest theories of population dynamics. Subsequent work through the nineteenth and twentieth centuries expanded these initial concepts. Lotka (1925) and Volterra (1926) developed theories of population ecology by studying population growth relative to competition and predation. Also during the twentieth century, biologists such as Fischer, Wright, and Haldane developed theories of population genetics. Their theories were based on a synthesis of the early work of Darwin and Mendel on natural selection and inheritance of morphological characteristics. The diverse aspects of population ecology and population genetics are combined in the overall subject of population biology.

The science of ecology is another essential tool used to define biodiversity. Ecology is the study of organisms and their relationships with their biotic and abiotic environments. This includes the way in which organisms compete for and use essential resources such as food, water, and space; how organisms find mates; and the underlying processes behind organism dispersal and the colonization of new regions and habitats. Haeckel (1869) was the first to define the term *ecology*, but even before that, biologists were aware of the importance and complexity of the interrelationships between organisms and their environment.

By the 1960s, scientists started to recognize that populations, species, and ecosystems were disappearing at a rapidly accelerating rate because of human activity. More recently, scientist have estimated the rate of biodiversity loss to be comparable to pervious periods of mass extinction, and refer to this as the Sixth Extinction (Eldredge, 1998; Pimm et al., 1995; McCann, 2000; see also Evolutionary Processes That Create and Sustain Biodiversity, below). In response to the seriousness of this issue, scientists from diverse fields have developed the field of conservation biology**.** This field integrates knowledge from both the natural and social sciences for the purpose of maintaining the earth's biodiversity. The discipline grew rapidly in the 1990s; simultaneously, the study of biodiversity has become a central and unifying theme of research in genetics, taxonomy, biogeography, ecology, anthropology, socioeconomics, and natural resource management. The study and protection of biodiversity also became an important part of global politics. The following areas of investigation are central to conservation biology activities, either at a regional or a global level:

assessment and inventory of the remaining biodiversity
evaluation of threats to biodiversity
analysis of how biodiversity is changing in response to threats
assessment of the importance of different aspects of biodiversity to humans
mitigation of biodiversity loss, and strategies to conserve the remaining biodiversity.

Evolutionary Processes That Create and Sustain Biodiversity

Any comprehensive definition of biodiversity also includes references to the processes that create and maintain biodiversity. The diversity of species, ecosystems, and landscapes that surround us today are the product of at least 3.8 billion years of evolution of life on earth (Mojzsis et al., 1996). Life may have first evolved under rather harsh conditions, perhaps comparable to those of the deep-sea thermal vents where chemo-autotrophic bacteria (which obtain their energy only from inorganic, chemical sources) are currently found. A subterranean evolution of life has also been suggested.

Rock layers deep below the continents and ocean floors, previously thought to be too poor in nutrients to sustain life, have now been found to support thousands of strains of micro-organisms. Bacteria have been collected from rock samples almost 2 miles below the surface, at temperatures up to 75 degrees centigrade. These chemo-autotrophic micro-organisms derive their nutrients from chemicals such as carbon, hydrogen, iron, and sulfur. Deep subterranean communities could have evolved in situ or originated on the surface and become buried or otherwise transported down into subsurface rock strata, where they have subsequently evolved in isolation. Either way, these appear to be very old communities, and it is possible that these subterranean bacteria may have been responsible for shaping many geological processes over the history of the earth (for example, the conversion of minerals from one form to another, and the erosion of rocks [Fredrickson and Onstott, 1996]).

As early as 3.5 billion years ago, the first photosynthetic bacteria evolved and started releasing oxygen into the atmosphere. Prior to that, the atmosphere was mainly composed of carbon dioxide, with other gases such as nitrogen, carbon monoxide, methane, hydrogen, and sulfur gases present in smaller quantities. Initially the oxygen produced by photosynthesis was absorbed by the oceans, where it reacted with dissolved iron to form iron oxide.

About 1.8 billion years ago, the oceans ran out of dissolved oxygen and the levels of oxygen in the atmosphere started increasing significantly (Mojzsis, 2001). Some of the early species probably became extinct, and others probably became restricted to habitats that remained free of oxygen. Some took up residence inside other, aerobic cells. The anaerobic cells might, initially, have been incorporated into the aerobic cells after those aerobes had engulfed them as food. Alternatively, the anaerobes might have invaded the aerobic hosts and become parasites within them. Either way, a more intimate symbiotic relationship subsequently evolved between these aerobic and anaerobic cells. In these cases the survival of each cell was dependent on the function of the other.

The evolution of this symbiotic relationship was an extremely important step in the evolution of more complex cells—the eucaryotes. Recent studies of rocks from western Australia have suggested that the earliest forms of single-celled eucaryotes are at least 2.7 billion years old (Anon., 2001). There has, subsequently, been plenty of time for some of the genes of the invading anaerobes to have been lost, or even transferred to the nucleus of the host aerobe cell. As a result, the genomes of the ancestral invader and ancestral host have become mingled, and the two entities can now be considered as one, from a genetic standpoint.

Complete accounts of the probable evolutionary history of eucaryote organisms on earth can be found in various standard references. The important thing to note is that evolutionary history has physically and biologically shaped our contemporary environment. Many existing landscapes are the remains of earlier life forms. For example, some existing large rock formations are the remains of ancient reefs, formed 360 to 440 million years ago by communities of algae and invertebrates (Veron, 2000).

The flora and fauna that form today's biodiversity are a snapshot of the earth's 3.8-billion-year history of life, representing just 0.1 percent of all the species that have lived on earth. Thus 99.9 percent—or virtually all of life that has existed on earth—has gone extinct (Raup, 1991). Extinction, an important part of evolution, does not occur at a constant pace. There have been at least five periods when large numbers of different species have disappeared from around the world. These are termed *mass extinctions*, and their timing is shown in Table 1.

Table 1
The Major Extinction Events

Era	*Period*	*Epoch*	*Duration**	*Time of Extinction Event*	*Extinction Event*
Cenozoic	Quaternary	Holocene	Present–0.01	Now	Sixth
		Pleistocene	0.01–1.6		
	Tertiary	Pliocene	1.6–5.3		
		Miocene	5.3–23.7		
		Oligocene	23.7–36.6		
		Eocene	36.6–57.8		
		Paleocene	57.8–66.4		
Mesozoic	Cretaceous		66.4–144	65*	Fifth
	Jurassic		144–208		
	Triassic		208–245	206*	Fourth
Paleozoic	Permian (Carboniferous)		245–286	245*	Third
	Pennsylvanian (Carboniferous)		286–325		
	Mississippian		325–360		
	Devonian		360–408	364*	Second
	Silurian		408–438		
	Ordovician		438–505	443*	First
	Cambrian		505–570		
Precambrian			570–4500		

* Approximate time in millions of years before present

Source: Center for Biodiversity and Conservation. 1999. *Humans and Other Catastrophes: Perspectives on Extinction*. New York: Center for Biodiversity and Conservation, American Museum of Natural History, p. 5. (Reprinted with permission)

Each of the first five extinctions represents a significant loss of biodiversity. The recovery from these extinctions has always been relatively good. It appears that the extinctions were followed by a sudden burst of evolutionary diversification on the part of the remaining species, presumably because these survivors started using habitats and resources that had previously been occupied by more competitively successful species that had gone extinct. However, this does not mean that the recovery from mass extinction was rapid; it has usually required some tens of millions of years (Jablonski, 1995).

It has been hypothesized that we are currently on the brink of a sixth mass extinction. However, this sixth extinction differs in a number of ways from previous events. The five other mass extinctions predated humans and were probably the products of some physical process (perhaps climate change as a result of meteor impacts) rather than the direct consequence of the action of some other species. In contrast, the sixth extinction is human-induced. Consequently, unlike previous events, the most recent extinction event can be slowed or reversed.

Characterization and Measurement of Biodiversity

To conserve biodiversity effectively, we need to be able to define what we want to conserve, determine where it currently occurs, identify strategies to help conserve it, and track over time whether these strategies are working. The first of these, defining what we want to conserve, is complicated by the fact that biodiversity can be divided into several categories.

Genetic diversity, organismal diversity, population diversity, and species diversity are principally concerned with the diversity of organisms themselves, whereas community diversity, ecosystem diversity, landscape diversity, and cultural diversity are concerned with the functional interrelationships among these organisms.

Genetic Diversity

Genetic diversity refers to any variation in the nucleotides, genes, chromosomes, or whole genomes of organisms. This is the "fundamental currency of diversity" (Williams and Humphries, 1996) and the basis for all other organismal diversity. Approximately 1 billion different genes are recognized from all the known species on earth (World Conservation Monitoring Center, 1992). But not all species have the same number of genes. The potential genetic diversity of a species can be measured by the total number and type of genes present within its entire DNA or genome. However, a greater total number of genes might not correspond with a greater observable complexity in the anatomy and physiology of the organism (that is, greater phenotypic complexity). For example, the genome of the cultivated subspecies of rice, *Oryza sativa* L. ssp. *indica*, is estimated at 46,022 to 55,615 genes (Yu et al., 2002), and the total size of the human genome is currently predicted to be not much larger, at approximately 67,000 genes.

Genetic diversity is key for conservation efforts, since higher genetic diversity usually represents a greater capacity to adapt to environmental changes. This is, for example, an important issue in the context of changing global climate.

Genetic diversity, at its most elementary level, is represented by differences in the nucleotide sequences (adenine, cytosine, guanine, and thymine) of chromosomal DNA (deoxyribonucleic acid). This nucleotide variation is measured for particular genes. Each gene comprises a hereditary section of DNA that occupies a specific place on the chromosome and controls a particular characteristic of an organism. Differences in the nucleotide sequences of a gene can be compared for different organisms. Most organisms are diploid, having two sets of chromosomes, and therefore two copies (called alleles) of each gene. However, some organisms can be triploid or tetraploid (having three or four sets of chromosomes).

Within any single organism, there may be variation between the two (or more) alleles for each gene. This variation is introduced either through mutation of one of the alleles, or as a result of sexual reproduction. During sexual reproduction, offspring inherit alleles from both parents, and these alleles might be slightly different. Also, when the offspring's chromosomes are copied after fertilization, genes can be exchanged in a process called sexual recombination. Genetic diversity can exist between the copies of genes possessed by a single organism. Increased genetic diversity can be achieved in an organism by having multiple copies of each gene within its genome (Pennisi, 2001). Mutations can kill an organism. However, when an organism has two copies of the same gene, it is possible for one to mutate without harming the organism's survival. Eventually, mutations may allow the evolution of new characteristics. (In populations, genetic variation can be added through migration or hybridization.)

Each allele codes for the production of amino acids that string together to form proteins. These proteins code for the development of the anatomical, physiological, and behavioral characteristics of the organism. Differences in the nucleotide sequences of alleles result in the production of slightly different strings of amino acids or variant forms of the proteins. The variation within genes, for individual organisms and between different organisms, can be measured indirectly by measuring the biochemical variation of the proteins produced by these genes. The technique for studying protein diversity is known as protein electrophoresis. This was one of the most important methods for studying genetic diversity from its inception in the late 1950s until the late 1970s, when new technologies were developed that allowed direct analysis of DNA sequences.

Besides having distinct combinations of genes, species may also have variation in the shape and composition of the chromosomes carrying the genes, and in the total number of chromosomes present. Examination of these features of the chromosomes (termed karyology) provides another way of describing genetic diversity.

Analyses of genetic diversity can be applied to studies of the evolutionary ecology of populations. Genetic studies can identify alleles that might confer a selective advantage on the host organism—for example, an allele that renders the host better equipped for digesting certain foods. This selective advantage means that the organism is more likely to survive and pass its genetic traits on to its offspring. Under these circumstances, particular alleles can spread through, and become established in, a population. The spread of this genetic diversity can then affect the ecological diversity of the habitat where the organisms live. In this example, the allele might enable the organisms to feed upon certain types of plants more effectively, leading to greater predation on those plants as preferred food. This higher predation on the plant could cause related changes in other parts of the food web within that habitat.

The presence of unique genetic characteristics distinguishes members of a given population. The size of a population can be estimated by analyzing the geographic range of organisms with specific genetic characteristics. If the population is large, and the individuals are not closely related (which is usually the case in large populations), then the overall gene pool is large, and many different alleles are likely to be present. A wide diversity of alleles indicates a greater potential for the evolution of new combinations of genes and, subsequently, a greater capacity for evolutionary adaptation to different environmental conditions. In contrast, a small population typically has a narrower diversity of alleles. The individuals are likely to be genetically, anatomically, and physiologically more homogeneous than in larger populations and less able to adapt to differing conditions. Populations with very low genetic diversity may be so susceptible to moderate environmental change or disease that they become extinct. For example, sub-Saharan populations of cheetahs show extremely low levels of genetic diversity, perhaps because their populations collapsed about 10,000 years ago when other large mammals were going extinct, creating a genetic bottleneck. Captive populations have been very susceptible to disease, suffering high mortality rates from diseases such as feline infectious peritonitis, which is not usually fatal to cats. Presumably, the virus is effective against a particular genotype that is shared by all cheetahs. Other traits apparently associated with the low genetic diversity are unusually high levels of spermatozoan abnormalities in males and a high infant mortality rate (see Hunter [2002] for discussion and references).

Organismal Diversity

Organismal diversity refers to any variation in the anatomical, physiological, or behavioral characteristics of different individual organisms. These are called phenotypic characters, or physical traits. They represent the outward expression of genes and the action of the environment on the way those genes are expressed in an organism. It is this phenotypic diversity that overwhelmingly interacts with biotic and abiotic (that is, living and nonliving) factors to create higher levels of biodiversity, such as community and ecosystem diversity. The phenotypic characters of organismal diversity, therefore, represent an important measure of the adaptation of the organism to its environment. Similar to genetic characters, variation of organismal characters can be used to measure the amount of diversity between individuals of the same population, different populations, or different species.

Variation in the genes that control certain features may be expressed as quite distinct phenotypes. For example, two organisms might be different sizes or colors as a result of genetic variation. However, that is not always the case. For some features, the phenotypic expression of genetic variation may be very subtle and difficult to detect.

Distinctive anatomical, physiological, and behavioral characters are the product of complex interrelationships between the form and function of various organs. For example, the distinctive appearance of some muscles might be closely correlated with their position, orientation, and function relative to adjacent muscles. Local environments can significantly alter organismal characters. The physiological (and anatomical) characteristics of the kidney in fishes, for example, can vary depending on the environment. Rainbow trout and flounder filter fluid through their kidneys at different rates, depending on the salinity of the water in which the fish are immersed (see Harrison [1996] for references). Therefore, interpreting the relationship between what something looks like and its underlying diversity is difficult. Phenotypic features can be less precise measures of diversity than genetics. However, analyses of organismal diversity can be more informative than genetic studies, because they provide direct information about the relationship between the diversity of the organism and the environment.

The behavior of an organism is controlled by genetic diversity. In some cases, the behavior of whole populations is closely related to the genetic diversity of the individuals in the population. For example, in some eusocial insects such as ants, which have a "queen" producing "worker" daughters, the daughters share three-quarters of their genes. Rather than produce daughters of their own, these workers can ensure that more of their genes are passed on through the population by assisting the queen in the care of new generations of their own sisters. Community or ecosystem diversity also shapes some behaviors. For example, feeding behavior is dependent on the relative availability of different types of prey.

Behavioral characteristics define population, community, and ecosystem diversity. The herding behavior of some mammals such as elephants or wildebeests helps determine the size and activity of populations. Moreover, the activity of these herds (for example, seasonal migrations) can significantly affect the overall ecology of an ecosystem.

Behavioral patterns are also associated with landscape/seascape and biogeographic diversity. For example, the long-range spawning migrations of eels are perhaps associated with the biogeographic and, hence, evolutionary history of the species (see Biogeographic Diversity). Similarly, the annual migrations of wildebeests are associated with physiographic aspects of landscape (for example, seasonal variation of climate) and biogeographic diversity.

The behavioral patterns of species are sometimes included in taxonomic and phylogenetic studies. One of the most difficult problems in applying behavioral characters to phylogenetic studies is how one establishes whether behavioral traits, shared by different species, are similar because of descent from a common ancestor (that is, homology), or whether the characters originated independently in phylogenetically unrelated taxa (that is, homoplasy) (Wenzel, 1992). McLennan (1993) mapped behavioral characters onto a phylogenetic tree for sticklebacks and showed where there was independent, convergent evolution of similar behavioral characters in unrelated species. This information is useful to behavioral ecologists because it indicates where further investigation of the characters would be informative, as well as analysis of the relationships between the organism and the environment.

Population Diversity

Population diversity refers to variation in the quantitative and spatial characteristics of populations, such as the numbers of individuals present and the geographic range of the population. An estimate of the overall population size provides a measure of the potential genetic diversity within the population; large populations usually represent larger gene pools and hence greater potential diversity.

The geographic range and distribution of populations (that is, their spatial structure) are key factors in analyzing their diversity, since they give an indication of the likelihood of the movement of organisms between populations and subsequent genetic interchange.

Isolated populations, with very low levels of interchange, show high levels of genetic divergence (Hunter, 2002, p. 145), and often show unique adaptations to the biotic and abiotic characteristics of their local environment—for example, competition with other organisms, local topography, and climate. Less isolated populations may show greater genetic exchange, and those populations are likely to be more homogenous.

Populations can be categorized according to the level of divergence between them. Isolated

Cottontail rabbit. Some rabbit species undergo population cycles of impressive abundance alternating with extreme scarcity, often influencing the population densities of their predators. (D. Robert and Lorri Franz/Corbis)

and genetically distinct populations of a single species may be referred to as subspecies. Presumably, in time, these populations, or subspecies, will become sufficiently genetically distinct that they can no longer interbreed and hence will represent different species. Populations that show less genetic divergence might be recognized as "variants" or "races." However, the distinctions between subspecies and other infra-subspecific categories can be somewhat arbitrary.

Studies of population diversity also include analyses of seasonal changes in population dynamics and distribution. These studies identify cyclical changes in population size, and whether certain populations migrate to different regions and habitats to reproduce or in search of food.

Individual organisms periodically disperse from one population to another. Groups of contiguous populations thereby form a larger so-called metapopulation. For instance, let us look at the distribution of five populations of field mice, randomly distributed over an area of 2,500 square meters.

Figure 2 represents a patchy distribution of populations of field mice in a landscape. Populations 1 and 5 are isolated from all other populations, are genetically quite distinct, and may be considered a subspecies. Populations 2 and 3 are adjacent to each other and closely related, with quite extensive genetic transfer between them. Populations 3 and 4 are also adjacent to each other, but a seasonal stream temporarily separates the two populations. Genetic exchange occurs only occasionally between 3 and 4, when the stream is dry; thus they represent partially isolated populations. In

Figure 2

Distribution of Five Populations

1				
			2	
		3		
			4	
5				

conclusion, we have five populations; but populations 2, 3, and 4 are subpopulations of a larger, linked, metapopulation. If we assume that population 4 can maintain itself only because of immigration from population 3, then we can say that population 3 is a source and population 4 is a sink. Population 3 might also be a constant source of immigration to population 2. If there is enough mixing between the populations, it is possible that over time, population 2 will become genetically indistinguishable from population 3. Then we will have only four main populations: 1, 5, (2+3), and 4, with (2+3) and 4 forming a metapopulation.

Species Diversity

Species diversity refers to variation in the number and phylogenetic diversity (or evolutionary relatedness) of species present in an area. This is probably the most frequently used measure of total biodiversity (see Surrogate Measures of Overall Biodiversity, below).

To count species, we must define a species. There are several competing theories or "species concepts" (Mayden, 1997). The most widely accepted are the morphological species concept, the biological species concept, and the phylogenetic species concept.

The morphological species concept is the oldest. Although it is largely outdated as a theoretical definition, it is still widely used. This concept, as described by various authors (see, for example, Du Rietz [1930]; Bisby and Coddington [1995]), states that species are the "smallest natural populations permanently separated from each other by a distinct discontinuity in the series of biotypes."

The biological species concept, as described by Mayr (1982) and Bisby and Coddington (1995), states that "a species is a group of interbreeding natural populations unable to successfully mate or reproduce with other such groups, and which occupies a specific niche in nature."

The phylogenetic species concept, as defined by Cracraft (1983) and Bisby and Coddington (1995), states that "a species is the smallest group of organisms that is diagnosably [that is, identifiably] distinct from other such clusters and within which there is a parental pattern of ancestry and descent."

These concepts are not congruent, and considerable debate exists about the advantages and disadvantages of all existing species concepts. Some systematists take a pluralist theoretical approach: a species is a group of phylogenetically distinct organisms (following the phylogenetic species concept) and reproductively isolated (following the biological species concept).

In practice, systematists group specimens together according to shared features (genetic, morphological, and physiological characters). When two or more groups show different sets of shared characters, and these differences cannot be attributed to intraspecific variation, the groups are considered different species. This approach relies on the objectivity of the phylogenetic species concept (that is, the use of intrinsic characters to define or diagnose a species) and applies it to the practicality of the morphological species concept, in terms of sorting specimens into groups. Kottelat (1995, 1997) used a similar approach for distinguishing species of European freshwater fish for which there was incomplete or confusing taxonomic information; he referred to his technique as the pragmatic species concept. By this, he meant that he was applying the most coherent and consistent way of defining species according to the taxonomic information available.

Regardless of their differences, all species concepts are based on the understanding that set parameters define a species and make it a discrete and identifiable evolutionary entity. If populations of a species become completely isolated, they can diverge, ultimately resulting in phylogenetic change and what is called speciation. During this process, we expect to see distinct populations representing so-called incipient species—species in the process of formation. These may be described as subspecies or some other infra-subspecific rank. However, it is very difficult to decide when a population is sufficiently different from other populations to merit its ranking as a subspecies. Difficulty also exists in defining the difference between a subspecies and a species. Categories such as subspecies, varieties, or populations are subjective measures of the magnitude of taxonomic difference and are not consistently discrete and identifiable evolutionary entities. Thus, in evolutionary terms, species are recognized as the minimum identifiable unit of biodiversity (above the level of a single organism) (Kottelat, 1997). This is the reason that species diversity represents an important and informative measure of biodiversity.

One aspect of species diversity is the number of species found in a particular region, often referred to as species richness. Global biodiversity is frequently expressed as the total number of species currently living on the earth. About 1.75 million species have been scientifically described thus far (Lecointre and Guyader, 2001), and estimates vary for the total number of species on the planet. This is partly because of differing opinions on the definition of a species. For example, the phylogenetic species concept recognizes more species than does the biological species concept. Some scientific descriptions of species appear in old, obscure, or poorly circulated publications. In those cases, scientists may accidentally overlook certain species when preparing inventories of flora or fauna, causing them to describe and name a known species.

More significantly, some species are very difficult to identify. For example, taxonomically cryptic species look very similar to other species and may be misidentified (and hence overlooked as being a different species). Thus several different but similar-looking species, identified as a single species by one scientist, are identified as different species by another scientist. That does not, however, mean that contemporary taxonomic research is unreliable. Quite the contrary. As taxonomists obtain new collections of organisms and develop more techniques for investigating genetic and organismal diversity, they revise and refine their interpretation of species diversity and provide more reliable estimates of the total number of species.

Scientists expect that the 1.75 million scientifically described species represent only a small fraction of the total number of species on earth today. Many additional species have yet to be discovered, or are known to scientists but have not been formally described. (For a species to be recognized as valid, it must be described, according to precise rules set down by an international committee, and named in a publication.) Viral, bacterial, botanical, and zoological nomenclatures, and the nomenclature of cultivated plants, all have separate rules and committees (Bisby and Coddington [1995]). Scientists estimate that the total number of species on earth could range from 3.6 million up to 111.7 million (Hammond, 1995). The total number of species for any taxonomic group can be estimated from the ratio of the number of new species described each year to the number of previously described species. Estimates can also be extrapolated from the number of species collected per unit area from field samples (Stork, 1997). The range between the upper and lower figures is large because of the difficulty in estimating total species numbers for some taxonomically lesser known groups, such as bacteria, or groups not comprehensively collected from areas where their species richness is likely to be greatest—for example, insects in tropical rain forests. Consequently, authors have produced varying estimates for these groups. A reasonable estimate for the total number of species on earth seems to be about 13.6 million (Hammond, 1995).

Table 2
Estimated Numbers of Described Species

Taxon	*Number of Described Species*	*Percentage of Total Described Species**
Bacteria	9,021	0.5
Archaea	259	0.01
Bryophyta (mosses)	15,000	0.9
Lycophyta (clubmosses)	1,275	0.07
Filicophyta (ferns)	9,500	0.5
Coniferophyta (conifers)	601	0.03
Magnoliophyta (flowering plants)	233,885	13.4
Fungi	100,800	5.8
Porifera (sponges)	10,000	0.6
Cnidaria	9,000	0.5
Rotifers	1,800	0.1
Platyhelminthes (flatworms)	13,780	0.8
Mollusca (mollusks)	117,495	6.7
Annelida (annelid worms)	14,360	0.8
Nematoda (nematode worms)	20,000	1.1
Arachnida	74,445	4.3
Crustacea	38,839	2.2
Insecta	827,875	47.4
Echinodermata	6,000	0.3
Chondrichthyes (cartilaginous fishes)	8,46	0.05
Actinopterygii (ray-finned bony fish)	23,712	1.4
Lissamphibia (living amphibians)	4,975	0.3
Mammalia (mammals)	4,496	0.3
Chelonia (living turtles)	290	0.02
Squamata (lizards and snakes)	6,850	0.4
Aves (birds)	9,672	0.6
Other	19,3075	11.0

*The total number of described species is assumed to be 1,747,851.

Source: Lecointre, G., and H. Le Guyader. 2001. *Classification phylogénétique du vivant*. Paris: Belin.

Although it is important to know the total number of species on earth, it is also informative to have some measure of the different types of species that compose this biodiversity (for example, bacteria, flowering plants, insects, birds, and mammals). We do this through what is called taxonomy, the genetic, anatomical, biochemical, physiological, or behavioral features used to distinguish species or groups of species and that demonstrate diversity between species. Once ordered into a logical system, or classification, taxonomic diversity indicates the relatedness of groups of species, based on their shared characteristics.

Using this taxonomic information, we assess the proportion of related species among the total number of species on earth. Table 2 contains a selection of well-known taxa.

This table provides a measure of the evolutionary or taxonomic diversity of the species present in any given region. These studies correct common misconceptions about global biodiversity. For example, most public attention is focused on the biology and ecology of large, charismatic species such as mammals,

A clownfish hides in the protection of a sea anemone's tentacles. Clownfish and anemones have a symbiotic relationship—each provides the other the benefit of protection from predators. (Jeffrey L. Rotman/Corbis)

birds, and certain species of trees (for example, mahogany and sequoia). Far less public concern is paid to groups such as molluscs, insects, and, to some extent, flowering plants. However, Table 2 indicates that mammals and birds represent only a small portion of the total number of species (0.3 percent and 0.6 percent, respectively). Molluscs, on the other hand, represent about 7 percent of the total number of known species, and flowering plants 13 percent. Insects represent 47 percent of the total number of species; there are approximately 300,000 species of beetles alone, representing 17 percent of all species on earth. The greater part of earth's species diversity is often overlooked.

Community Diversity

A community comprises the populations and species that naturally occur and interact in a particular environment to effect a transfer of energy between members of the community. Although some communities, such as a desert spring community, have well-defined boundaries, others are larger, more complex, and less defined, such as mature forest communities. Biologists are selective when applying the term *community*, sometimes using it for a subset of organisms within a larger community. For example, some biologists may refer to the community of species specialized for living and feeding entirely in the forest canopy, whereas other biologists may refer to this as part of a larger forest community. This larger forest community includes those species living in the canopy, those on the forest floor, and those moving between those two habitats, and the functional interrelationships between all of them.

The diversity of a community depends on the natural resources available to support its populations and species. Therefore the most effective way of measuring community diversity is to examine the energy cycles/food webs that unite the populations and species within their community. The extent of community diversity is then expressed by the number of links in the food web. However, in practice, it can be very difficult to quantify the functional interactions between organisms, populations, and species that share a habitat. It is easier to measure and quantify the diversity of the organisms themselves and use that as an indication of functional diversity of the system. The quickest way to evaluate community diversity is to count the number of populations and species present. The evolutionary or taxonomic diversity of the species present is another way of measuring the diversity of a community.

Communities are most easily classified by their overall appearance, or physiognomy. In some cases this is based on a diagnostic, physical feature of the community's habitat, such as the riffle zone community of a stream. However, in most instances the classification is based on the dominant types of species present—for example, a fringing reef community, or a Mediterranean scrubland community. Multivariate statistics provide more complex methods for diagnosing communities, by arranging species on coordinate axes that represent gradients in environmental factors such as temperature or humidity.

Christen Raunkiaer, a Danish botanist, developed a classification of plants that provides a useful measure of community diversity. Raunkiaer's five main life forms are shown in Table 3, with one additional life form (epiphytes) not originally included in his classification. The number of species, for any community, that fall into the different categories of life forms is expressed as a proportion of the total number of species in the community, and this gives a measure of the ecological heterogeneity of the community.

Table 3
Raunkiaer's Life Forms

Life Form	*Characteristics*
Therophytes	Annual plants with complete life cycle lasting one season; plants survive unfavorable conditions as resistant seeds
Geophytes (Cryptophytes)	Buds on bulb or rhizome underground
Hemicryptophytes	Perennials with shoots or buds near the ground, possibly covered with leaf litter
Chamaephytes	Perennials with shoots or buds from 0–25 cm above ground surface.
Phanerophytes	Perennials with buds more than 25 cm above ground Trees, shrubs, and vines.
Epiphytes*	Plants growing on other plants. Aerial roots

*Not originally included in Raunkiaer's life forms, now included in contemporary classifications.

Source: Modified from Smith, R. L. 1990. *Ecology and Field Biology*, 4th ed. New York: Harper Collins, table 24.1.

Communities exhibit diversity in the amount of vertical stratification of species present. For example, a heavily vertically stratified community such as a mature forest can have a variety of distinct layers—for example shrub, understory, and canopy, each with its own group or guild of interacting species. Similarly, horizontal heterogeneous communities contain species present in different parts of the total range of the community. Species diversity at the edge of a community might be significantly different from that in the middle of the community. For example, the environmental conditions on the edge of an exposed, high-altitude forest are quite different from those in the more protected middle of the forest, and that is likely to affect the species present in those two areas.

Ecosystem Diversity

An ecosystem is the entire complement of species and communities found in a given region, and the functional interrelationships that exist between these organisms and the other biotic and abiotic characteristics of the region. The diversity of an ecosystem is dependent not only on the biological and physical entities that it contains, but also on the ecological interrelationships between those entities (predation or parasitism between species, competition between species for the available natural resources).

Ecosystem diversity is also dependent on the type of physical resources available within a particular habitat and the way in which the resident organisms use those resources. For example, the aquatic larvae of caddis flies build a protective casing from small stones and other debris collected from the streambeds where they live. Their distribution is restricted to parts of streams where the particle size of the sediment is suitable for building the protective cases. This, in turn, determines the presence or absence of other species that feed on the caddis fly larvae.

The physical characteristics of ecosystems can be modified by the actions of the organisms themselves. For example, beavers alter the hydrology of aquatic ecosystems by damming rivers, which affects the flora and fauna of the region (Butler, 1995; and see Butler for discussion of the geomorphic influences of other vertebrates and invertebrates). Similarly, beavers change the physical structure of forests by felling trees. Recent studies of North American prairie dogs show that their presence can significantly affect the diversity and productivity of the vegetation in the areas where they are present (Miller et al., 1994; Thacker, 2001). In the Arctic, some cetaceans (such as killer whales) and pinnipeds (ringed seals) maintain breathing holes and lees in the ice. This not only shapes the physical structure of the environment but also attracts predators, such as polar bears, to these patches of open water.

The diversity of an ecosystem is often described in terms of the complexity of the food web (trophic relationships). This gives a general idea of the overall complexity (and ecological stability) of the ecosystem. Another way to describe the ecological diversity of an ecosystem is to identify keystone species. These are important because some aspect of their presence in the ecosystem allows many other species to coexist in the ecosystem. The presence of a specialized and important keystone species may indicate the presence of a complex habitat and ecosystem. However, it is difficult to quantify and measure the diversity of ecological interrelationships within an ecosystem, as noted in the preceding discussion on community diversity. Therefore, the number of populations and species present and the taxonomic diversity of those species are often used as proxy measures of overall ecosystem diversity.

The functional complexity of the ecosystem (the complexity of the trophic and other ecological interconnections between constituent species) increases with the number and taxonomic diversity of the species present. In an ecosystem with very few species, the loss of even a single species or a small part of the habitat can affect the ecological interactions between a significant proportion of the remaining species in the ecosystem. The ecosystem will no longer function properly and may collapse as a consequence (Myers, 1996). In a large ecosystem, a small amount of damage would affect the ecological interactions between a relatively small proportion of the populations and species present. Thus the larger ecosystem is less likely to collapse; the increase in functional complexity is assumed to make the ecosystem more resilient to environmental change. However, new research suggests that an increase in species richness might not necessarily confer greater ecological resilience (Pfisterer and Schmid, 2002).

Ecosystems may be classified according to the dominant type of habitat present—for example, a salt marsh ecosystem, or rocky shore intertidal ecosystem. Comparisons between ecosystems usually focus on how the biological complexity of the ecosystem (for example, the number and diversity of species present) might be constrained by the physical complexity of the ecosystem—whether, for example, the ecosystem is a high-energy environment such as a torrential stream or exposed coastline, or a low-energy environment such as a sheltered salt marsh. These factors can result in considerably different types of ecosystems, either locally—as in the stunted vegetation and low species diversity on exposed hilltops compared with the more prolific vegetation and high species diversity in sheltered valleys—or globally. Temperate climate ecosystems tend to be simpler than tropical climate ecosystems in terms of numbers of species and taxonomic diversity. The European freshwater fish fauna, for example, is estimated to include about 360 species, representing about 29 families of fish; the neotropical region of Central and South America includes between 5,000 and 8,000 species in at least 55 families; and tropical Asia has about 3,000 species in 121 families (Kottelat, 1997; Lundberg et al., 2000).

Landscape Diversity

A landscape is "a mosaic of heterogeneous land forms, vegetation types, and land uses" (Urban et al., 1987). Therefore, assemblages of different ecosystems (the physical habitats and the species that inhabit them, including humans) create the landscapes on earth. The scale of a landscape varies from about 100 square kilometers—about the size of a national park—to more than 1 million square kilometers—the size of a large physiographic region such as a river basin. Species composition and population viability are controlled by a landscape's structure (patch size and connectivity of habitats within the landscape; perimeter-area ratio) and function (nutrient cycling rates; hydrologic processes) (Noss, 1990). Certain animals and plants, including endangered species such as jaguars, wolves, and quetzals, range widely across several different ecosystems. Therefore, conservation management should be directed at whole landscapes to ensure that these species survive.

Landscape diversity depends on local and regional variations in environmental conditions, and the species supported by those environments. Landscapes are significantly affected by the activity of the species present. For example, although bacteria are some of the smallest organisms on earth, many species that live in rocks are thought to be important in the process of erosion, which shapes landscapes. The activity of modern humans has been one of the most significant factors affecting the appearance of landscapes in the past few thousand years, and substantially so in the past few centuries. More than half of all accessible surface freshwater is put to use (Vitousek et al., 1997). Industrial agriculture around the Aral Sea in the last thirty years has approximately halved that lake's surface area and depth, and tripled its salinity; and only two of Japan's 30,000 rivers are neither dammed nor modified (for references, see Harrison and Stiassny, 1999). Landscape diversity is often incorporated into descriptions of so-called ecoregions, which are geographically defined areas that integrate environmental conditions such as climate and geology, and support distinct assemblages of species and communities (Stein et al., 2000).

Biogeographic Diversity

Biogeographic diversity refers to the relationship between the evolutionary history of the biota of a region and the geological and geographic history of that region. Analyses of biogeographic diversity include two fields (Wiley, 1981):

> Historical biogeography. This is the study of spatial and temporal distributions of organisms (usually species or higher taxonomic ranks); it attempts to provide explanations for these distributions based on earth history events.
>
> Ecological biogeography. Ecological biogeography is the study of the dispersal of organisms (usually individuals or populations) and the mechanisms that influence them.

Studies of historical biogeography are important for describing what are called *biogeographic provinces*, regions defined by their characteristic flora and fauna. For example, examination of the freshwater fish fauna of South America has revealed several distinct faunistic regions, such as the Magdalenean, Orinoco-Venezuelan, Guyana-Amazonian, Paranean, and Patagonian (Gery, 1969). These regions were isolated from each other at various times over the last 90 million years of South America's geological history, because of events such as the formation of inland seaways and the Andean mountain range (Lundberg et al., 1998). Consequently, distinct fish faunas evolved in these regions. According to historical biogeography, the evolutionary history of the fish faunas, and their current distributions, can be explained by the geological history of the continent. However, historical biogeography is not the complete explanation. Ecological biogeographical studies show that recent dispersal of some species has occurred between areas. In addition, some groups of marine fishes have invaded the freshwaters of South America.

Historical biogeography also explains the diversity of species distributions between continents. For example, different species of freshwater lungfishes are found in Australia, Africa, and South America. This disjunct distribution occurs because these continents were joined (as the supercontinent Gondwanaland) about 90 million years ago. It is presumed that the ancestor to the different species was distributed across Gondwanaland; speciation, resulting in the current taxa, occurred after the breakup of the continents.

Cultural Diversity

An important part of human diversity is our cultural diversity, which determines the way we interact with each other as well as the way in which we interact with other species and habitats. Approximately 4 percent of the world's human population live in regions rich in nonhuman species or habitats. The effect of human cultural activity on the ecology of these and other regions is an important aspect of biodiversity.

The factors that determine how humans interact with the environment are complex. They vary historically, affected by the development of advanced agricultural, industrial, and engineering technology, and geographically, depending on the climate and physical geography of the area. The relative size and economy of any human community can also affect how that community uses its natural resources. Also, human use of natural resources is diverse, even locally, and varies significantly within and between communities and cultures, driven by the requirements, values, or interests of individuals within a culture, rather than by the culture as a whole.

Surrogate Measures of Overall Biodiversity

The discussion above illustrates the many different ways of defining biodiversity, and each way depends on how we want to characterize biodiversity. For example, we may want to show the genetic diversity between populations from different regions, or we may want to show the diversity of trophic levels represented by the species in different ecosystems. But how do we provide an account of the overall biodiversity of an area in terms of the diversity of the organisms, communities, ecosystems, and interactions present? It is usually difficult, if not impossible, to measure all these aspects of the biodiversity of a region, so we must select some representative or surrogate measure of the overall diversity.

What do we mean by surrogate? Essentially we need to measure an aspect of biodiversity that is feasible to quantify, and we need to choose something that best represents the nonmeasured aspects of biodiversity. We take baseline information on these surrogates and monitor them over time to determine changes in the status of biodiversity based on a management strategy.

The number of species present in an area, or the species richness of an area, is one of the most common surrogates for estimating overall biodiversity. A greater number of species implies a greater level of genetic, organismal, and ecosystem diversity. However, species richness can oversimplify the extent of diversity, because it does not account for possible variation in the types of species present—that is, the taxonomic or phylogenetic diversity of the species present. Table 4 compares three different regions with three communities of species.

Table 4
Comparison of Species in Three Regions

Region A	*Region B*	*Region C*
Plant 1	Plant 1	Plant 1
Plant 2	Snail 1	Plant 2
Plant 3	Fish 1	Plant 3
Plant 4	Lizard 1	Plant 4
Plant 5	Bird 1	Plant 5
Bird 1		Snail 1
Bird 2		Fish 1
Bird 3		Lizard 1
Bird 4		Bird 1
Bird 5		

Region A is clearly more diverse than region B in terms of species richness, because it has twice as many species. However, region B is more taxonomically diverse, having representatives from five different taxonomic groups (plants, mollusks, fishes, lizards, and birds) compared with only two groups (plants and birds) in region A. This greater level of taxonomic diversity for region B implies that it is genetically and ecologically richer, despite the fact that it has fewer species.

Let us consider the relative contribution that each of the different taxonomic groups makes to the overall species diversity for regions A and B. In region A, plants and birds both contribute 50 percent of the total number of species present, and 50 percent to the taxonomic diversity. In region B, each of the taxonomic groups contributes 20 percent to the total number of species present, and 20 percent to the taxonomic diversity. Now let us compare region B with region C. Region C has the same number of taxonomic groups as region B, but it differs by having multiple species of plants. So each taxonomic group still contributes 20 percent to the taxonomic diversity (as in region B), but plants contribute 56 percent to the total number of

Table 5
Abundance of Species* in Three Ecosystems, with Measures of Richness and Evenness

Species	*Ecosystem A*	*Ecosystem B*	*Ecosystem C*
1	220	80	120
2	170	65	65
3	120	50	10
4	70	0	0
Richness (S)[1]	4	3	3
Shannon's Diversity Index (H)[2]	1.3086	1.0807	1.0323
Evenness (E)[3]	0.94	0.98	0.94

* Number of specimens per hectare

Sources: Gibbs, J. P., M. L. Hunter Jr., and E. J. Sterling. 1998. "Problem-solving in Conservation Biology and Wildlife Management. Exercises for Class, Field, and Laboratory." Boston: Blackwell Science; Gross, L. J., et al., eds. "Alternative Routes to Quantitative Literacy for the Life Sciences," a project supported by the National Science Foundation through award DUE-9752339 to the University of Tennessee, Knoxville, August 1, 1998–July 31, 2000. The Institute for Environmental Modelling, University of Tennessee, Knoxville. http://www.tiem.utk.edu (cited June 21, 2002) for discussion and examples; Magurran, Anne E. 1988. *Ecological Diversity and Its Measurement*. Princeton: Princeton University Press also provides discussion of the methods of quantifying diversity.

[1] The total number of species in an area.

[2] Shannon's Diversity Index (H) = $-\Sigma p_i \text{ In } p_i$, where p_i is the proportion of the total number of specimens of species $_i$ expressed as a proportion of the total number of specimens for all species in the ecosystem. The product of ($p_i \text{ In } p_i$) for each species in the ecosystem is summed and multiplied by -1 to give H.

[3] The species evenness index (E) is calculated as H/H_{max}, where H_{max} is the maximum possible value of H and is equivalent to In(S). Thus E = H/In(S)

species, and all other taxonomic groups contribute only 11 percent.

Another factor to compare against species richness (that is, the total number of species present in an area) is the evenness with which species are represented. Table 5 shows abundance of species (number of individuals per hectare) in three ecosystems and gives the measures of species richness and evenness and the Shannon diversity index.

Ecosystem A shows the greatest diversity in terms of species richness, but ecosystem B could be described as being richer, insofar as all the species present are more evenly represented (The E value is larger). This example also illustrates a condition that is often seen in tropical ecosystems, where disturbance of the ecosystem causes uncommon species to become even less common, and common species to become even more common. Disturbance of ecosystem B may produce ecosystem C, where the uncommon species 3 becomes less common, and the relatively common species 1 has become more common. There may even be an increase in the number of species in some disturbed ecosystems, but, as noted above, this may occur with a concomitant reduction in the abundance of individuals or local extinction of the rarer species.

Also, individuals of any one species might be abundant in one part of the region under consideration but absent in all other parts. Another species might have the same number of individuals, but they are more widespread over the entire area. For example, if we can consider an ecosystem with a total area of 1 hectare, containing 60 specimens of two species (species X and species O shown in Figure 3). If we divide the ecosystem area into a grid of 100 smaller units, each 0.01 hectares in size, we might see a distribution of the two species similar to that in Figure 3.

There are 60 specimens of both species in the 1-hectare grid, but species X shows all the

Figure 3

Distribution of Two Species across a 1-Hectare Grid

XXXXXXXXXXX XXXXXXXXXXX XXXXXXXXXXX									OOO OOO
XXXXXXXXXXX XXXXXXXXXXX XXXXXXXXXXX	OO OO OO								
					OOO OOO				
OOO OOO									
								OOO OOO	
		OOO OOO							
						OOO OOO			
				OOO OOO					
							OOO OOO		
			OOO OOO						

X represents one specimen of species X
O represents one specimen of species O

individuals grouped as a single population in one location, whereas species O is fragmented into several isolated populations. If these populations are reasonably isolated, with relatively little gene flow between them, the fragmented populations of species O will be more genetically diverse than a single population.

Thus, even when using elements of species richness as surrogates for overall biodiversity, we should still carefully consider the following:

the number of individual organisms present that form the populations
the number of populations present
the number of species present
the taxonomy (or evolutionary relatedness) of the species

Phylogenetic diversity is another important surrogate for evaluating biodiversity in some instances. Some regions may be the home of a burst of phylogenetic (or evolutionary) diversity, producing many closely related species. Various authors (for example, Seehausen, 2002) use as an example Lake Victoria, which has 500 to 1,000 closely related species of cichlids that evolved rapidly, perhaps within the last 14,600 years. Such areas are interesting not just because of their species richness but also because of our interest in understanding what conditions led to such a high rate of speciation. However, there are other reasons for using phylogenetic diversity as a surrogate. Stiassny (1997) explains that some regions may be very low in species richness but are the home to the basal (primitive) members of some groups of species. For example, Madagascar has very few species of cichlids, but those that are present appear to be the most primitive representatives of the group. Stiassny has shown that Madagascar is also home to basal representatives of other groups of fishes. The basal representatives are very important because they can tell us a great deal about the way in which certain features evolved in the group. In other words, we can look at the way that a particular feature (or character) is expressed by different representatives of the group; we can look at how the character is expressed in the most primitive member of the group, and from this, we can raise some hypotheses about the way that character has changed during the course of evolution of the group. Thus, although Madagascar may not be as species rich as other areas of comparable size, there is a special value to the diversity of the species found there, based on their phylogenetic or evolutionary history.

Species that are endemic to a certain region—that is, those that are found in one region of the world and nowhere else—are often used as a surrogate measure of the biodiversity value of a region. For example, Madagascar is often rated as one of the highest conservation priorities in the world, because a large majority of the species found there are endemic. One hundred percent of the primates, 80 percent of the flowering plants, and 95 percent of the plants found in the southern spiny forest are endemic.

Some areas may be home not just to individual endemic species but also to the only known representatives of entire groups of species. For example, the aye-aye, also found in Madagascar, is the only living representative of the primate family, Daubentoniidae. This is another aspect of using taxonomic or phylogenetic diversity as a particular measure of biodiversity.

The tuatara (*Sphenodon*) is a large, lizardlike animal that occurs only on islands off the coast of New Zealand. It is the only surviving representative of an entire order of reptiles, and it is also a phylogenetically basal representative of living reptiles. Therefore it confers special importance to the reptile biodiversity of these islands.

Mapping Biodiversity

Thus far, we have focused on the so-called organizational dimension of biodiversity (Wals and Van Weelie, 1998). This refers to variation in the genetic, biochemical, anatomical, or physiological composition of organisms, and to the population and species compositions of communities and ecosystems. However, when setting priorities for conservation, we often compare the diversity of species (or ecosystems and landscapes) across areas. That gives us an idea of how biodiversity is distributed across the earth.

Species-area Curves

A comparison of species richness relative to the area sampled (the species-area relationship) is one of the most important methods for quantifying the spatial distribution of biodiversity. This can be plotted (usually logarithmically) showing the number of species against area, and it gives a species area curve. Generally speaking, as you sample a larger area, you find more species. However, this species-area relationship can vary depending on whether one is sampling a small part of a single biota or a more extensive ecosystem or landscape. Four main species-area relationships are recognized:

1. Species-area relationships among tiny pieces of a single biota; below a certain area, there might not be a close correlation with species number.
2. Species-area relationships among large pieces of a single biota; larger areas are sampled than in (1), including more habitats.
3. Species-area relationships among islands

of a single archipelago; larger areas are sampled than in (2), containing more habitats, and the species-area relationship is affected by immigration and extinction of species from the islands (see Island Biogeography, below).

4. Species-area relationships among biogeographic provinces that have had separate evolutionary histories; the species-area relationship is affected by a higher rate of speciation and lower rate of extinction than the more restricted island archipelagos in (3).

Species-area relationships are important insofar as they show that any decrease in available habitat area will also result in a decrease in the number of species that can be supported by that habitat. When human activity results in the fragmentation of habitats into isolated regions of reduced area, then we expect a parallel decrease in the biodiversity of these habitats.

Island Biogeography

MacArthur and Wilson (1967) investigated the species-area relationship for islands in an archipelago (number 2, above) when they developed their theory of island biogeography. There is a consistent relationship between the area of an island and the number of species living on it. MacArthur and Wilson noted that the number of species present on an island represents a dynamic equilibrium between the rate of extinction and immigration of species. At equilibrium, the number of new species arriving equals the number of species going extinct. The taxonomic diversity of the island fauna may be changing (with different species arriving and disappearing), but the species richness stays constant.

The rate at which species immigrate to an island is most closely correlated with the distance of the island from the nearest land. The immigration rate (in number of species per year) is approximately the same for islands of different size but equal distance from the nearest land mass. That is because the colonizing organisms have the same distance to travel to reach any of the islands. However, the extinction rate is negatively correlated with the size of the island; a larger island can support a larger viable population, with less risk of extinction. Therefore, on large islands, the extinction rate reaches equilibrium with the immigration rate only after many species have colonized the island. Large islands will have a greater number of species than smaller islands at the same distance from the nearest landmass.

If we now consider islands of the same size but at different distances from the nearest land mass, we can see that the extinction rate is approximately the same for all islands. This is because the islands have the same available space for supporting viable populations. However, the immigration rate is negatively correlated with the distance of the island from the nearest land; the organisms have farther to travel to reach the more isolated islands. Thus, on distant islands, the extinction rate reaches equilibrium after only a few species have reached the island. The distant islands will have a smaller number of species than a less isolated island of the same size.

This theory of island biogeography has been applied to fragmented habitats and ecosystems. Using this theory, we can estimate the number of species a fragmented landscape can support, and predict whether that number will be enough to prevent the ecosystems from collapsing or prevent the extinction of a species.

Alpha, Beta, and Gamma Diversity

Whittaker (1972) created a system to describe biodiversity over different spatial scales. He called these alpha, beta, and gamma diversity. Alpha diversity refers to the diversity within a particular area or ecosystem, and it is usually expressed by the number of species in that ecosystem. This is equivalent to measuring the species richness of an area. For example, we might be interested in monitoring aquatic biodiversity on the offshore side of a fringing coral reef on Mauritius in the Indian Ocean. The alpha diversity of this reef is measured by the total number of species found in the area that we are monitoring. If we extend our survey along a transect running inshore from the reef, we cover some new ecosystems; the reef becomes shallower and less exposed as we move from the main fringing reef to an inshore lagoon ecosystem. If we extend our survey far enough, we may reach some submerged coastal mangrove forests. These different ecosystems will have different species and communities. We can compare the degree of species change as we move along the transect from one ecosystem to the next—this comparison of so-called between-area diversity is referred to as *beta diversity*. Gamma diversity is a measure of the overall diversity within a large region, and so in some respects it is an expanded version of alpha diversity. Thus, if we chose to survey all the reefs of Mauritius and measure species diversity over the whole area, that would be gamma diversity. We could expand the survey even further to include the reefs of the neighboring Mascarene Islands of Reunion and Rodrigues; the gamma diversity would then include the species for all those islands.

Spatial Gradients in Biodiversity

By studying spatial patterns of biodiversity we can identify some distinct spatial gradients in biodiversity. The most striking gradient is a global one; there is an increase in species richness as one moves from high latitudes at the poles to the lower latitudes of the tropics. A similar pattern is seen for higher taxonomic groups (genera, families). Various hypotheses have been raised to explain the greater species richness at the tropics (for example, environmental patchiness, solar energy, productivity) (Blackburn and Gaston, 1996). Most conservation activity is focused in the tropics, where there are more complex (and hence biologically richer) ecosystems, with more species to conserve. However, some of the species that are found near the poles are evolutionarily or ecologically unique and so are also especially deserving of conservation action.

Similarly, there is a biodiversity gradient with altitude. There are fewer species at higher elevations. This pattern is not as uniform for different taxa as the patterns of species across latitudinal species gradients. In oceans and freshwaters there are also fewer species as one moves to increasing depths below sea level.

Identifying Areas of Endemism and High or Low Biodiversity

By mapping biodiversity we can also identify areas of special interest, such as areas of endemism, areas that have unusually high levels of diversity (sometimes called hotspots), or areas with very low diversity (biodiversity coldspots).

Because endemic species are unique to one region, they are usually of special concern for conservation. High areas of endemism are also usually associated with high species richness (see Gaston and Spicer [1998] for references).

Biodiversity hotspots are priorities for conservation because they represent concentrations of diversity (Sechrest et al., 2002). Although a biodiversity coldspot is low in species richness, it can also be important to conserve, as it may be the only location where a rare species is found. For example, extreme environments (in temperature, pressure, or chemical composition) inhabited by just one or two specially adapted species are coldspots, but they still warrant conservation because they represent unique and biologically and physically interesting environments.

Conservation managers should consider all levels of spatial diversity when developing conservation policy, especially the alpha and beta diversity. Hunter (2002) provides a concrete example: a program to create forest clearings can increase the beta diversity of an area by creating additional forest edge areas that are colonized by more numerous species than are found in uncut forest. This will increase the beta diversity of the forest region. However, some species that are deep-forest specialists may be displaced as a result of the forest clearings, and so the alpha diversity of the forest itself is reduced.

Ecoregions

Since the 1980s, there has been an increasing tendency to map biodiversity over ecoregions. An ecoregion is "a relatively large unit of land or water containing a geographically distinct assemblage of species, natural communities, and environmental conditions" (WWF, 1999). Several standard methods of classifying ecoregions have been developed, with climate, altitude, and predominant vegetation being important criteria (Stein et al., 2000). Ecoregions may be relatively small (for example, the Crete Mediterranean forest ecoregion, covering about 8,000 square kilometers), or they may cover entire landscapes (for example, the east Siberian taiga, covering almost 4 million square kilometers).

Ecoregions are based on a comprehensive account of the biotic and abiotic components of the ecosystems they comprise. Therefore, they represent important units on which to base conservation planning. Conservation biologists have identified several ecoregions

A male poison arrow frog calling. The poisonous secretions of these Central and South American frogs, long used to produce poisonous arrows, are being investigated for possible use as a painkiller. (Michael and Patricia Fogden/Corbis)

that have high levels of species richness or endemism, contain unique or rare habitats, or show some other unusual ecological or evolutionary characteristic. The large geographic size of ecoregions means that they can provide the basis for developing extensive regional conservation programs. Indigenous human cultures may also be associated with ecoregions, with local communities relying on a variety of the natural resources for food, shelter, medicines, or other extrinsic purposes such as spiritual and cultural traditions. Therefore, the conservation management of these ecoregions is usually planned with the involvement of these local communities.

Comparing Concepts: Biodiversity and Other Concepts of Conservation Biology

Biodiversity is used as a measure of the complexity and biological health of a region and the ecosystems that it contains. Consequently, we can compare the biodiversity of different regions and make decisions for which regions are priorities for conservation. Similarly, there are some other conceptual approaches to describing the biological health of a region—namely, biotic integrity, ecosystem integrity, and sustainability. Hunter (2002) provides a discussion of the similarities and differences in the ways these concepts describe biological health. These are summarized here.

Biotic Integrity

Biotic integrity refers to the completeness of a biological system in terms of the organisms present and the interrelationships between them. Therefore, it is conceptually similar to some of the organizational and functional aspects of biodiversity discussed above (that is, genetic, organismal, population, species, and community diversity). Biotic integrity may be used to compare the condition of a community or ecosystem that has been changed in some way with a former condition. For example, the biotic integrity of a meadow can be changed by the introduction of cattle; the grazing cattle will change the types of plants present, which will consequently affect the types of animals feeding on the plants or using the undergrowth for shelter.

Ecosystem Integrity

Whereas biotic integrity is concerned with the populations and species and the interactions between them, ecosystem integrity also considers the relationships between these organisms and the surrounding environment. Ecosystem integrity is similar to the organizational and functional aspects of ecosystem diversity discussed above. As with biotic integrity, ecosystem integrity may be used to compare the condition of an ecosystem that has been changed in some way with a former condition. For example, the reintroduction of beavers to an area from which they had previously been extirpated represents an increase in the species diversity of that region. However, if the beavers had been absent for a very long time, then the local hydrology and associated flora and fauna might have changed to a condition quite different from that when the beavers were previously present. Therefore, unless carefully managed, the reintroduction of the beavers could represent a disruption to the integrity of these ecosystems.

Sustainability

Sustainability assumes that populations and ecosystems are biologically healthy if they can sustain themselves at a steady level over time. This concept is therefore more concerned with maintaining biodiversity at an existing steady state than attempting to change the structure of the populations, species, and ecosystems back to some former level. Again,

The io moth* (Automeris io)*, also known as the peacock moth, has spots on its hind wings that look like eyes and may serve as a defense against predation. (Jim Zuckerman/Corbis)

reintroducing a previously extirpated species would increase the biodiversity of a region but perhaps compromise the sustainability of the existing biodiversity. However, sustainability tends to focus on a few key populations, species, or resources in an ecosystem rather than considering the dynamics and diversity of the system as a whole. Thus the concept of sustainability can sometimes oversimplify an assessment of the biological health of an environment.

Setting Priorities for Biodiversity Conservation

Throughout most of the world, the practical and economic resources for conserving biodiversity are extremely limited. Therefore we need to set priorities for conservation action. To do this, we must decide what aspect of biodiversity we want to conserve, and we must use the appropriate surrogate to measure the biodiversity in the areas under comparison. For example, if we are working on freshwater fishes, we know that the Amazon Basin probably contains the most numerous and diverse fish fauna on earth, exceeding 1,000 species (Lundberg et al., 2000). However, we may be particularly interested in conserving endemic species that live in unusual habitats. In that case, we might be more inclined to put a premium on regions of Australia and New Guinea that are not rich in species (with about 500 species recorded) but do contain some unusual endemics found only in very restricted habitats, such as warm desert springs or ephemeral pools. As noted above, if we are particularly interested in conserving phylogenetically basal members of certain groups of fishes, such as cichlids and mullets, then we would direct our conservation efforts toward the rivers of Madagascar.

In some cases, the prioritization of regions for conservation is based, more pragmatically, on the relative threat of extinction to the species present. Thus, if we have $50,000 for conserving freshwater fish in either Brazil or Australia, our first inclination might be to use the money in the Brazilian Amazon, because there are more species there. But if we examine the 2000 IUCN Red List of Threatened Species (http://www.redlist.org), we can see that Australia has eight species of freshwater fish that are listed as "critically endangered," while Brazil has none. The biodiversity of Australia's freshwater fish is not as great as that of Brazil, but it is of special importance because proportionally more of the species are threatened. Thus there is an imperative to focus on the Australian freshwater fish for conservation work.

However, the example above represents an oversimplification. When any two regions are compared for prioritization of conservation action, conservation biologists look at all the other species present in the two regions, and they usually categorize areas based on the diversity or uniqueness of the entire ecosystem, rather than an individual species. Additionally, the quality of biodiversity data is highly variable for different continents. Some regions, such as parts of the Brazilian Amazon, may be imperiled by severe habitat loss, but there is inadequate data available to show that. The biodiversity of these regions may appear stable and unthreatened (with no species included on the IUCN Red List) simply because they have been undersampled and inadequately studied. Conservation biologists then choose to collect baseline information about the biodiversity of areas that are potentially important sites for conservation (Samways et al., 1995).

The choice of what surrogate to measure is never neutral. What you measure and how you measure it places a higher value on some particular element of biodiversity. By choosing one level, or unit, you draw attention and resources away from another. Ultimately, conservation decisions are influenced by many factors—political, economic, scientific, and social. Clear definitions of what level and aspects of biodiversity to target can help strengthen the effectiveness of science in the decision-making process.

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Why Is Biodiversity Important?

Human beings depend upon biodiversity in obvious, as well as in unimaginable, ways. We spend increasingly more time in built environments, immersed in our virtual worlds, surrounded by houses and offices, streets and shopping malls, with "nature" contained in aquaria in our living rooms or manicured parks to which we drive. These environs disconnect us from the natural world to the point that we forget how important biodiversity is for us. Children in the United States now need to be taught that food in the grocery store did not spring forth packaged, ready to cook and serve. Yet if we were to put a bubble over these built environments and tried to survive with no input from the natural world, we would perish in a heartbeat.

When we hear about species going extinct or ecosystems being destroyed, we somehow figure that other species or ecosystems are around to take their place, or that technology will help us invent a solution, or that in the end it doesn't really affect us. What we do not think about are the interconnections in the natural world, that any change in an ecosystem sooner or later causes a chain of reactions that reverberates throughout the system.

As an example, in the early 1950s, the World Health Organization undertook a mosquito eradication project in Borneo to reduce the incidence of malaria among the Dayak people. They sprayed large amounts of the insecticide DDT to eradicate the mosquitoes. It was quite successful; however, the DDT also killed a parasitic wasp that controlled thatch-eating caterpillars, causing the thatched roofs of the Dayak houses to cave in. Then, the DDT-poisoned insects were eaten by geckoes, which in turn were consumed by cats. As the cats began to die, the rat populations increased, and the Dayak were faced with outbreaks of sylvatic plague and typhus.

We rarely feel individually culpable for the loss of biodiversity, although human activities are the leading threat to the earth's biodiversity (see Threats to Biodiversity). Ironically, that same biodiversity is critical for human survival; yet few people realize the value of biodiversity to us.

Valuing Biodiversity

The "value" of biodiversity is a highly subjective concept that is at times difficult to understand and often causes fierce debate. There are two main categories of value for biodiversity: (1) utilitarian/instrumental or extrinsic value and (2) intrinsic or inherent value.

A living thing's utilitarian value is determined by its practical use or application. Usually we frame this in terms of its use for humans, such as for medicine or food, but it could also represent the value of an organism to other living things. Native bees, for example, serve as pollinators for many plants. Utilitarian values are often categorized as goods, services, information, spiritual, cultural, aesthetic, and recreational. In contrast to utilitarian value, intrinsic value describes the inherent worth of an organism, independent of its value to anyone or anything else. Those who believe in intrinsic value argue that all living things have intrinsic value—essentially a right to life—regardless of their extrinsic value.

Although the utilitarian/intrinsic/instrumental groupings are often used (Meffe and Carroll, 1997), there are other ways of categorizing the value of biodiversity. Frequently, people also distinguish things with economic, or market, value from those without it (Primack, 1998). In a somewhat more complex system, Kellert (1996) describes nine basic values that humans hold for nature and biodiversity: utilitarian; naturalistic or outdoor; ecologistic-scientific; aesthetic; symbolic; humanistic; moralistic; dominionistic; and negativisitic (see Table 1).

We will focus on two main categories of biodiversity value: utilitarian and intrinsic.

Utilitarian Value

Goods

The earth provides an abundance of goods essential to human life, including food, timber, fuel, fiber, and medicine, to name a few. Some highlighted examples follow.

Food. Humans have spent most of their existence as hunter-gathers, dependent on

Table 1
Three Methods of Categorizing the Value of Biodiversity

Meffe and Carroll	*Primack*	*Kellert*
Intrinsic/Utilitarian/Instrumental	Economic Values	Basic Values
Goods: food, fuel, fiber, medicine	Direct economic: consumptive (local) use; productive (market) use	Utilitarian: basic needs
Services: pollination, recycling, nitrogen fixation	Indirect economic: nonconsumptive (protection of water and soil resources regulation of climate; waste disposal; species relationships; recreation and ecotourism; education and science; environmental monitoring)	Naturalistic: discovery and recreation
Information: genetic engineering, applied biology, pure science	Option value: potential for future economic benefit	Ecologist–Scientific: knowledge
Psycho-spiritual: aesthetic beauty, religious awe, scientific knowledge	Existence value: amount people will pay to prevent species extinction	Aesthetic: beauty, inspiration
		Symbolic: communication
		Humanistic: connection to nature
		Moralistic: spiritual reverence
		Dominionistic: dominance over nature
		Negativistic: alienation from nature

Sources: Kellert, Stephen R. 1996. *The Value of Life: Biological Diversity and Human Society.* Washington, DC: Island; Meffe, Gary K., and C. Ronald Carroll. 1997. *Principles of Conservation Biology,* 2d ed. Sunderland, MA: Sinauer Associates; Primack, Richard B. 1998. *Essentials of Conservation Biology,* 2d ed. Sunderland, MA: Sinauer Associates wild plants and animals for survival. Around 10,000 years ago the first plants were cultivated, marking a fundamental shift in human history. Biodiversity continued to play a central role, providing the original source of all crops and domesticated animals. And today people still depend upon biodiversity to maintain healthy, sustainable agricultural systems. World crop exports alone were worth an impressive $432 billion in 2000, according to the Food and Agriculture Organization (FAO). Unlike agriculture, in which wild species have been domesticated, the world's marine fisheries are still dominated by wild-caught fish, representing 73.7 percent of the 125.2 million tons produced in 1999, according to the FAO.

Although humans have used more than 12,000 wild plants for food, twenty species now support much of the world's population (Burnett, 1999). It is still unclear why certain species were cultivated and not others. Of all the plants that we depend upon, none are more important than the grass family, Gramineae. The grass family includes the world's principal staples: wheat, rice, and corn (maize). Rice and corn formed the basis of civilizations in the Far East and the Americas, while wheat (together with barley) formed the basis of the civilizations of the Near East.

Wheat (*Triticum sp.*) is believed to have been one of the earliest cultivated plants, being highly suited for the making of bread because of the amount and quality of its gluten. Natural hybridization between different types of wild grasses helped produce the first wheat strains. For example, einkorn wheat and a goat grass hybridized to produce "emmer." Later, emmer would form a hybrid with another wild grass to produce the so-called bread wheats. Each of these hybridizations brought new characteristics that made wheat more suitable for cultivation. The grains of wild wheat tended to fall out of the sheath individually, which was useful for seed dispersal but not for harvesting. Modifications to wild wheat eventually created a plant that could no longer spread its own seeds without the help of humans and whose grains were easy to gather. Bread wheat was also unique for its plump grains. Hybridization with grass species that were not used for food created the qualities we revere today in common bread wheat. The stories for rice and corn and other species with a long history of cultivation are similar.

Less familiar wild plants exist that could be important foods in the future. For example, peachpalm (*Guilielma gasipaes*, Arecaceae) from Central America produces one of the most balanced foods for human nutrition, being composed of an ideal mixture of carbohydrates, protein, fat, vitamins, and minerals. Peachpalm can produce more protein and carbohydrate per hectare than corn (Vietmeyer, 1996). Even among species related to our common staples, only a handful are currently in cultivation. There are 235 species of potatoes, but only seven are cultivated. Sorghum, emmer, and spelt were once widely grown grains, but they have been largely replaced by wheat. However, because of their unique environmental adaptations—sorghum, for example, can be grown in climates that do not support wheat—these grasses may become more important in the future.

Wood and Forest Products. The worldwide production of timber and related products is a multibillion-dollar industry. Wood is used to construct homes and furniture; it is also made into mulch, chipboard, paper, and packaging. The wood from each tree species has unique characteristics suitable for different purposes: white ash is used for baseball bats; locust and cedar, both very rot-resistant, are valued as fence posts; Brazilian rosewood is favored for guitars; and black walnut has been used for gunstocks because of its strength and decay resistance. Fabric manufacturers harvest wood for its fiber, using wood cellulose to make Tencel and rayon. Other useful tree products include cork, rubber, latex, and resins, as well as fruits, nuts, and oils. According to the World Resources Institute, 63 percent of all harvested wood is used as fuel, either burned directly or after being converted to charcoal

Medicine. According to the World Health Organization, about 80 percent of the world's population still use plants as a primary source of medicine, and many Western medicines were developed from a plant or animal source: 57 percent of the 150 most commonly prescribed drugs originate from living organisms (Grifo et al., 1997). For example, the antibiotic penicillin is derived from a fungus (*Pencillium notatum*) that is a common bread mold. Aspirin and common acne medicines are derived from salicylic acids, first taken from the bark of willow trees (*Salix sp.*). Although these drugs are now synthesized more efficiently than extracted from the wild, we still depend on the chemical structures in nature to guide us in developing and synthesizing new drugs.

Some drugs are still synthesized in whole or in part from wild sources. For example, Taxol, a potent drug used to fight ovarian and breast cancers, was first derived from the bark of the Pacific yew (*Taxus brevifolia*). In fact, the bark of six trees (each of at least 13.2 cm in diameter) was needed to produce enough Taxol for only one cancer patient; stripping the bark killed the trees. Fortunately, researchers found that the leaves of the European yew (*Taxus baccata*), a close relative of the Pacific yew, produce a similar chemical substance that can be used to produce Taxol both sustainably and less expensively. At this time the production of Taxol remains partially dependent on wild sources.

A less well known, more recent example of how we depend upon nature comes from the biotechnology industry. The polymerase chain reaction (PCR) is used in genetic research to replicate and manipulate DNA in large quantities over short periods of time. PCR has revolutionized genetic engineering, bringing it into the realm of industry and opening new possibilities for improved health and agriculture. The special enzymes used to catalize PCR withstand extremely high temperatures and originate, appropriately enough, in the hot springs of Yellowstone National Park. Needless to say, scientists are now researching these and other extreme environments to identify other enzymes that could be of help to the biotechnology industry.

Services

Ecosystems, and the plant and animal species that compose them, provide a host of services to all living things. These services include the regulation of atmospheric gases that affect global and local climates, including the air we breathe; maintenance of the hydrologic cycle; control of nutrient and energy flow through the planet, including waste decomposition and detoxification, soil renewal, nitrogen fixation, and photosynthesis; a genetic library, providing a source of information to create better agricultural crops or livestock; maintenance of reproduction, such as pollination and seed dispersal, in plants that we rely upon for food, clothing, or shelter; and control of agricultural pests. Often the values of ecosystem services are not considered in commercial market analyses, yet they are critically important to human survival. Humans can rarely replace these services—or, if they can, only at considerable cost. According to a study by Costanza et al. (1997), the earth provides a minimum of $16 to $54 trillion worth of "services" to humans per year.

Biodiversity plays a critical role in regulating the earth's physical, chemical, and geological properties, from influencing the chemical composition of the atmosphere to modifying the climate. Earth's atmosphere has a unique composition, being made up primarily of nitrogen (77 percent) and oxygen (21 percent)—unlike the atmospheres of Venus and Mars, which are almost entirely composed of carbon dioxide (95 percent). Initially, like those of Venus and Mars, the atmosphere of Earth lacked oxygen. About 3.5 billion years ago, early life forms (bacteria) helped to create an oxygenated atmosphere by means of photosynthesis, taking up carbon dioxide and releasing oxygen (Schopf, 1983). Eventually, these organisms altered the composition of the atmosphere and paved the way for organisms that use oxygen as an energy source (aerobic respiration). Thus, organisms and their environment evolved together, achieving a balance between living and nonliving things, a state known as *homeostasis*.

The atmosphere is continually influenced by biodiversity. Phytoplankton (microscopic marine plants) in our oceans play a central role in regulating atmospheric chemistry. The oceans are the major reservoir for carbon on the planet, and they regulate carbon levels in the atmosphere. Carbon is continually exchanged between the atmosphere and the oceans. Phytoplankton transform carbon dioxide into organic matter during photosynthesis. This carbon-laden organic matter settles either directly or indirectly (after it has been consumed) to the deep ocean, where it stays for centuries or even thousands of years. This movement of carbon through the oceans removes excess carbon from the atmosphere and regulates the earth's climate. Over the last century, humans appear to have affected the atmospheric balance by releasing large amounts of carbon dioxide. The excess carbon dioxide, along with similar so-called greenhouse gases, is believed to be heating up our atmosphere and changing the world's climate.

Besides influencing global climate by modifying the atmosphere's composition, biodiversity affects climate in other ways. The extent and distribution of different types of vegetation over the globe, for example, modify climate by affecting the reflectance of sunlight (radiation balance), through the release of water vapor (evapotranspiration), and by changing wind patterns and moisture loss (surface roughness). The amount of solar radiation reflected by a surface is known as its *albedo*; surfaces with low albedo reflect a small amount of sunlight; those with high albedo reflect a large amount. Different types of vegetation have different albedos: forests typically have low albedo, whereas deserts have high albedo. Thus vegetation cover influences the amount of energy that reaches the earth. Deciduous forests are a good example of the seasonal relationship between vegetation and radiation balance. In the summer, the leaves in deciduous forests absorb solar radiation through photosynthesis; in winter, after their leaves have fallen, deciduous forests tend to reflect more radiation. These seasonal changes in vegetation modify climate in complex ways by changing evapotranspiration rates and albedo.

Vegetation absorbs water from the soil and releases it back into the atmosphere through evapotranspiration, the major pathway for water to move from the soil to the atmosphere. This release of water lowers the air temperature. In the Amazon region, vegetation and climate are tightly coupled; evapotranspiration of plants is believed to contribute 50 percent of the annual rainfall. Deforestation in this region leads to a complex feedback mechanism: it reduces evapotranspiration, decreasing rainfall and increasing the area's vulnerability to fire (Laurance and Williamson, 2001). Deforestation is also influencing the climate of cloud forests in the mountains of Costa Rica. The Monteverde Cloud Forest is nominally well protected within a network of reserves, and it harbors a rich diversity of organisms, many of which are found nowhere else. However, deforestation in lower-lying lands is changing the local climate and lifting the clouds above the mountains, leaving the cloud forest cloudless. Removing the clouds from a cloud forest dries the forest, so that it can no longer support the same vegetation or provide appropriate habitat for many of the species originally found there. As these areas dry up, there is literally nowhere for the cloud forest species to go, and they may disappear permanently. Similar patterns may be occurring in other, less well known montane cloud forests around the world.

Different vegetation types and topographies have varying surface roughness—that is, average vertical relief; small-scale irregularities of a surface change the flow of winds in the lower atmosphere, which in turn influences climate. Lower surface roughness tends to reduce surface moisture and to increase evaporation. Models examining the conversion of African savanna to grassland and agriculture found that precipitation declined by 10 percent in the new landscape (Hoffmann and Jackson, 2000). This decline was caused equally by changes in the surface albedo and the surface roughness. Farmers apply this knowledge when they plant trees to create windbreaks. Windbreaks reduce wind speed and change the microclimate, increasing surface roughness, reducing soil erosion, and modifying temperature and humidity. For many field crops, windbreaks increase yield and production efficiency. They also minimize stress on livestock from cold winds.

Biodiversity is also important for global soil and water protection. Terrestrial vegetation in forests and other upland habitats helps to maintain the water quality and quantity of the hydrologic cycle, and it also helps to control soil erosion. Plant leaves slow the descent of raindrops, so that by the time the water reaches the ground it is less likely to wash away soil and more likely to percolate into the ground. Roots hold soil in place, which increases water absorption and decreases soil erosion during heavy rains. Plants pump water from the soil back into the atmosphere, completing the cycle. In watersheds (land areas drained by a river and its tributaries) where vegetation has been removed, flooding prevails in the wet season and drought in the dry season. Soil erosion is also more intense and rapid, causing a double effect: removal of nutrient-rich topsoil and siltation in downstream riverine or, ultimately, oceanic environments. This siltation can harm riverine and coastal fisheries as well as damage coral reefs. In the Mississippi River delta ecosystem, for example, a buildup of sediment and pesticides has created an anoxic area (that is, an area without oxygen), known as the dead zone, in the Gulf of Mexico (Turner and Rabalais, 1994). The source of these sediments and pesticides is upriver, far from the delta. Another example comes from East Africa, where sediment discharges caused significant damage to the Malindi-Watamu fringing reef complex along the Kenyan coast (van Katwijk et al., 1993), smothering the corals and leading to excessive algal growth.

Wetlands, natural communities linking land and water, are also instrumental for the maintenance of clean water and erosion control. Wetlands are defined as lands where water is present at or near the surface of the soil, or within the root zone, all year or for a period of time during the year; they are characterized by vegetation adapted for those conditions. Microbes and plants in wetlands, some of the most productive ecosystems on earth, absorb nutrients and in the process filter and purify water before pollutants can enter aquatic ecosystems.

Wetlands help reduce flood, wave, and wind damage. They slow the flow of flood waters and accumulate sediments that would otherwise be carried downstream or into coastal areas. Wetlands also serve as breeding grounds and nurseries for fish, and they support thousands of bird and other animal species.

Nutrient cycling is yet another critical service provided by nature. Fungi and microbes in the soil help to break down dead plants and animals. This process converts elements and compounds—such as nitrogen and phosphate—into nutrients that most plants use and thus enriches the soil. Nitrogen-fixing bacteria, for example, transform atmospheric nitrogen into nitrates or nitrites. Nitrogen is essential for plant growth, and an insufficient quantity limits biomass production in both natural and agricultural ecosystems. In addition to decomposition, microbes also detoxify waste, changing waste products into forms less harmful to humans.

Humans cultivate only a small fraction of the plant and animal species on earth. To ensure that we can sustain these systems, we depend on biodiversity, especially the wild counterparts of cultivated foods and domesticated animals, as a genetic library that we can use to create new varieties or breeds better able to combat pests or disease, more suited to certain environmental conditions. Thus biodiversity acts as a kind of insurance for agriculture. For instance, corn (*Zea mays*), along with wheat and rice, is one of the world's most important cultivated plants. The annual global market for corn is nearly $60 billion, yet this crop is susceptible to several viral diseases. In the late 1970s, teosinte (*Zea diploperennis)*, the closest wild relative of corn, was discovered and found to be resistant to viral diseases that infect *Z. mays*. The new species has the same chromosome number as *Z. mays* and can therefore hybridize with it. When that occurs, some of the viral resistance is transferred to domestic corn. Four viral-resistant commercial strains have since been produced, highlighting the importance of wild counterparts to cultivated food crops.

As a further example of ecosystem services, an estimated 90 percent of flowering plants depend on pollinators, such as wasps, birds, bats, and bees, to reproduce. Without these pollinators, many plant species would face extinction. Plants and their pollinators are increasingly threatened around the world, however (Buchmann and Nabhan, 1995). Yet pollination is critical to most major crops and virtually impossible to replace. For instance, imagine how costly orange juice would be (and how little would be available) if its natural pollinators no longer existed, and each orange flower had to be fertilized by hand.

Agricultural pests (principally insects, plant pathogens, and weeds) destroy an estimated 37 percent of U.S. crops (Pimentel and Levitan, 1986). The level of destruction varies depending on the crop, where it is grown, and the type of pest. According to Oerke et al. (1994), production losses caused by pests, pathogens, and weeds amount to 15 percent, 14 percent, and 13 percent on average, respectively, for the principal cereals and potatoes. Without natural predators that keep pests under control, these figures would be much higher. Natural pest control saves farmers billions each year, and pesticides are no replacement for the services provided by these crop-friendly predators.

Some animal species are important dispersers of plant and tree seeds. Loss of these species may have a "domino effect," leading to the loss of those plants and trees that depend upon them for reproduction. In the pine forests of western North America, for example, corvids (including jays, magpies, and crows), squirrels, and bears play a role in seed dispersal. The Clark's nutcracker (*Nucifraga columbiana*) is particularly well adapted to the dispersal of whitebark pine (*Pinus albicaulis*) seeds. The nutcracker removes the wingless seeds from the cones, which otherwise would not open on their own. Nutcrackers hide the seeds in clumps. When the uneaten seeds eventually grow, they are clustered, accounting for the typical distribution pattern of whitebark pine in the forest.

Information

We value biodiversity for its ability to inspire creativity and to help us to solve problems. The term *biomimicry* is used for research into how humans use models from the natural world to solve problems in agriculture, medicine, manufacturing, and commerce. Humans have long drawn inspiration from the wild for commercial products. Velcro, for example, was patterned after cockleburs, which attach to clothes as people walk through a meadow. A closer look at hedgehog spines, whose supple, strong structure enables them to bend without breaking, led to the development of lightweight wheels in which the tires have been replaced with an array of spines that effectively absorb shocks. Millipedes—invertebrates with multiple pairs of legs fringing their long bodies—are being studied to help design robots to carry heavy weights in cramped conditions where significant twisting and turning are necessary (Beattie and Ehrlich, 2001). Halobacteria that thrive in the salt ponds of San Francisco Bay contain a molecule called bacteriorhodopsin, which may revolutionize computer optics.

Scientists study nonhuman primates, such as baboons, chimpanzees, and howler monkeys, in the wild to learn how they "self-medicate" against diseases like schistosomiasis, and how they use secondary compounds from plants, for instance, to regulate reproduction. This information can help scientists in the search for new drugs for humans. Similarly, studies of how natural prairies are structured and function are illuminating new methods for fertilizing crops and protecting them from pests (Benyus 1997).

Spiritual, Cultural, Aesthetic, and Recreational

Although many of the utilitarian values discussed previously have an economic basis, biodiversity is valued for noneconomic reasons as well. Most cultures place distinct aesthetic, spiritual, or recreational value on natural areas. People look to the natural world as a source of inspiration, beauty, and rejuvenation. They seek out natural areas in which to relax, surrounded by the sights, sounds, and smells of nature. Some people believe that individual living organisms are valuable for their beauty, rarity, complexity, and adaptations (Rossow, 1981, reprinted in Van DeVeer and Pierce, 1998). Nature provides insight and understanding of our role in the world.

Biodiversity plays a central role in human spiritual traditions. Religions help define the relationships between humans and their environment. Nature is used in religious imagery, and many religious traditions view the contemplation of nature as an important spiritual value (Chevalier et al., 1997). In Thailand, trees are marked with yellow cloth to denote their sacredness to the Buddhist faith. This practice has saved some sacred groves from illegal logging, since to destroy these trees is a serious crime. Ancient Greek temples were situated in places noted for their natural beauty. Similarly, in Japan, Shinto temples are often located in large groves of trees, where spiritual forces are believed to exist. In the islands of the South Pacific, fishing families have a unique relationship with certain ani-

A grizzly bear on the Alaska tundra. People look to the natural world and the creatures that inhabit it as sources of inspiration and rejuvenation. Some people believe that living organisms are valuable for their beauty, rarity, and complexity, even if they have no obvious utilitarian value. (John Conrad/Corbis)

mals, usually turtles or sharks. For each family, these special species (or groups of species) are considered sacred, and it is taboo to hunt them; this relationship is carried on through the generations. The idea of kinship between animals and people is known as totemism, and it is found in many parts of the world. Because totems are usually associated with taboos, they can help to control the harvest of species. In some fishing communities, taboos linked to the life cycle of certain species may restrict hunting when fish are breeding.

The natural world also provides a rich source of symbols used in art and literature. Plants and animals are central to mythology, dance, song, poetry, rituals, festivals, and holidays around the world. Different cultures can exhibit opposite attitudes toward a given species. Snakes, for example, are honored by some cultures and reviled by others. Rats are considered pests in much of Europe and North America, delicacies in many Asian countries, and sacred in some parts of India. Of course, within cultures individual attitudes can vary dramatically. For instance, in Britain many people dislike rodents, and yet there are several associations devoted to breeding them, including the National Mouse Club and the National Fancy Rat Club.

Natural areas provide a source of inspiration and a place to relax. Because of this, forests, lakes, mountains, and beaches offer opportunities for commercially valuable outdoor activities such as ecotourism, fishing, and hiking.

Costanza et al. (1997) estimate that the total recreational value of the world's resources could be as high as $800 billion annually. The growing ecotourism industry generates an enormous amount of money and is fast becoming a lucrative industry for some developing nations. For example, in Costa Rica tourism has expanded rapidly since the mid-1980s; it is now the leading source of foreign revenue, surpassing the banana industry.

Intrinsic Value

Intrinsic value is generally defined as the inherent worth of something, independent of its value to anyone or anything else. One way to think about intrinsic value is to view it as similar to an inalienable right to life. The Endangered Species Act in the United States protects many species that are not "valuable" to humans in any readily definable way (for instance, the dwarf wedge mussel [*Alasmidonta heterodon*] or the swamp pink [*Helonias bullata*]). These species are protected based on the idea that they have a right to life, just as all humans do. Conservationist Aldo Leopold is one of the most famous supporters of the idea that wildlife and wildlands hold value in and of themselves (Lorbiecki, 1996).

Intrinsic value is a frequently misused term. Some believe that values not easily defined, such as aesthetic values, are intrinsic values. As discussed earlier, aesthetic value is a kind of extrinsic/utilitarian value. Others believe that the value of a species to the structure and function of an ecosystem (such as an invertebrate decomposer's ability to cycle nutrients) is its intrinsic value, because it does not have any obvious value to humans. But here intrinsic value is incorrectly defined as one organism's usefulness to another organism.

The concept of intrinsic value is one of the most difficult to understand, as it is heavily philosophical. Many economists and some ethicists believe that intrinsic value does not exist, arguing that all values are human-centered. Generally, two contrasting ideologies frame a continuum along which our beliefs fall. On one extreme is the idea that humans are the center of the universe and that nature exists (and is used) for human benefit (a view called anthropocentrism); at the other is the notion that life is the center of the universe and that humans are a separate but equal part of nature (biocentrism, or ecocentrism). The latter viewpoint, forwarded by the deep ecology movement (Naess, 1989), holds that all species have intrinsic value and that humans are no more important than other species.

That humans have no right to wantonly destroy biodiversity is an assertion justifiable from certain religious standpoints. If God or some other deity or sacred process created the natural world alongside humans, then all creatures are imbued with sacredness: all have intrinsic value. This "most fundamental" postulate of all—that biotic diversity has intrinsic value, irrespective of its utilitarian value—is key to many motivations for biodiversity conservation. If one accepts the idea that biodiversity has intrinsic value, then species conservation requires less justification.

Measuring the Value of Biodiversity

As we can see, there are equally diverse and valid ways to value biodiversity. Throughout most of human history, there has been no need to quantify these values. However, given the recent, overwhelming impact of human activity on biodiversity, in part because of population growth and our technological capability, developing ways to measure biodiversity has become a necessity. We live in a world in which tradeoffs and decisions have dire implications for biodiversity.

Apart from family, humans interact with each other as both community members and as consumers (Sagoff, 1988). Within these frameworks, we have developed ways to "measure" the importance of biodiversity related to other values, either through deliberation and priority-setting in a democratic process or in economic terms. To date, the most commonly employed method has been economic.

To determine biodiversity's importance in economic terms, economists group biodiversity's values into two categories: use and nonuse. Use values include direct use values (for goods), indirect use values (as in ecosystem services such as flood control), and option values (protecting biodiversity for some unknown future human need). Nonuse values include bequest values (the value of the legacy left to the future) and existence values (the value of the knowledge that certain species or wilderness areas will continue to exist). Economists have not found a way to capture intrinsic values in a meaningful economic way, so this value has been excluded from any economic determination scheme (Moran and Pearce, 1997).

Each of these use or nonuse value groupings (other than intrinsic) can be assigned a monetary value. This is most often done by determining how much people are willing to pay, or what they are willing to accept, as compensation for the gain or loss of a benefit of biodiversity.

In some cases, willingness to pay (or to accept compensation) can be determined directly, by asking people what they prefer. One of the most common of these methods is the Contingent Valuation Method. In this method, the public is surveyed to determine what value they place on a particular natural asset. For example, how much will they pay for a scenic view, or to live in a community with cleaner air, or to prevent a species from going extinct. This method was used to determine the nonuse values of the marine ecosystem that was damaged by the *Exxon Valdez* oil spill in 1989. People living outside Alaska were asked how much they were willing to pay to avoid an oil spill in Prince William Sound with similar environmental impacts. The median was $31.00 per household, or $2.8 billion when all U.S. households were totaled (Peterson and Lubchenco, 1997).

Willingness to pay can also be determined indirectly. In place of directly asking how much people would pay to live in an area, the hedonic price technique determines the difference in housing costs between an area with clean air and one with polluted air. The difference in price is assumed to be the value of the clean air.

Another example of indirect valuation is the travel cost method, in which the value of a particular resource is inferred by the cost of travel to that resource. Travel cost and other related expenses have been used to estimate the economic worth of a horseshoe crab fishery in providing ecotourism opportunities. Each spring thousands of migratory shorebirds, en route to their arctic breeding grounds, stop along Delaware Bay to feed on horseshoe crab eggs. Many bird-watchers come to the region to view the shorebirds and the crabs. The "value" of the crab population has been determined indirectly, in part by calculating what the birders spend to see the birds and crabs. This valuation includes the bird-watchers' travel, lodging, and food costs, as well as equipment costs and park fees (Manion, West, and Unsworth, 2000).

Replacement value is another example of indirect monetary determination. A replacement value analysis assigns a monetary value to an ecosystem function based on what it would cost to replace it if the service were no longer available. For instance, New York City's water supply comes from the Delaware and Hudson River watersheds farther to the north.

In 1996 the water coming into the city was no longer meeting Environmental Protection Agency standards, as sewage, pesticides, and fertilizers were interfering with natural water purification processes such as soil microbe activity, natural filtration, and sedimentation. The city decided against constructing a new, multimillion-dollar purification treatment center within the city limits, instead concentrating on investing in the preservation of so-called natural capital (that is, watershed land) in the Catskill Mountains. To replace the services provided by the watershed would cost roughly $6 to $8 billion, as well as $300 million annually for maintenance. That is the replacement value of the ecosystem's services. To ensure the sustainability of these watersheds, New York City administrators developed a comprehensive plan to control activities within the watershed that affect water quality. This somewhat controversial plan included reducing pollution from agriculture, minimizing nonpoint pollution, restoring streams and wetlands, protecting buffer lands through land acquisition and stewardship, and developing community education programs.

Although these and other economic assessment techniques can be useful tools, they do not fully determine the value of biodiversity for a number of reasons. People's decisions about their so-called willingness to pay are based upon different preferences and constraints, ultimately affecting the final dollar value. People usually expect more compensation for the loss of something they already have (for example, clean air) than they are willing to pay to improve an existing situation (such as cleaning up polluted air) (Van Deveer and Pierce, 1998). In addition, the value of these assessments also depends upon how much—and what kind of—information people are given to help them make their determination. The quality of available information can alter their response and the final valuation (Sagoff, 1988).

Economic cost determinations seldom include true environmental costs. Typical cost determinations include raw materials, wages, and the cost of processing, production, and distribution. Costs usually not included (termed "externalities") are the waste or pollution generated by production, the depletion of natural resources, and other social impacts on the population (for example, smog that leads to poor health). Instead, these costs are passed on to society. As Van DeVeer and Pierce (1998) explain, "If a firm wishes to dump a ton of sulfur dioxide into the atmosphere, it is under no obligation to determine whose health or whose view might be impaired by this use of the environment."

The market economy considers only costs and benefits to humans, and works with a short-term view of the world. How do we factor in the costs to wildlife or natural processes and the impacts that accrue over a longer ecological time frame? How can we predict what might be "valuable" to us, or the world, in the future? Current economic theory is based on the assumption of unlimited abundance, whereas in reality the earth and its resources are finite.

Ecological economics is a relatively new field, working to address these concerns and to do a better job of incorporating ecological concepts into economic theory. In contrast to conventional economics, ecological economics is defined as multiscale, focuses on all species (including humans) and whole ecosystems, and has a goal of maintaining our natural world. Designing ecologically sustainable economic activities will require modifying existing techniques or developing entirely new tools. An important proposed revision to current economic standards is the incorporation of natural resource accounting to

A flock of emperor penguins in the Antarctic landscape. The economic costs for the products and services we use seldom include the environmental costs—the price paid by species and their habitats. The market economy considers only costs and benefits to humans and works with a short-term view of the world. How do we factor in the costs to wildlife or natural processes? How can we predict what ecosystems and species might be "valuable" to us, or the world, in the future? (Galen Rowell/Corbis)

determine gross national product (GNP). This modification, the index of sustainable economic welfare, developed by Herman Daly, adds the contributions of natural resources (for example, the value of forests, topsoil, farmlands, and so forth) to determinations of economic growth. Ecological economists believe that this is necessary because the GNP typically counts all economic activity as good, regardless of whether that activity has high environmental costs, such as pollution (Costanza, Daly, and Bartholomew, 1991).

Despite these efforts to improve the techniques of applying economics to ecological valuation, some argue that certain things, such as health, safety, freedom, nature, and human life, cannot be viewed in monetary terms. According to Sagoff (1988) and others, the values of nature are better determined by a democratic, deliberative process allowing for discussion and compromise.

Why Do Values Matter?

We often ask why we should care if one species is lost out of many in an ecosystem. One answer is that natural communities are finely tuned systems in which each species has a role to play. Removing one species may have immediate consequences, or we may not see the effects until decades or centuries later. For example, kelp "forests" (composed of a brown seaweed of the Family Laminariales), found in shallow, rocky habitats from temperate to subarctic regions, are important ecosystems for many commercially valuable fish and invertebrates. In the northern Pacific, prior to hunting by humans, these communities encompassed vast forests of kelp and other marine plants. The kelp was eaten by herbivores such as sea urchins (Family Strongylocentrotidae), which in turn were preyed upon by predators such as otters (*Enhydra lutris*). Hunting during the eighteenth and nineteenth centuries brought sea otters to the brink of extinction. In the absence of sea otters, sea urchin populations burgeoned. Sea urchins grazed down the kelp forests, at the extreme resulting in "urchin barrens," in which the kelp was completely eradicated. Other species dependent upon kelp (such as abalone *Haliotis spp.*) were affected, too. Legal protection of sea otters in the twentieth century led to partial recovery of the system. Unfortunately, however, sea otter populations in Alaska seem more recently to be threatened by increased predation from killer whales (*Orcinus orca*). It appears that whales may have shifted their diet to sea otters when populations of their preferred prey, seals and sea lions, declined. The exact reason for the decline in the seal and sea lion populations is still unclear, but it seems to be the result of declines in their prey, in combination with increased fishing and higher ocean temperatures. As a result of the loss of sea otters, increased sea urchin populations are grazing down kelp beds again.

Interestingly, a similar scenario in kelp forests in southern California did not show immediate effects after the disappearance of sea otters. That is because the system was initially more diverse. Other predators (California sheephead fish, *Semicossyphus pulcher*, and spiny lobsters, *Panulirus interruptus*) and competitors (abalone) of the sea urchin helped maintain the system. However, when those predators and competitors were overharvested as well in the 1950s, the kelp forests declined drastically as sea urchin populations boomed. In the 1970s and 1980s, a sea urchin fishery developed that then enabled the kelp forest to recover. However, it left a system with little diversity. The interrelationships among these species and the changes that reverberate through systems as species are removed are mirrored in other ecosystems on the planet, both aquatic and terrestrial.

As this example illustrates, biodiversity is incredibly complex; successful and comprehensive conservation efforts cannot focus on just one species, or even on events of the recent past. Yet we cannot possibly design conservation strategies that take into account all species and their interconnections—we just do not have the resources or the knowledge to do so. Thus we make choices when we measure biodiversity or set conservation priorities. These choices depend upon what we currently hold as valuable. What we value today will influence the scope of the natural world for future generations, as laws, policies, and conservation decisions are based on our current value system.

The issue of what elements of biodiversity are most valuable arises at different scales, from individual to global. For instance, conservation biologists often have to decide in which countries a nongovernmental organization should invest its resources. Within a country or region one has to decide which areas should receive conservation attention, and which to include within a protected area system. Globally, nationally, and regionally, we need to decide which species or populations to study, monitor, and manage. In deciding where to place our resources, we face questions such as these: Should we value areas with greater numbers of species over those with many endemic species (those that are found only in

The actions of individuals—decisions about where to live, what to buy, what to do on and with our land, and how to vote—will have profound effects on the future of biodiversity. (Todd Gipstein/Corbis)

that one place in the world)? Would it be better to value the conservation of phylogenetic diversity (species that are maximally different from an evolutionary standpoint) over the degree of threat to a species? Would it be better to plan for greater security for one type of ecosystem in case of catastrophic events by conserving two or more representatives of that ecosystem, or to have a greater representation of more types of ecosystems? Should we give priority to a species or ecosystem that is nationally endangered but globally common or to one that is nationally common and globally rare? There are no correct answers to these questions—the responses depend upon what the decision-makers value most at the moment they are making the decision.

The responses also depend on the information available for making decisions. Scientists working with the National Centre for Ecological Analysis and Synthesis in the United States have recently raised the question of whether there might also be an inadvertent scientific bias toward "cute, unique, or spectacular" species. In most countries, conservation efforts focus on the species listed as endangered and threatened, although those lists to date include mainly vertebrates and vascular plants. Since we know so little about other components of biodiversity (invertebrates, nonvascular plants, microbes, and so forth), our current endangered species lists may be omitting information critical to better decision making.

Ordinary citizens are involved in similar biodiversity-related decision-making on the local scale as well. Communities across the globe make decisions about whether and how to protect natural lands and their biodiversity. Should a village sell the timber from its forested lands, or should it preserve the forest for its nontimber products (such as fruit and nuts, animal products, medicinal plants, and shade)? Should a municipality permit development or protect open space?

Some feel that governments and corporations have more influence than individuals over local and global biodiversity. However, governments and corporations are organized and run by individuals. In democratic societies, at least, individuals have the responsibility to understand the ramifications of their choices on biodiversity, along with the responsibility to participate in local decision-making. The actions of individuals, whether acting alone or in concert with others, will have the most profound effects on the future of biodiversity.

Some of the most critical priority setting is done every day by individuals in their own lives—decisions about where to live, what to buy, what to do on and with their land, or even how to vote. Yet polls show that while 70 percent of U.S. citizens are concerned about the environment, exit polls record that only 28 to 29 percent of voters actually consider the environment when voting (Dowrie and Shabecoff, 2001/2002).

Few individuals truly realize the impact of their daily decisions. In the book *Stuff, the Secret Life of Everyday Things,* authors John Ryan and Alan Durning trace all of the environmental costs involved in drinking a cup of coffee. The decision whether to drink coffee at all; which brand to purchase; and how that coffee was grown, harvested, shipped, distributed, packaged, and prepared—all come under consideration. Because many of the steps in coffee production occur elsewhere in the world, there are global ramifications to the simple decision to drink a cup of coffee.

Ultimately, each of the decisions people make, consciously or not, is based upon what they as individuals value, and those are the values that will be learned by their children. As Mark Sagoff (1988) writes: "If individuals in the future have no exposure to anything we consider natural or unspoiled, they will not acquire a taste for such things. What they want will be more or less what we leave to them."

However, it is not merely a question of what we want. We must never forget that biodiversity is vital to human survival. It is essential for the future of life on the planet that we realize this value.

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Threats to Biodiversity

Over the last century, humans have come to dominate the planet. Our rapidly expanding population and economies place increasing demands on the world's resources. One-third to one-half of the world's terrestrial surface has been substantially altered by human activity (Vitousek et al., 1997). Many species persist on a greatly reduced area of their former range and on increasingly fragmented landscapes. Ecosystems suitable for agriculture, such as tropical dry forests and tall-grass prairie, have almost completely disappeared from our planet. Dams are disrupting freshwater ecosystems, while the marine world is threatened by overfishing and habitat destruction. Humans are also transporting plants and animals around the globe both deliberately and unintentionally. These "invaders" threaten other species or change entire ecosystems. David Quammen (1998) aptly notes that we are living on an increasingly "weedy planet," filled with species that can survive only in human-modified landscapes. Human influence reaches even the farthest corners of the globe; species in the Arctic and Antarctic are contaminated by pollutants created thousands of miles away and carried through the atmosphere. We are even modifying the functioning of the entire planet, changing the earth's atmosphere through the industrial release of carbon dioxide (which may dramatically change the earth's climate) and diminishing the ozone layer through the production of chlorofluorocarbons.

Only by understanding the principal threats to biodiversity can we hope to meet the challenge of conserving biodiversity. Direct threats to biodiversity are relatively straightforward. They include habitat fragmentation, invasive species, pollution, overexploitation, and global climate change. The underlying causes of biodiversity loss, on the other hand, are often more complex and stem from many interrelated factors. The most important of these are overpopulation and overconsumption, which are compounded by social, economic, and political forces. Existing socioeconomic structures and policies contribute to biodiversity loss or hinder conservation efforts by reducing incentives to conserve. Furthermore, weak governance structures, policies, and legislation, coupled with corruption and a lack of enforcement, often exacerbate the threats to biodiversity.

Underlying Causes of Biodiversity Loss

Overpopulation and Overconsumption

As of 2001 there were nearly 6.1 billion people on the planet. Although there are signs that the rate of world population growth is slowing in many parts of the world, even with lower growth rates the earth's population is expected to reach 10 billion by the year 2050—nearly doubling what it is today. This growth will be concentrated in less developed countries. Expansion of agricultural lands, sprawling urban areas, and increased demand on water, forests, and other resources are tied to growing human populations. As our population grows, human influence increasingly encroaches on the last remaining remnants of biodiversity.

The impact of human population on the environment is complex, depending not just on the total number of people on the planet but also their distribution and consumption rates. Developed countries consume 10 to 100 times more resources than developing countries. As individuals we require a certain amount of land and resources to support our consumption and waste production; this impact on the earth is called our ecological footprint. The world's average ecological footprint is 1.8 hectares per person. Children born in India will each need on average 0.4 hectare to support their consumption and waste, compared with 5.4 hectares in the United States. Thus a child born in a developed country will have a much greater impact on the environment. This unequal distribution of the world's resources has many consequences.

Socioeconomic Structure and Policy Failures

Poverty and inequality strain resources and minimize the incentive to conserve. The poorest people in many countries are often forced onto marginal lands with infertile soil or at higher altitudes that are difficult to cultivate. Unable to subsist on these lands and lacking other economic alternatives, they turn to the resources around them to survive, often hunting or pushing resources to their limit. A lack of access to land or land tenure rights further strains resources. There is no motivation to conserve land that has no clear owner. In many countries, forested land is public property, while cleared land is considered "improved" and guarantees the right to the land; thus to claim land, settlers are forced to deforest areas.

Although poverty may cause people to misuse resources, wealth also puts strains on resources by leading to increased consumption. Globalization of trade and markets has expanded production in some developing countries to meet international demand, often at the expense of biodiversity. Conversion of wetlands for shrimp aquaculture, deforestation for cattle, coffee, or soybean production are just a few examples of how globalization has contributed to biodiversity loss. Global markets also mean that consumers are often unaware of where the items they buy are from, or how they were harvested, though specialized labeling of food, paper, and wood products, sometimes called "green-labeling" or "eco-labeling," can allow consumers to choose products that are managed sustainably. Markets do not necessarily reflect the full value of something or its full cost to the environment. Existing policies and government incentives often encourage overuse of resources. The phrase "perverse subsidies" was coined to describe these incentives. Governments heavily subsidize four main areas: energy, road transport, water, and agriculture. Farmers usually pay a discounted price for water, and as prices do not reflect its true value, farmers have little incentive to conserve. Industries rarely have to pay the full cost of polluting the environment. Society usually incurs these costs.

Weak Government Structure, Policy, and Legislation

Lack of coordination between government agencies and conflicting policies, either within countries or regionally, hinders biodiversity conservation. Responsibility for biodiversity conservation often overlaps within government agencies. For example, one government department may be delineating a protected area, while another is building a road or dam through that same area. The central government may control mining and logging concessions, often to the detriment of protected areas and biodiversity, and without providing any benefit to local people. Furthermore, wildlife does not recognize political boundaries, so ecosystems and species that cross provincial or country borders are especially at risk when policies and laws are inconsistent.

Even when the appropriate laws exist to protect biodiversity, these are often not enforced, or the penalties are too low to deter people from breaking them. Illegal extraction of wildlife and timber is common in many protected areas. International laws that limit hunting of certain species are rarely enforced. Markets around the world openly display illegally harvested wildlife. For example, swordfish cannot be harvested until they reach a certain size, according to international law, but few countries enforce that law, and by the time the fish is sold consumers have no way of knowing if it was caught legally.

Human migration and civil unrest are often linked to a combination of government policies and socioeconomic factors; both also threaten biodiversity in many parts of the world. People migrate for many reasons: lack of economic opportunities, resource scarcity, civil unrest, or government policies. They may also be attracted to other areas because of better economic opportunities, free land, or similar incentives. Migration often brings social and cultural change. New colonists tend to manage resources with a short-term outlook, and traditional resource management may disappear. For example, migrants may use more destructive fishing methods, such as dynamite, that are not accepted by existing fishing communities. Migrants may settle in or near protected areas or increase population pressure on an area, leading to resource overuse.

Civil unrest is often a threat to biodiversity because it is typically associated with limited economic opportunities or political power, poverty, and migration. Civil unrest may also arise because of competition over scarce biological resources. Conflicts over fishing rights have occurred in many parts of the world, such as between England and Iceland in the 1970s and off the eastern coast of Canada in the 1980s and 1990s. The introduction of the Nile perch to Lake Victoria caused the extinction of many native fish important as local food sources, resulting in ongoing political, social, and economic unrest in the region. Several Central American countries have been decimated economically by mismanagement of the environment, leading to deforestation and intense soil erosion. Such dire economic conditions foster social unrest and political repression.

Direct Causes of Biodiversity Loss

The principal direct threats to biodiversity are habitat loss and fragmentation, invasive species, overexploitation, pollution, and global climate change.

Habitat Loss and Fragmentation

Habitat loss and fragmentation have been termed the greatest worldwide threats to wildlife and the primary causes of species extinction (Simberloff, 1986). Although habitats can be fragmented or lost because of natural disturbances, such as earthquakes or geological forces, humans are the principal threat. People have modified landscapes for thousands of years for agricultural production. Today, agricultural activities are the major cause of habitat loss and fragmentation

The charred remains of logging slash in a Brazilian rain forest. Tropical forests worldwide were severely reduced in area and fragmented during the latter half of the twentieth century. (Stephanie Maze/Corbis)

throughout the world. Human settlement, resource extraction, and industrial development generally result in small, isolated areas or patches of natural habitat surrounded by developed land (Gascon et al., 1999). Humans also alter landscapes through the construction of fences, parking lots, roads, buildings, and hydroelectric dams.

Tropical forests worldwide have been severely reduced in area and fragmented during the latter half of the twentieth century. Much of the world's natural prairie grasslands and steppes have been replaced by wheat, corn, and other crops. Wetlands have been drastically reduced in area and number in many regions of the world as they are drained or filled. Although we often think of fragmentation only in a terrestrial context, fragmentation also occurs in the marine environment. Mangroves, seagrasses, salt marshes, coral reefs, kelp forests, and rocky shorelines are fragmented by natural forces such as wave action, currents, tides, and storm surge, as well as human activities such as dredging, boating, and nutrient enrichment.

Many of the world's major riverine systems are highly fragmented, or their flow has been modified by human intervention. According to the World Register of Dams, between 1950 and 1986 the number of large dams in the world increased sevenfold. Dams fragment habitat and change natural water-flow patterns. In the Pacific Northwest, dams have seriously affected salmon populations by preventing salmon from returning to their native streams to reproduce. Humans also affect riverine systems by diverting their flow for reservoirs or irrigation.

Natural versus Human Fragmentation

Several differences exist between human-caused and naturally fragmented landscapes. In human-modified landscapes, most patches are usually unsuitable for wildlife. A naturally patchy landscape has a complex structure with many different types of patches, all suitable for wildlife. A human-fragmented landscape tends to have a simplified patch structure with distinct edges and a few small patches of natural habitats in a large area of developed land. In natural landscapes there is less contrast between adjacent patches, and therefore there are potentially fewer "edge effects" (see below). Certain features of human-fragmented landscapes, such as roads, are novel in the evolutionary history of most wild species and pose unusual threats. Besides fragmenting the environment, roads, especially those that are heavily traveled, are a direct threat to wildlife. Roads also make remote areas more accessible to hunters and aid invasion by exotic species.

Effects of Habitat Fragmentation

There are four major consequences of habitat fragmentation: increased habitat loss; decreased patch size; increased number of edge effects; and increased patch isolation.

Habitat loss. Habitat loss is the (permanent) conversion of land to other uses. Habitat loss drives habitat fragmentation, and the two are tightly linked. Fragmentation of habitats is typically a consequence of habitat loss. However, the level of fragmentation may vary even if the same amount of habitat is lost. For example, assume that 100 hectares of trees will be removed from a 200-hectare forest reserve. This habitat loss could occur in one location, leaving one large fragment of 100 hectares. Alternatively, the trees could be removed from several locations across the reserve leaving 100 forest fragments of one hectare each. In both cases the reserve has lost 100 hectares of forest, but in the second scenario there is a much higher level of fragmentation. The total area of remnant forest in the landscape is the same, but the degree of fragmentation and thus the consequences for plants and animals are quite different.

Decreased patch size. The size of the fragments that remain in a landscape is a critical factor in determining the number and type of species that can survive there. Some species (such as bears, tigers, elephants, and migratory birds) require large areas of continuous habitat and simply cannot survive in small patches. They are referred to as area-sensitive species. Larger patches can support larger populations of a given species and thereby buffer them against extinction, inbreeding depression, and genetic drift. For all species—large or small—that cannot cross a forest edge or leave a patch, all requirements to complete their life cycles must be met within the patch. This is especially important for species with complex life cycles. Amphibians, for example, have an aquatic larval stage and an upland adult phase, and require distinct habitats to meet those needs.

Increased edge effects. Many studies have examined the effects of edges on the physical environment and on biological communities that remain after fragmentation (Laurance and Bierregaard, 1997).

Some of the most significant edge effects are the microclimatic changes that take place along a fragment's edge. Edge areas are warmer, more exposed to light and wind, and drier than interior forest. These microclimatic gradients extend from the edge of the fragment into the interior, approximately 15 to 75 m. Changes to the microclimate along the edge can have secondary effects, such as altering vegetation structure and eventually plant and animal communities.

Increased wind along the edge of the fragments can physically damage trees, causing stunted growth or tree falls. This is especially obvious when a fragment first forms, since interior plant species are often not adapted to handle high wind stress. Furthermore, wind tends to dry out the soil, decrease air humidity, and increase water loss (evapotranspiration rates) from leaf surfaces, creating a drier microclimate. This drier environment may increase the risk and frequency of fires.

Along the edge of a fragment, biotic changes, such as changes in plant communities and nutrient cycling, invasions by generalist animal species, and transmission of disease from domesticated animals to wildlife, often extend much farther than the physical changes. In one study, invasion by a disturbance-adapted butterfly species extended nearly 250 m into the forest (Laurance et al., 2000).

Edges are more susceptible to invasion by generalist or "weedy" plant species (such as lianas, vines, creepers, and exotic weeds) that are better adapted to handle disturbance and the new microclimate. Simultaneously, long-lived interior canopy species, epiphytes, and other mature forest taxa decline in abundance. Wind can also increase the transfer of seeds from outlying areas, thereby aiding invasion of foreign, generalist, or weedy species. The increased light along the edges affects both the rate and type of plant growth, favoring light-loving species at the expense of shade-loving ones.

Since many tree species have long life spans, it may take hundreds of years to truly understand the dynamics and effects of fragmentation. The longest running and perhaps the most detailed study of fragmentation effects ever conducted is the Biological Dynamics of Forest Fragments project, which began in 1979. This pioneering project, located in the Amazon region north of Manaus, Brazil, has generated many of the findings described here and has informed much of our understanding in general of the effects of forest fragmentation. Forest fragments from this area experienced a dramatic loss of plant biomass. Although secondary vegetation (especially vines and lianas) proliferated, the new biomass did not compensate for the loss of "interior" tree species. Loss of biomass in the tropics could also be a source of increased greenhouse emissions from decomposition.

Edge effects alter insect communities and as a result have a profound effect on leaf litter decomposition and hence nutrient cycling (Didham, 1998). Beetles (Carabidae, Staphylinidae, Scarabaeidae) common to continuous interior forest disappear from forest fragments, which is surprising, given their small size and generalist habitat requirements. Possibly this is a result of the drier microclimate or loss of species they depend on (that is, less mammal dung and fallen fruit on which to reproduce). Another reason for the change is that these insects actually travel tremendous distances in search of decaying material for their reproduction, and they may not be able to cross the area between patches. Whatever the cause, the implications for ecosystem function are significant. Unless there is another organism to fill their role as decomposers, more decaying matter is left on the ground for a longer time, and nutrient cycling may be slowed. Also, the incidence of disease may be elevated as dung is left on the ground longer, allowing flies to breed there.

Increased patch isolation. The degree of isolation of a patch helps determine what biological communities can be sustained in it. In a very isolated patch, species that cannot disperse may become separated from other populations and thus prone to genetic inbreeding and possibly local extinction. The degree of connectivity between patches is similarly important in maintaining sustainable populations of some species. Although patches may appear isolated, their actual biological connectivity depends on whether the habitat that separates them (called the matrix) is hostile to plant and animal dispersal. Note, however, that if the matrix contains similar elements of the patches (for example, forest patches surrounded by grassland or savanna), many species will travel out of the patches for extended periods, thereby greatly expanding the effective area of patches. This movement will generally not occur where dissimilar habitats meet (for example, forest and crop land).

In a given landscape, the effects of connectivity and isolation vary greatly from species to species. For example, species that fly (birds, bats, flying insects) are less affected by patch isolation than less mobile species (such as frogs and beetles).

Fragmentation and Species Diversity

Fragmentation causes the loss of animal and plant populations by a process termed *faunal relaxation*. During relaxation, species loss is nonrandom with respect to their place on the food chain or trophic role, with species at higher trophic levels, such as large-bodied vertebrates, being most vulnerable and typically among the first species to disappear. Thus predators are often lost before their prey, and those species that do manage to persist in small fragments (often herbivores) tend to become far more abundant than populations of the same species in larger, species-rich fragments. Increased abundance is partly a result of decreased competition: when competing species are removed, the resources they utilized become available to the remaining species. Another reason for increased abundance is that prey populations are no longer limited by predators. The overabundance of herbivores on small fragments weeds out palatable plant species and converts the landscape into a forest of "herbivore-proof" plants. Fragmentation thus triggers distortions in ecological interactions that result in changes in community composition and structure. Such distortions drive species loss, ending in a greatly simplified ecological system lacking much of the initial diversity.

Species Vulnerable to Fragmentation

Behavior, resource needs, reproductive biology, and natural history can be used to identify species that are most vulnerable to fragmentation (Laurance and Bierregaard, 1997). Examples of species that are expected to be most affected by fragmentation include rare species with narrow distributions or small populations; species with large home ranges, such as top carnivores or large animals; species that need heterogeneous landscapes; species that avoid matrix habitats or that have very specialized habitat requirements; species with limited dispersal abilities or low fecundity; and coevolved species (that is, plants with specific pollinators).

Invasive Species

Invasive species are the second most important threat to biodiversity conservation globally, threatening individual species and even entire ecosystems. Furthermore, as humans carry species from one part of the world to another, we potentially endanger the fundamental root of the world's biodiversity—the evolution of new species. Spatial barriers that isolate populations from one another create and maintain biodiversity, fostering the evolution of new species. By transferring species to and fro across these barriers, we break down the natural process of evolution. The frequency, geographic scope, and sheer number of species that humans have carried from one area to another have increased tremendously as transportation and commerce have evolved.

Multiple terms are used interchangeably to describe invasive species; some of these terms are synonymous, while others are distinct. One major distinction lies between exotic species and invasive species. An exotic species lives outside its native range (Hunter, 2001). Terms such as *nonindigenous*, *nonnative*, *alien*, *adventive*, *neophyte* (for plants), and *introduced* are synonyms for *exotic*. Invasive species, on the other hand, can be exotic or native species whose populations have expanded dramatically and out-compete, displace, or extirpate native species, potentially threatening the structure and function of intact ecosystems. Not all exotic species are invasive. Many populations of exotic species do not survive for long in their new environment. Others become established but do not substantially disrupt their new host environment. Similarly, not all invasive species are exotic. Scientists are increasingly documenting native species whose populations grow out of control or substantially increase their range because of human-induced change in their environment. These range shifts may also be the result of natural changes, since it is difficult to distinguish between human-driven and natural changes. These species often prey on or parasitize species at a higher rate than previously, or they hybridize with or outcompete close relatives. Some examples from North America include the coyote in the eastern United States and the brown-headed cowbird throughout the United States, subarctic Canada, and northern Mexico. Cowbirds are a native species that were once restricted in their range to the Great Plains, where they followed bison herds. Human alteration of landscape has allowed their range to expand and thus impact other native bird species. Cowbirds are brood parasites that don't build their own nest but lay their eggs in the nests of other bird species. These birds then raise the cowbird young, often to the detriment of their own offspring. So little is known about native invasives that the rest of this section will focus mainly on exotic invasives.

Research into why and how some species become invasive is still preliminary, in part because of the complex process of invasion. The most comprehensive works on exotic invasive species (for example, Elton, 1958; Cox, 1999; Mooney and Hobbs, 2000) are compendia of case studies—predictive models still in development that detail the species most likely to become invasive and the potential consequences their invasion (Pimm, 1989). There appear to be three major stages in the process of invasion by exotic species: dispersal, establishment, and integration (Cox, 1999).

Dispersal Stage

The first stage—the dispersal stage—comprises how species move from one area to another. Characteristics of the donor region, of the dispersing organism, of the natural and human agents that affect dispersal, and of the colonized region all influence the success of exotic species at this stage. The inexorable globalization of human societies has afforded exotic species myriad avenues for dispersal into new environments. Humans have unwittingly brought "stowaways" along in containers such as ships' hulls and ballast water, on muddy shoes, or in our digestive tracts that have profoundly changed the face of their new environment. Classic examples of these stowaways include rodents, such as the Norway and black rats, and the house mouse, which have contributed to the demise of innumerable native species around the world, most notably island species; diseases such as smallpox and measles that decimated indigenous human populations when carried to the New

World and Australia by European explorers and colonists; marine invaders such as European green crabs that may have arrived in the United States in bilge water and are changing the structure of intertidal communities along the West Coast; and plant invaders such as the southern Russian or Ukrainian leafy spurge, which arrived in the United States as a contaminant of grain and is now crowding out the remaining native plant species in prairies.

Humans also deliberately brought exotic species with them when they settled new lands. These species served for food and commerce, fiber and fuel, medicine, sport, scientific interest, wind breaks or erosion control, and simple enjoyment. Sometimes species have been introduced to help contain outbreaks of other invasive species—unfortunately often with unanticipated consequences. On occasion, single individuals have caused the extinction of a whole species. A particularly predatory cat belonging to the lighthouse keeper on Stephen's Island, between the North and South Islands of New Zealand, evidently hunted and killed every last individual of the Stephen's Island wren, ironically just as it was identified as a species new to science (Hunter, 2001). Domestic cats in the United States (more than 60 million of which are pets and perhaps 30 to 40 million more that are feral) are estimated to kill more than a billion small mammals and at least 200 million birds annually. They are partly responsible the endangerment of at least six species of North American birds and small mammals, and for the extinction of more than twenty animal species in Australia.

Establishment

The second stage in the process of invasion—establishment—encompasses how biotic and abiotic factors in the colonized region affect the initial survival, reproduction, and expansion of invasive species in a new area. An overwhelming majority of exotic species are unsuccessful in establishing populations when introduced to mainland settings. Some scientists have argued that tropical oceanic islands are more susceptible to invasions, but the evidence for that seems equivocal. Many organisms arrive in a new region and are swiftly eliminated by any number of physical or biotic agents. Others survive but do not expand their populations or become harmful to the environment.

Integration

The final stage in the invasion process—integration—embraces how exotic species interact with the communities and ecosystems they invade, and the factors that affect their rates of expansion both in population size and over space. As noted above, some exotic species settle into their new environment and become naturalized. They do not depend upon reimmigration from their natural range to persist. A few of these species then become invaders. Scientists estimate that, of every 1,000 species that reach a new region, some 100 will settle temporarily, 10 will establish long-term populations, and 1 will become a problematic invasive species (Cox, 1999). The transition from naturalized immigrant to invader often encompasses a long delay, or lag phase, followed by a phase of exponential increase that diminishes only when a species reaches the boundaries of its new range. Many extinctions of immigrant populations take place during this time. It is often difficult to predict which species will remain as naturalized immigrants and which will become invasive.

What Makes an Invasive Species Successful?

Unfortunately, it is currently next to impossible to predict the success of invasives, nor can we even come up with a comprehensive list of attributes of common invaders. Some evidence points to greater success for species with higher numbers of invaders, for those that are widespread in their native habitat, as well as for those that settle in already heavily disturbed areas. The European starling was released in New York City around 1890 by someone who wanted to bring all the birds mentioned in the writings of Shakespeare to North America. The initial release of starlings was unsuccessful, and several more individuals were brought over. From these relatively modest beginnings, the European starling has become arguably the worst invasive bird in the United States. Fifty years after its release, its population size was estimated at 120 million birds. Starlings are displacing native birds, particularly cavity nesters, throughout the eastern United States.

In terrestrial ecosystems, the most successful intruders seem to be those that are significantly different from native species. For example, *Myrica faga,* an exotic tree, has successfully settled in Hawaii and is affecting the entire ecosystem that it invaded. This tree is a member of the legume family and harbors symbiotic bacteria that convert atmospheric nitrogen to ammonia, a trait not present in native plants in the ecosystem. The introduced tree forms dense canopy stands beneath which other plants don't grow. Because of its nitrogen-fixing capabilities, it can colonize nutrient-poor volcanic sites faster than native plants and prevent native communities from establishing.

Ecological Consequences of Invasive Species

The list of consequences of invasive species on their host environment is as lengthy as it is depressing. Invasive species can cause local or global extinction of species as well as complete disruption of an ecosystem's structure and function. As predators (including herbivores such as cows, goats, pigs, and rabbits), invasive species often benefit from encountering "naive" prey that have not yet developed appropriate defenses. A well-known example is the brown tree snake, which was introduced inadvertently on many Pacific islands and subsequently caused the extinction of a number of native birds, bats, and lizards. Similarly, the newness of exotic species to a region may also mean that they themselves escape predation, as potential predators do not yet look upon them as prey. Freed from their natural predators, competitors, and diseases, populations of exotic species flourish in their new environment.

Exotic invasive species often outcompete native species for food, water, shelter, nutrients, light, and space. The North American gray squirrel is outcompeting and replacing the native red squirrel in Britain and mainland Europe. Particularly successful invaders include zebra and quagga mussels, which were introduced into the Great Lakes region of North America sometime in the 1980s. These mussels can achieve densities of 524,000 per square meter or greater, blanketing whole lake bottoms and other surfaces. In Lake Erie, where zebra mussels extirpated a healthy population of native, freshwater bivalves (Unionoidea), some shells were covered by 15,000 zebra mussels—the equivalent of five times the weight of the living bivalve (ibid.). Zebra mussels are extremely efficient filter feeders, and as a result they substantially modify the aquatic systems they invade.

Invasive species may impact native species abundance through hybridization. Mallard ducks in North America have spread through introduction by sport hunters into new areas and by expansion of their range as natural areas are converted to agricultural lands. As mallards encounter closely related ducks in these new areas, they interbreed with them, often coming to dominate the gene pool of smaller populations, as is the case with the Mexican duck and the mottled duck. North American mallards are also hybridizing with the New Zealand gray duck and the Hawaiian duck. Similarly, "new" species generated through genetic engineering may pose a threat via hybridization after their release into the wild, as is suggested for escaped fish from aquaculture operations.

Although not often considered in discussions of invasives, diseases are a special class of invasive species that affect wildlife and human populations the world over. In the Hawaiian Islands, avian pox and malaria have led to an almost complete extermination of endemic birds in lowland forests. Similarly, emerging infectious diseases may play a role in the recently noted global amphibian decline.

Invasive species have transformed whole ecosystems, affecting fertility, productivity, and stability. For instance, plant invaders can alter ecological processes such as fire regimes, nutrient cycling, and hydrological cycles, or replace the dominant species in a community. In the fynbos ecosystem of South Africa's Cape Province, native plant species have evolved to withstand the difficult environment. These plants efficiently process water—particularly during dry summer months. They can live in nutrient-poor soils, and their roots bind the soil and minimize erosion. Much of the vegetation has fire-resistant leaves or bark, and their overall low biomass minimizes the impact of the fires that occasionally move through the area. Eucalyptus, pine, acacia, and other invasive species in the fynbos scrubland are heavy water users. They have threatened the extinction of many endemic plants, increased the overall biomass and water demands in the ecosystem, raised fire intensity, and reduced the amount of water for agricultural production and the limited water available to Cape Town and Port Elizabeth.

Invasive species seem to be particularly successful in establishing in and significantly changing the structure and function of freshwater lakes and stream ecosystems. Introduction of game or commercial fish in lakes and streams around the world has wreaked havoc on local fish species. The San Francisco Bay and Delta was rated the most invaded aquatic system in North America by the U.S. Fish and Wildlife Service. In many bay and coastal communities from Canada to Mexico, exotic species outnumber native species.

Biotic invasions affect economic systems in two major ways. First, they influence potential economic output—that is, causing loss in crop and livestock production and fisheries profits. Second, the cost of battling invasions (including invasives that are threats to human health), from quarantine to control to eradication efforts, is enormous. Accurate assessments of these costs are difficult to calculate, but estimates exceed $138 billion per year (Pimentel et al., 2000).

Controlling Invasive Species

There are two major ways to limit the effects of invasive species. The first is to prevent new invasions, and the second is to minimize their impact once they have colonized a region. Initial invasions can be held in check by using quarantine techniques, but these techniques are hampered by our inability to predict which species might become invasive. In addition, countries such as the United States and Australia apply an "innocent until proven guilty" approach to incoming species, mostly to avoid limits on trade (Mack et al., 2000). In other words, all species are let in until we know they are harmful. A major problem with this approach is that once we know a species is harmful, it is often too late to control its spread.

Attempts to control invasive species have focused on chemical methods (for example, herbicides), mechanical methods (for example, hand removal of giant land snails), and biological methods (such as introduction of native parasites). Each of these has a suite of problems associated with it, ranging from cost (mechanical) to limiting the side effects of applications (chemical and biological). Control efforts have been most successful at the beginning of an invasion, when populations are smaller and localized. Once populations take hold and produce huge numbers of individuals, any attempt at control is usually unrealistic financially and logistically. Efforts to control invasive species are frequently stymied by public concern, either for the species being eradicated (as in the case of mute swans or feral cats) or the proposed method. Considerable effort should be directed at educating the public about invasive species and their effects on biodiversity.

Overexploitation

Natural resource consumption rates and human population size exert tremendous pressure on the world's plants and animals. Although direct use of wildlife is essential for human survival, overexploitation of resources (or using resources at an unsustainable rate) is a critical problem in conservation. Although habitat loss may be the greatest threat to most species, the overexploitation or nonsustainable use of wildlife is closely linked and plays an increasing role in the loss of biodiversity. Overharvesting, nonsustainable use, and the illegal trade in some species are threatening not only their continued survival but also that of ecosystems and the livelihoods of communities and local economics that depend upon them.

There is no question that overexploitation has led to species extinctions in historic as well as modern times. Unsustainable hunting, fishing, logging, or gathering of wild populations leads to their commercial, ecological, or global extinction. Commercial extinction occurs when populations are too depleted or scattered to be harvested economically; ecological extinction indicates populations that may still be present in low numbers but no longer play important functional roles in the ecosystem. Global extinction signifies that no living individuals of the species remain anywhere in the world.

In theory some level of exploitation should be manageable. The difficulty is in determining what level is sustainable (in part because sustainability is an ambiguous term) and in keeping exploitation to that level or below. As with other aspects of conservation, short-term perspectives often call for higher rates of use than long-term perspectives.

Overexploitation can be divided into two major categories: direct and indirect exploitation. Direct exploitation ranges from commercial activities such as logging operations or trade in endangered species to subsistence hunting. Indirect exploitation encompasses the unintentional mortality of nontarget species such as fish or turtles killed as by-catch in fishery operations. Both endanger species around the world.

Direct Commercial Overexploitation

Although not all commercial ventures lead to overuse of resources, commercial exploitation is a major cause of overexploited resources. Natural resources are generally communal and therefore vulnerable. With communal resources, the cost of overexploitation is borne by the whole community, not just the person using the resource, whereas the benefits go to the exploiter alone. It is in the best interest of individuals—in this case commercial venturers—to overexploit communal resources until there is nothing left; Hardin (1968) dubs this phenomenon the "Tragedy of the Commons." There are numerous examples of commercial overexploitation, and we will limit discussion to two very important ones: overexploitation of marine fisheries and wildlife trade.

Marine fisheries. The oceans were once considered a limitless resource. This philosophy, coupled with a policy of open access to the oceans, set the stage for overexploitation, as predicted by Hardin (ibid.). According to the Food and Agriculture Organization, the world's total capture fishery harvest reached 86 million tons in 1998, with marine catch accounting for 90.1 percent of the harvest. Among the major marine stocks exploited, 47 to 50 percent of species are considered fully exploited and are close to their maximum harvest; another 15 to 18 percent are overexploited; and 9 to 10 percent are depleted. Major fisheries have collapsed around the world, from the Peruvian anchovy fishery in the 1970s to the cod fishery in eastern North America in the 1990s. These collapses followed similar patterns. Initially these fisheries were so plentiful that they were judged impossible to overharvest. We systematically removed the largest, oldest fish from the populations. The largest fish are often the top predators, and removing them affects the prey species and other predators. The oldest fish generally have the highest reproductive capacity, and their loss led to declining populations. Over time, boats had to travel farther and fish longer to harvest the same catch. At the same time, the average size of the fish caught began to decline substantially. In 1963 the average swordfish caught off the East Coast of North America weighed 250 pounds (113.6 kg); by 1996 that had dropped to 90 pounds (40.9 kg).

As one species becomes overexploited, fishing pressure has simply shifted to other species—overharvested top predators are replaced with target species farther down the food web. Between 1950 and 1994, there has been a gradual shift in mean trophic level fished—from long-lived bottom fish that eat other fish, to lower trophic level invertebrates and open-water species that eat plankton. This shift—termed "fishing down marine food webs"—has been most noticeable in the Northern Hemisphere; while it initially leads to an increase in catch, it is followed by declines (Pauly et al., 1998). As we systematically remove the top predators and their prey from marine systems, we have put the oceans in a perilous state for recovery.

Recent research into historical and archaeological evidence has highlighted the toll of overexploitation on many marine systems. The resulting impoverished state of these marine systems leaves them more susceptible to major disturbances (for example, epidemic diseases, hurricanes, and climate change) and less productive for current and future human needs (Jackson et al., 2001). For instance, in Caribbean coral reefs, populations of predatory and large herbivorous fish were overfished during the seventeenth to twentieth centuries. The loss of these fish made those reefs more susceptible to other threats. An introduced disease killed off most of the sea urchins (*Diadema antillarum*) in 1983 and 1984, removing the other major herbivore in the reef system. With the loss of these herbivores, Caribbean corals perished under the overgrowth of macroalgae.

As in other cases of commercial overexploitation, technological advances have significantly contributed to overharvesting of marine fish. Engines, refrigeration, sonar, geopositional systems (GPS), and acoustic Doppler profilers have made it easier to locate, catch, and store fish, and to fish farther from shore and for longer periods of time. New fishing gear has allowed us to harvest faster and in areas that were once inaccessible. Longlining has enabled fishermen to catch in three days the same amount of swordfish previously harvested in two weeks by harpooning. New trawling techniques—such as “rockhoppers” with wheels on the net that enable it to effectively trawl the ocean floor despite rocky terrain—afford access to areas previously out of reach.

Several regulations have been imposed to try to control the exploitation of fish, although with mixed success. In the 1970s, a 200-mile limit was imposed around the world’s coastline to enable countries to regulate fishery harvest in their waters. Quotas on the number and size of fish caught, restrictions on fishing gear, and limitations on the number of boats allowed into a fishery have been used to help control harvest rates.

Aquaculture was considered a solution to already overfished oceans. Unfortunately, the species farmed are often carnivores and require wild-caught fish as food. It takes five pounds of wild fish to raise one pound of farmed salmon. So rather than reducing the harvest, aquaculture has placed a new burden on fisheries to supply fishmeal. Aquaculture can also pollute the environment with excess nutrients or antibiotics, or by introducing disease into wild populations, though new methods of raising fish to minimize some of these problems are being tested.

Wildlife trade. Trade in wildlife is pandemic, occurring in local, regional, and international settings. TRAFFIC, an international organization established by the World Wildlife Fund and the World Conservation Union, monitors the trade in wildlife and wildlife products. Based on declared import values, they estimate that the global wildlife trade is huge, with an annual turnover of billions of dollars and involving hundreds of millions of individual plants and animals. The Convention on the International Trade in Endangered Species of Wild Fauna and Flora (CITES) regulates international trade in some 30,000 species of plants and animals through a system of certificates and permits. Interpol estimates the illegal trade at $12 billion a year, second only to drugs. A large proportion of the world’s wildlife trade is domestic and does not cross international borders, especially for products such as medicinal plants, timber, wild meat, and fisheries. The magnitude of the domestic trade for most wildlife species remains unknown.

Hunting for commercial bushmeat, prevalent across tropical Asia, Africa, and the neotropics, is a specific element of wildlife trade that has received increased attention of late (Robinson and Bennett, 2000). As humans colonize formerly remote regions, few places are immune to the effects of the bushmeat trade. In some communities harvesting of wild plants and animals fulfills a secondary role in the household economy, whereas in others these resources are irreplaceable. It is increasingly difficult to distinguish subsistence hunting from commercial hunting, traditional from modern, and sport from necessity. Each situation embraces its own nuances, making the search for sustainability—and particularly a formula for sustainability—complicated. The bushmeat trade has increased because of the replacement of traditional weapons with modern ones, new logging roads and other activities that increase access into formerly remote areas, and more permanent settlements along roadsides. Fundamentally, however, rising human populations and consumption rates drive this transition from subsistence to commercial hunting.

Hunting has a significant effect on wild populations and communities, lowering population densities and the average body size of individuals as well as decreasing the representation of large-bodied species in a community. Overhunting has led to the extinction of the passenger pigeon, flightless birds, tortoises and other island species, and the near extinction of the bison.

Indirect Overexploitation

Nontarget species may inadvertently be exploited as commercial species are harvested. For instance, many fishing methods are not selective, catching other species besides the intended one. This indirect harvest—or "by-catch"—can be substantial. Total global by-catch is estimated at 16 to 40 million tons per year. Shrimp harvest has one of the highest by-catches of any fishery; for every pound of shrimp harvested, five pounds of by-catch is caught and wasted. Longlining for tuna and swordfish produces significant by-catch of sharks, sea turtles, and marlin. Nets positioned to catch schools of tuna have caught and drowned dolphins, prompting public outcry and consequent modifications of tuna fishing practices.

Fishing techniques that use cyanide or dynamite are nonselective and also result in substantial by-catch. Dynamiting on coral reefs not only kills the fish and invertebrates nearby but also destroys the physical structure where these species live and breed, causing long-term damage to the entire community.

Wildlife trade offers another example of indirect overexploitation, though in this instance individuals of the same species are in a sense indirectly exploited. Many animals die during capture and shipment, so traders must bolster the number they capture to ensure that an adequate supply reaches the market destination. Sadly, experts calculate that the mortality rate can reach up to 60 to 70 percent for some birds and reptiles and 80 to 90 percent for reef fish.

Pollution

Everyday, thousands of pollutants are discharged into our environment. Many pollutants lack regulation, and their lingering presence threatens biodiversity, affecting individual species or degrading entire ecosystems. Pollutants resist categorization because of their varied forms and effects. Some, such as lead or PCBs, directly toxify the environment, while others, such as fertilizer runoff, are nontoxic but harm aquatic systems by causing excessive plant growth. Noise and light pollution threaten species by disrupting their behavior. Pollutants are also classified by the environment they affect, regardless of their form, such as air, water, and soil pollution. Many pollutants cycle through all of these environments at some stage, entering the air and ending up in water or soil. Classification of pollutants may also derive from where they enter the environment: a so-called point source pollutant enters at a discrete location and is nonmobile, such as effluent from a sewage treatment plant, whereas a nonpoint source pollutant enters from many locations or is mobile, such as surface runoff into the coastal zone from cars (motor oil) or lawns (fertilizers and pesticides). Typically, it has been easier to regulate "point source" pollutants.

What makes something a pollutant? Pollutants tend to persist in the environment. Because of this, even after a pollutant has been banned, its legacy is felt by the environment. Pollutants are often widespread and can be transported over large distances. Pollutants accumulate in an animal's tissues or interfere with vital processes such as the reproductive or immune systems. Some pollutants are toxic in low concentrations and at the extreme will kill an animal. Pollutants can also substantially alter entire ecosystems. Here, we will examine some of the leading pollutants of our environment, including toxic contaminants, organic biostimulants, solid wastes, noise, and light pollution. Because so many pollutants infiltrate our air, water, and soil, it would be difficult to cover them all.

Aerial view of an oil slick spilling into the ocean from the Liberian tanker* Ocean Eagle*, which split in two at the entrance to San Juan Harbor, Puerto Rico, in 1968 (Bettmann/Corbis)

Toxic Contaminants

Toxic contaminants include trace metals (for example, cadmium, copper, lead, and mercury); biocides/pesticides (for example, DDT, TBT [tributyl tin]); industrial organic chemicals (for example, PCBs, tetrachlorobenzene); and by-products of industrial processes and combustion (for example, polycyclic aromatic hydrocarbons [PAHs] and dioxins). Toxics can be lethal or can interfere with an organism's immune, endocrine, and reproductive systems. Existing toxicity tests for new chemicals rarely reveal the consequences of toxic contaminants on the environment.

Chlorinated hydrocarbons, such as the insecticide DDT (dichloro-diphenyl-trichloro ethane) and PCB (polychlorobenzene), are renowned for their toxic effects on the environment. A particularly troubling characteristic of these pollutants is their ability to persist over long time frames and spread over large areas. When DDT was introduced in the 1940s, it was a marvel; it was cheaper and more effective than any other insecticide. However, its effectiveness came at a price. During the 1950s and 1960s, populations of predatory birds in North America, in particular those that ate fish, including eagles, pelicans, and ospreys, declined rapidly. Analysis of the birds revealed that DDT in their bodies was a million times more concentrated than that in the water where they lived. This discovery led to the concept of bioaccumulation—that is, animals higher up the food chain concentrate contaminants in their bodies. Why is DDT such a powerful toxin? First, it cannot be broken down by the body and is fat soluble, allowing it to accumulate in animal tissue. Second, DDT interferes with calcium deposition in eggs; thus birds were laying thin, fragile eggs that often broke during incubation. Because DDT affected the birds' reproduction, it had an immediate and powerful effect on populations. DDT also disperses readily in the atmosphere and has even been found in organisms of the Arctic and Antarctic (Wania and Mackay, 1996). Even though DDT was banned in 1972 in the United States, it continues to persist in the environment. One notable place is in Palos Verdes, off the coast of California, where DDT manufacturers were allowed to dump their supply of DDT into the ocean—more than 200 tons covering a 20-square-mile area. Manufacturers export DDT and other pesticides that are banned in the United States to developing countries.

Many pesticides, including DDT and PCB, as well as DBCP (dibromochloropropane), DDE (dichloro-diphenyl-dichloro ethylene), kepone, heptachlor, chlordane, dieldrin, mirex, lindane, toxaphene, dioxins, Bisphenol-A, and phthalates, are endocrine disrupters—that is, chemicals that mimic or inhibit the effects of hormones. Most of these pesticides are long-lived compounds and bioaccumulate. The toxin tributyltin (TBT) used in antifouling paint on ships interferes with sexual development in some mollusks (for example, females develop male organs), even at concentrations of 10 parts per trillion. Declines in marine snail populations have been found along the coasts of North America and Europe because of heavy contamination with TBT (Nehring, 2000).

Atrazine, a common weed killer used heavily on corn crops in the United States, pervades the environment, contaminating runoff and groundwater. Atrazine, even in low doses, has recently been shown to affect frog development (Hayes et al., 2002). The study found that 20 percent of frogs exposed to doses of just 0.1 part per billion (well below the limit allowed for drinking water) developed abnormal reproductive parts, such as multiple sex organs or both male and female organs. At slightly higher doses of 1 part per billion, 90 percent of males lacked vocal chords, which are essential for attracting mates. Atrazine appears to affect the production of the enzyme aromatase, which converts the male hormone testosterone into the female hormone estrogen.

Sulfur and nitrogen oxides are released into the atmosphere when fossil fuels, such as coal in power plants, or oil in vehicles, or wood, are burned. These combine with water in the atmosphere to create sulfuric and nitric acid, which fall to earth as "acid rain" (these pollutants also create smog in urban areas). Because of prevailing wind patterns and geological characteristics, certain regions (including the northeastern United States, Canada, and northern and central Europe) have been especially affected by these pollutants. Some soils and rock types, however, neutralize or buffer the acid. For example, calcium carbonate in limestone acts as a natural buffer, reducing the damaging effects of acid rain. On the other hand, areas with granite and quartz tend to be very sensitive. Freshwater lakes in those areas are particularly susceptible. Initially the changes affect only some species of invertebrates, but with increasing acidity fewer and fewer species survive, until eventually the lake is dead. That has been widespread in the Adirondacks of New York and lakes of northern Sweden and Canada. Acid rain also dissolves other harmful metals, such as mercury, which plants and animals then absorb. On land, pollution by acid rain and other air pollutants (ozone) tends to affect plants more than animals. Lichens, bryophytes, and fungi suffer the most. Decline of a certain species may be due to acidification of the soil, direct toxicity, or competition from more resistant species. Animals, such as otter and deer, tend to be indirectly affected by acid rain pollution brought about by changes in their prey or the bioaccumulation of mercury in their tissue, which is released at higher acidities.

Organic Pollutants/Biostimulants

Organic pollutants or biostimulants, primarily from agricultural fertilizers and sewage waste, have a major impact on aquatic environments. When these excessive nutrients enter aquatic systems, they stimulate plant growth. Rapid phytoplankton growth or algal blooms create diverse problems. Plant growth is so rapid that animals don't have a chance to eat it. The phytoplankton then falls to the seafloor, where it decomposes. This decomposition depletes oxygen, creating hypoxic (that is, low-oxygen, less than 2 mg/liter) or even anoxic (no oxygen) environments in which few organisms can survive. Large concentrations of algae also reduce water clarity, preventing light from reaching the bottom and reducing the growth of seagrasses. Changing phytoplankton communities also affect shellfish populations. A long-term increase in excess nutrients into an ecosystem is known as eutrophication. More than 50 percent of the estuaries along the U.S. coast are affected by eutrophication, some—such as the Mississippi River delta, Chesapeake Bay, and the Long Island Sound—severely. Eutrophication is a worldwide phenomenon affecting coastal areas from Europe to Asia.

Aquaculture operations also produce organic waste through uneaten food, feces and urine, and dead fish. Although still a minor organic pollutant, it can have a major local impact. Areas with offshore salmon pen farming (such as L'Etang Inlet, New Brunswick, Canada; and Puget Sound in Washington state) have significant nitrogen and phosphorous inputs brought about by aquaculture. Directly beneath the pens, there is often an anoxic area that extends 30 to 150 m from the caged area. Effluent from pond aquaculture (such as that used for shrimp and catfish) also contaminates nearby waterways. Besides releasing organic nutrients, aquaculture is also a source of chemical and biological pollutants. Antibiotics, parasiticides, pesticides, hormones, anesthetics, pigments, minerals, and vitamins are added to the feed for various types of pen and pond aquaculture systems. Especially in pen aquaculture, which is completely open to the surrounding water, uneaten food enters the water, where it can contaminate wild species. Similarly, escaped fish are a form of biological contaminant. Farm-raised fish have been bred with certain traits; when they escape they can reproduce with and alter the wild population.

Our ecosystems have been fundamentally changed by pollution. It was long thought that it is normal for temperate forests to lose nitrogen into soil and stream waters in inorganic forms such as nitrate and ammonium. However, recent studies of ancient and unpolluted temperate forests in Chile and Argentina reveal that it may be an artifact of pollution (Perakis and Hedin, 2002). South American forests are dominated by the release of dissolved organic nitrogen. Their North American counterparts (in this study the Smokey Mountains of Tennessee and Tionesta National Forest in Pennsylvania) release high levels of inorganic nitrogen. The cycling of nitrogen in North American temperate forests appears to be a consequence of excessive fertilizer use and nitrogen deposition from acid rain.

Solid Waste

Solid waste is generated from household and industrial sources, and it includes everything from food to plastics. Solid waste is usually disposed of in landfills. Landfills take up space and, if not properly contained, can leach toxins into the soil and poison groundwater. In countries with limited space, solid waste is burned at high temperatures. But incineration is expensive, creates very hazardous ash, and pollutes the air with toxic chemicals. Solid waste can be minimized through recycling and composting. Certain materials, such as metals, glass, and paper, are, in fact, easier to recycle. The composting of organic materials, such as food and paper, is an effective way to reduce solid waste—and it produces fertilizer.

Mining is a major source of solid waste. In the United States, mining produces more than 1.7 billion tons of waste, compared with the 180 million tons produced by all municipalities combined. Extraction of minerals, coal, and oil destroys and fragments habitat, and it is very polluting; in the worst instances it can lead to catastrophic spills. Open-pit mining is an extremely wasteful process. Metals, such as gold or copper, or mineral substances, such as coal, are extracted from ore found close to the surface. Most ore contains only small amounts of the target metal; the remaining excavated rock is wasted. The amount of waste depends on the metal and the region being mined, but typically it is huge. Some 3 tons of ore are needed to produce enough gold for just one ring. Copper mining is also wasteful; for every ton extracted, 99 tons of waste rock are produced. New technologies to extract and process minerals found at low concentrations in ore are increasing the waste produced by the mining industry and making it possible for new areas to be exploited. Much mining waste is also hazardous, polluting the environment with heavy metals, acid-producing sulphides, and other contaminants. Additional waste, known as tailings, is also produced during processing. Tailings are also highly toxic, being made up of heavy metals and chemicals, such as cyanide and sulfuric acid. Mining waste and tailings are stored in special containment areas or ponds near the mining site. Pollutants often leach from these sites into soils, groundwater, and nearby lakes and streams. If these sites are not well maintained, disasters may occur. For example, in southwestern Spain in 1998, a mining accident released 5 billion liters of toxic sludge into the Guadalquivir River. Contamination spread over a huge area downstream, damaging the wetlands of Coto Doñana and the Doñana National Park.

Solid waste originating on land also pollutes the marine environment (Coe and Rodgers, 1997). Plastics and fishing gear threaten many marine species. Turtles appear to confuse plastic bags with jellyfish, one of their main prey animals. The plastic blocks their digestive track, killing the turtles. Studies of stranded sea turtles off the coast of Brazil found that the most common debris ingested were transparent and white plastic bags; the turtles also showed evidence of damage on their carapaces from fishing activities. Recent studies of thirty remote island sites around the world revealed that floating marine debris is mostly made up of plastics. In addition to harming the marine mammals that swallow them, these plastics act as rafts, spreading invasive species, like barnacles and mollusks, around the globe (Barnes, 2002). Lost or discarded fishing gear, another major source of marine pollution, can remain a danger for many years, entangling turtles, seals, seabirds, and fish. Gear also damages the reef and benthic habitats that support marine life.

Noise Pollution

Transportation (cars, trains, airplanes, shipping) and industry (construction or factory) are the leading sources of noise pollution. Animals rely on hearing to communicate, avoid predators, and obtain food. To avoid noise, wildlife may alter their behavior, possibly leaving critical habitat or forage areas, though responses will vary with the kind of noise and the species. Waterfowl, for example, are particularly disturbed by low-flying aircraft. Noise can cause hearing loss and interfere with communication, and long-term exposure may have physiological effects because of increased heart rate and metabolism.

Many studies have examined the effects of noise on wildlife. Magnificent frigatebirds (*Fregata magnificens*) in the Florida Keys appear to be disturbed by low-altitude aircraft at their nesting sites. Birds flushed from their nests when they hear a noise may even break their eggs or injure the young. Caribou calves exposed to overflights suffer higher mortality rates. Bighorn sheep in the Grand Canyon are particularly sensitive to helicopter passes in summer, apparently because they graze at higher elevations and are closer to the source of the sound. Many desert animals have acute hearing and depend on it for hunting. Desert iguanas and the endangered kangaroo rat experience hearing loss caused by motorcycle noise.

Noise from shipping, fishing, recreation, dredging, military activities, or oil exploration disturbs marine animals. Whales and dolphins, which rely on sound for communication and navigation, appear particularly affected. Whales startled by noise (especially at low frequencies) may dive suddenly, swim faster, or change their vocalizations. At the extreme, noise may even lead to the animals' death. In March 2000, nine Cuvier's beaked whales (*Ziphius cavirostris*), three Blainville's beaked whales (*Mesoplodon densirostris*), two unidentified beaked whales, two Minke whales (*Balaenoptera acutorostrata*), and one spotted dolphin (*Stenella frontalis*) were stranded in the Bahamas, some bleeding from their ears, and at least seven of them died. According to the U.S. Navy and the National Marine Fisheries Service, testing of sonar in the area appears to be linked to the strandings. The marine mammals were confined to a narrow channel during calm conditions, which tend to amplify sound. Recent studies show that whales, like human divers, are susceptible to diving illnesses. Noise from sonar or explosives causes marine mammals to dive deeper. On long, deep dives, more nitrogen enters the blood from the lungs in the form of bubbles; too much nitrogen in the bloodstream can kill an animal. In humans, this illness is known as the bends.

Light Pollution

Satellite images of the planet at night dramatically reveal the extent of light pollution. Urbanization literally lights up the planet every night. The effect of light pollution is well documented in nesting turtles and hatchlings, which normally use the moonlight to guide them back to the ocean, but instead walk toward the brighter artificial lights on land. At night during foggy weather, when visibility is low, migrating birds can become disoriented by radio towers, especially those with heights greater than 200 m. In the United States there are more than 40,000 towers; where bird studies have been conducted, mortality rates have ranged from 375 to 3,285 per tower per year, and sometimes 1,000 birds have been killed on a single night. It is common knowledge that lights attract moths and night-flying insects, but few realize that they may be affecting their populations. The energy that moths spend attracted to artificial lights may prevent them from finding mates or good places to lay their eggs. Declines in moth populations may be linked to the effects of artificial lights on their reproduction. Plants whose reproduction is controlled by the lengths of day and night may not flower as a result of artificial lighting.

Global Climate Change

Global climate change is expected to impact plants and animals worldwide (IPCC, 2001a; Malcolm and Pitelka, 2000). What these changes will be depends largely on the amount and rate at which the world's climate warms. New studies and improved models are increasing our understanding of global climate change. Over the past 140 years, the global average surface temperature has increased 0.6 (+/–0.2) degree centigrade (IPCC, 2001b). Most of the warming has occurred during two periods, from 1910 to 1945 and 1976 to 2000. In the last century, the 1990s were likely the warmest decade on record, and 1998 the warmest year. Although the average global surface temperature has increased by 0.6 (+/–0.2) degree centigrade, there has however been great regional variation, with some regions experiencing much larger increases, and others smaller or no increases in temperature. The average minimum temperature has also increased at a faster rate than the average maximum temperature. Although it is difficult to examine temperature change on longer time scales, recent studies indicate that the temperature increase in the Northern Hemisphere is likely the largest of any century in the past 1,000 years; unfortunately, less data is available for the Southern Hemisphere.

Besides increasing temperatures, there are other indications that the earth's climate is warming. Satellite data reveal that snow cover has declined by 10 percent since the 1960s. During the twentieth century, there has been a continued retreat of the world's mountain glaciers, and at mid and high latitudes in the Northern Hemisphere, the time that lakes and rivers remain frozen has decreased by an average of two weeks. In late summer through early autumn, the thickness of Arctic sea ice appears to have thinned by 40 percent. Sea level rose 0.1 to 0.2 meter during the twentieth century, largely because of thermal expansion (water expands at higher temperatures) and loss of land ice. It is also very likely that continental precipitation has increased by 5 to 10 percent in the Northern Hemisphere over the last century, although it has decreased in other regions, such as North and West Africa and the Mediterranean. Increasing temperatures have been accompanied by shifts in the period of seasons, with earlier springs and longer autumns. As a result, over the last forty years the growing season in the Northern Hemisphere has lengthened from one to four days per decade.

Current global circulation models predict that in the future, the globally averaged surface temperature will have increased by 1.4 to 5.8 degrees centigrade between 1990 and 2100, while sea level will have risen between 0.09 and 0.88 m. These averages are for the entire planet, and a large degree of regional variation is anticipated. Notably, climate change is expected to have a disproportionate effect at higher latitudes, which will have larger temperature increases. Although the mass media frequently mention increased storms as a consequence of climate change, models of global climate change cannot generally predict finer-scale climate events such as storms or hurricanes.

What does climate change mean for the world's ecosystems and species? Climate is central to the geographic distribution of the world's vegetation types and animal species. As the climate warms, we expect to see shifts in vegetation patterns and species distributions. These shifts may fundamentally alter ecosystem composition and function. An increase in temperature of 3 degrees corresponds to an altitude shift of 500 m or a latitude shift of 250 km; this speed of change is similar to the change in climate during the Pleistocene era, which was too rapid for many species to adapt to. Alpine species may disappear entirely as they are pushed to their distributional limits. Those species that can adapt fast enough may encounter other barriers, such as human development, that hinder their ability to adjust to climate change.

Parmesan et al. (1999) found that European butterflies were changing their ranges in response to climate change. Of the thirty-five species examined, 63 percent had shifted their range north by 35 to 240 km. Only 3 percent had shifted their range southward. This shift reflects changes in colonization and extinction rates at the boundaries of the species range. Europe has warmed an average of 0.8 degree centigrade this century, reflecting a northward shift in climate of about 120 km. Warming temperatures may also allow some insect pests to widen their range, such as the mosquitoes that transmit malaria and dengue fever.

Species that live close to their temperature limit are particularly vulnerable to climate change. Corals flourish at temperatures between 16 and 25 degrees centigrade. Excessive temperatures stress corals and at the extreme lead to so-called bleaching events. Bleaching occurs when corals expel their symbiotic dinoflagellates (zooxanthellae). Bleaching was once considered a rare, isolated event from which corals often recovered. During the 1980s, however, large-scale bleaching events caused extreme loss of coral, and since then bleaching as occurred somewhere in the world every year. The 1997–1998 bleaching was the most severe and widespread ever observed, affecting reefs in the Pacific and Indian Oceans, Red Sea, Persian Gulf, and the Caribbean (Wilkinson, 1998). Bleaching is usually confined to the surface areas (depths of less than 15 m); in this instance, the damage extended to depths of 50 m.

Similarly, species and communities that live at high elevations, adapted to the climatic conditions in those regions, need to move continually higher as warmer temperatures move up the mountains. At some point these communities will have nowhere else to go and they will perish.

Migratory species are also vulnerable to climate change. Sea birds time their migrations carefully to take advantage of prey resources along their route, such as the spawning of horseshoe crabs or krill. Warming temperatures alter this timing and may cause a species to miss these key resources on route. A long-term study in the American Southwest has revealed a trend toward earlier breeding in the Mexican jay (*Aplelocoma ultramarine*) (Brown et al., 1999). Similar patterns have been observed in the United Kingdom. It is unknown what effect this will have on their reproductive success.

At higher latitudes, increasing temperatures are altering the environment and affecting ecosystem function. In Canada's Hudson Bay, the weight and reproductive condition of polar bears have been declining since the early 1980s. At the same time, rising spring temperatures have led to earlier ice breakups. Polar bears need solid ice to hunt effectively, and in the spring their main prey are young ringed seal pups. Before the ice thaws in the spring, polar bears must gain sufficient weight to last through the fasting period in the summer, when they are unable to catch prey on the open water (Stirling et al., 1999).

Sea level has risen 10 to 20 cm in the last 100 years and is expected to increase by 0.09 to 0.88 m by 2100; the rise may have dramatic consequences for coastal environments. Rising sea levels are caused by a combination of thermal expansion and loss of glaciers in mountainous areas, and potentially the loss of polar ice sheets—though there is still much uncertainty about how ice sheets will respond to climate change. As with temperature change, sea level rise is expected to vary regionally. Low-lying coastal areas and small island states are particularly vulnerable to sea level change, because it increases the risk of coastal flooding and the impact of storm surge. Other consequences of sea level rise are the loss of beach, wetland, and mangrove habitats.

Finally, climate change may exacerbate already endangered systems. Species that are confined to a small fragmented habitat are particularly at risk to climate change, as these species will not be able to migrate as vegetation and habitats shift. For example, wetlands have the potential to migrate landward as sea level rises, but this migration is seriously hampered by coastal development.

Synergistic Effects and Conclusions

Any one of these threats to biodiversity might not be enough to drive a species to extinction, but combined they may. Around the world, temperate estuaries have been permanently changed by humans. Estuaries, such as the Chesapeake Bay off the coast of Virginia, are severely affected by nutrient pollution from agriculture and sewage runoff. These excess nutrients cause phytoplankton blooms, some of them toxic, which in turn are decreasing or eliminating oxygen from the bottom sediments, making them uninhabitable to marine life. Historical analysis of the sediments reveals that as early as the late eighteenth century, human settlement in the watershed was affecting nutrient loads to the estuary and consequently the type of phytoplankton that was growing. However, sediments were still not experiencing low oxygen conditions, because the bay also had acres of oysters. Oysters could filter the entire bay in a matter of days, removing the excess phytoplankton and maintaining oxygen levels. But humans then began harvesting oysters at increasing rates, until the bay was nearly depleted of oysters by the 1930s. Without oysters to control the impact of excess nutrients from the land, the system collapsed, and the Chesapeake is now substantially and possibly irreversibly altered. That is not the only place where multiple disturbances brought about the collapse of an entire ecosystem. For instance, the Hawaiian Islands harbor one of the earth's most spectacular biotas, but also one of the most fragile and endangered. Introductions of exotic species, in combination with habitat disturbance by humans, have transformed more than 90 percent of the natural areas in Hawaii and led to countless extinctions. In the Amazon region, the water lost from plants through evapotranspiration is believed to contribute 50 percent of the annual rainfall. Deforestation reduces evapotranspiration rates, leading to decreased rainfall, and subsequently increases the area's vulnerability to fire (Laurance and Williamson, 2001). Fire can quickly burn acres of forest. Deforestation thus leads to additional forest loss through its indirect affect on the climate.

Now more than ever, we are realizing that all life on earth is interconnected. Humans are affecting not just the species that will go extinct today but also what will evolve in the future. The future of earth's biodiversity depends on us. As we begin to understand our impact on biodiversity and its importance to human survival, we are also discovering how to save biodiversity.

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Stemming the Tide of the Sixth Global Extinction Event: What We Can Do

More than 3 billion years of evolutionary trial and error have scattered across the globe a bounty of millions of species of organisms—a kaleidoscopic array of forms, functions, colors, smells, and textures. The equally ancient, constantly shifting ecological fabric that is assembled of those species, from swarming algae to the solitary albatross, connects us all in a web of mutual interdependence.

However, this intricate fabric of life is beginning to fray. The cumulative impacts of humanity's actions are degrading the biosphere and pushing species everywhere to the limits of their ability to survive. Many have already succumbed. The dodo, the Stellar's sea cow, the passenger pigeon—these are a few of the celebrities of the roll call of recently extinct plants and animals. But the list is already a long one, and full of lesser-known, but no less wondrous, species. Consider the Robbins milk-vetch, Kerr's noctuid moth, the Tennessee riffleshell mussel, and Nelson's rice rat, to name but a few of Nature's other actors who have left the ecological stage for good.

Of all ecological and evolutionary phenomena, only extinction promises to be irreversible. No passage of time or level of genetic variability will ever again allow us to hear the call of the dusky seaside sparrow or see the Xerces Blue butterfly emerge from its chrysalis. Sadder still is the fact that with the passage of each species comes the end of an evolutionary lineage, erasing all possibilities for future descendants and variants. Not only are we losing the fruit of Creation—with each extinction, we diminish Creation's capacity to create anew.

It is true, of course, that throughout time species have faded into the shadows of extinction. Indeed, over the last 3.5 billion years more of earth's species have emerged and gone extinct than currently grace us with their presence. The fossil record hints, though, that before human civilization, species were on the scene, on average, for between 1 and 10 million years before going extinct. Current rates of extinction are estimated to be 100 to 1,000 times faster (Pimm et al., 1995). What this means in terms of how many species vanish each day or each year is difficult to know, since we are not sure, even to within an order of magnitude, how many species there are on earth. But surely the toll is climbing higher daily.

There are many warning signs that the fabric of biodiversity is indeed becoming threadbare at an accelerating rate. Some 70 percent of the freshwater mussels in the United States

Workers clean oil from the feathers of a black scoter duck caught in an oil spill, Wales, 1995. The cumulative impacts of humanity's actions are degrading the biosphere and pushing species everywhere to the limits of their ability to survive. (Ecoscene/Corbis)

are either extinct or threatened (Stein et al., 2000). Since the 1990s we have documented declines of frog species in all parts of the world. Typically, evidence is accumulating that a variety of human activities, including pollution, a chytrid fungus (spread by humans), and increasing ultraviolet radiation (caused by thinning of the ozone layer) are contributing to the dwindling numbers of frogs. In fact, according to the World Conservation Union's 2000 Red List of Endangered Species, more than 11,000 species of organisms are known to be at immediate risk of extinction (IUCN, 2000), and there are surely many more species that deserve to be counted among the endangered but are simply too poorly known to evaluate.

We now find ourselves being sucked into the whirlpool of what may well be the sixth great extinction event of evolutionary history. Like the previous five great extinctions of the last 500 million years, the current one promises to erase a large proportion of species on earth and may well require millions or perhaps tens of millions of years before evolution is able to restore biodiversity to its previous levels. In the meantime, ecological upheaval and rearrangement will be the rule rather than the exception.

Unlike the last five extinction spasms, however, the sixth has as its cause a single species—*Homo sapiens*. Rather than tectonic upheaval, volcanism, or asteroid impacts, this time it is the collective activities of billions of people who are poisoning, crowding out, and consuming the world's biota. In just a few thousands of years—

a blink of an eye in evolutionary time—we humans have become the cause of the demise of untold numbers of species.

It is, however, in this fundamental difference between the current and previous extinction events than we can also find our greatest hope for avoiding global crisis. Humans, the most self-conscious of animals, are uniquely capable of foresight, deliberation, and moral thought. Human societies can radically transform themselves—and indeed they repeatedly have throughout history. The rise of agrarianism, democracy, and capitalism are but three examples of our ability to remake ourselves in the face of new circumstances.

It would seem that the vast complexity of natural ecosystems and human economic and societal imperatives would overwhelm our abilities to simultaneously comprehend all the causes, feedbacks, inputs, outputs, and results of the environmental crisis at hand. Amazingly, though, we are not limited by a lack of understanding of the problems or, for the most part, how we can begin to solve them. Instead what limits us now is a means to finding a consensus and collective will to turn things around.

Solutions can be found at many levels of the problem. This means that an effective approach will involve actors as diverse as international organizations, individual nations, nongovernmental organizations, academic institutions, local grassroots groups, and, most important, individuals. As individuals, our power lies in our everyday actions, through which we elect either to contribute to the problem or to the many possible solutions.

What follows is a collection of several of the most urgent and most promising steps that we must undertake if we are to preserve Creation. To be sure, it is scarcely a partial blueprint of the things that must be done. In fact, there is no precedent for the type of concerted global change that must be achieved. Yet if we can overcome our egotism for long enough to see the importance of maintaining biodiversity, while at the same time realizing that our dominant position in the biosphere means that we must also accept the responsibility for managing the planet, then there truly is hope. And where there is hope there can be action.

A protest in Vancouver, British Columbia, against the use of old-growth trees by the timber industry. Solutions to environmental crises must involve international organizations, academic institutions, local grassroots groups, and, most importantly, individuals. (Joel W. Rogers/Corbis)

Global Issues

Stabilize Global Population

If any sustainable balance among the world's biodiversity, ecological systems, and humans is to be found, we must stabilize human pop-

Students clean litter from the roadside in Colorado on Earth Day 1990. Once we accept the importance of maintaining biodiversity and understand our dominant position in the biosphere, we must also accept the responsibility of caring for the planet. (D. Robert and Lorri Franz/Corbis)

ulation. Although the consumption of the world's resources is dominated by the minority of people living in the rich, developed countries, the needs of the growing billions living elsewhere are taking an enormous toll on the global environment. Humans already capture more than a third of the earth's terrestrial productivity and more than half of the world's freshwater. As food production has doubled in the last thirty-five years, we now release more nitrogen and phosphorus into the environment than all natural sources combined (Vitousek et al., 1997). Simply feeding the world's people requires that food production increase at the same pace as population. Almost a billion hectares of land will be converted for crops and pastures between now and 2050—roughly half of the remaining suitable land (Tilman et al., 2001).

Human population grew gradually from the dawn of human civilization until roughly 1800, when for the first time there were 1 billion people on the planet. It took less than 200 years to add the second billion (which occurred around 1930), and since then the billion-people milestones have passed quickly on the path to 6.1 billion humans in 2002. World population is expected to swell from 6.1 billion to roughly 9.3 billion in 2050. All of that growth will occur in the world's developing nations. According to the UN Population Division, the population in the forty-nine least developed nations will almost triple from 668 million to 1.86 billion by 2050 (United Nations, 2001). The pressure on natural resources and biodiversity in these poorest regions of the world promises to be crushing, as more and more people scrape for shelter, land to farm, and firewood for cooking in a self-reinforcing cycle of environmental degradation and poverty. Even water, the most basic of needs, will soon become a scarcely available commodity to almost half of the world's people (UNFPA, 2001).

Fortunately, there are many actions we can take that will help bring about demographic transitions in the fastest growing nations and bring us closer to attaining a stable population. The following is a partial list of some of those actions:

1. Improve the educational and political status of women. Women around the world have less access to education than men and fewer opportunities to participate in the political process, and they often do not have the right to own property or earn income. Two-thirds of the world's roughly

1 billion illiterate adults are women. Just 12 percent of parliamentary seats worldwide are held by women. Studies have repeatedly shown a correlation between higher levels of education among women and smaller, healthier families. Similarly, when women are able to enter the political process, family-friendly and family-planning legislation is more often enacted (Population Reference Bureau, 2001). When women are intellectually, economically, and politically empowered, they can make decisions about how many children they wish to have.

2. Improve the survival and health of children. The African leader Julius Nyere is often quoted as saying that "the most powerful contraceptive is the confidence by parents that their children will survive" (Gore, 1992, p. 313). Low infant mortality rates and improved prospects for healthy children who grow to adulthood allow parents to have smaller families while still ensuring that there will be enough children on hand to care for their parents, run family businesses, and carry on family names.
3. Provide easy access to family planning resources. When parents are educated in family planning options and when access to a variety of contraceptives is readily available, family size becomes a matter of reason and decision rather than one of chance or ignorance. Education on spaced births, delayed marriage, breastfeeding, and other cultural institutions as well as birth control measures all combine to allow parents to choose when and whether to start families and how large those families will be.

Turning the tide of population growth has been a highly politicized topic in much of the world. Some argue that encouraging family planning goes against the tenets of a number of the world's religions. Others make the point that developed nations ought not to demand that the people in developing nations have fewer babies while the environmental impact of a single child gobbling energy and resources in the United States, for example, is equal to that of dozens of children born to peasants in Cambodia. Although these may be valid arguments, few arguments can seriously call into question the goals of alleviating poverty, increasing the health and survival of children and mothers, and reducing the rate of population growth in the poorest nations.

Consumption

The world's growing population is just one part of the crisis we face. Any discussion of the problems of a swelling global population must be accompanied by a parallel discussion of the patterns of human consumption of earth's resources. We are cutting the world's forests, drinking its freshwater, mining its minerals, and trawling its seas at rates that would have seemed inconceivable just a few decades ago. Today we use nearly twice the amount of energy we did in 1970, and it is expected that energy use will increase by another 60 percent by 2020 (EIA/DOE, 2002).

Although the number of people that the earth can support is a matter of heated debate, the answer ultimately comes down to the sort of life we would wish those people to have. If we aspire to a global community that enjoys the level of comfort of today's average U.S. or European citizen, then we have already greatly exceeded the carrying capacity of the planet. On the other hand, if we were all to emulate the consumption patterns of the average citizen in Bangladesh or Bolivia, we could envision a world in which many more people could live sustainably.

Half the world still exists on less than $2 per day (UNFPA, 2001). This difference in purchasing power translates into unequal consumption patterns of every conceivable resource. For example, as the consumption of energy exploded over the last century and a half, the distribution of that energy use also underwent a dramatic transformation. In 1700 a farmer in North America probably did not use much more energy than his counterpart in Asia or Africa. Today, however, the average citizen of North America uses almost thirty times the energy of the average African.

What You Can Do—Change the Way You Eat

Food is a huge component of the world's economy, and the way we eat can have a tremendous impact on the earth's biodiversity. Land conversion for agriculture; topsoil erosion; fertilizer, pesticide, and herbicide runoff; reliance on meat-rich diets; and wasteful packaging all damage ecosystems and reduce our ability to provide for future generations. Our everyday purchasing decisions at the supermarket can either help or hurt biodiversity. Here are a few things that you can do to help:

Eat foods that are lower on the food chain
Choose organic foods
Buy produce that is grown locally
Buy fewer processed foods
Buy produce that is in season
Buy foods with less packaging or no packaging at all
Avoid eating overexploited species
Broaden your diet to include a greater diversity of food items
Bring your own reusable cloth bag to the market instead of using disposable bags
Minimize your food waste

Sources: American Museum of Natural History. 1998. *Biodiversity and Your Food: A Guide for Green Consumers*. New York: Center for Biodiversity and Conservation. For more information, visit: http://research.amnh.org; Riebel, Linda, and Ken Jacobsen. 2002. *Eating to Save the Earth*. Berkeley, CA: CelestialArts.

Heavily consumptive habits are engrained in our daily lives. Often they are almost imperceptible to us, but cumulatively they wreak havoc on the natural world. Urban sprawl, for example, chews up 1 million acres of open space in the United States each year, fragmenting wildlife habitat and isolating populations of species (Sierra Club, 2002). This dispersed pattern of settlement also requires residents to use more energy to get to work, shopping, and school (it further requires increased energy use for garbage pickup, mail delivery, and the provision of goods and services), which contributes to reduced air quality and global climate change.

The way that we eat reflects the increasing amount of resources we use in our daily lives, as well as the large disparity in the resources it takes to feed a single person in different societies. For example, the Audubon Society recently reported that the earth could feed 10 billion people eating as the citizens of India do, 5 billion who eat as the Italians do, but just 2.5 billion eating as do the citizens of the United States (remember that there are already 6.1 billion people). Nowhere is this more apparent than in the world's meat consumption. As economies grow and populaces become more affluent, meat consumption tends to increase. In 1900, 10 percent of the world's grain went to feed animals. By the 1990s that proportion had risen to 45 percent (Riebel and Jaconsen, 2002, p. 14). As we transition to meat-heavy diets, it takes almost four times more calories to feed each person, with most of those calories cycled through animals (ibid., p. 25). Rather than consume local produce, we eat food that is transported huge distances before it arrives on our tables—a ham-

What You Can Do—Change Your Energy Use

The amount of energy we use and the ways we use it affect earth's biodiversity in every corner of the globe. As we burn fossil fuels to generate electricity, run our cars, and heat our homes, we release gases that contribute to global climate change, acid rain, and air and soil pollution. Ultimately, our reliance on fossil fuels is leading to a less habitable planet for ourselves and other species. By using energy more wisely and transitioning to cleaner, renewable energy sources, we promote a healthier environment and benefit biodiversity. Here's how you can help change the way you use energy:

1. Reduce, reuse, and recycle
2. Support renewable energy
3. Unplug your gadgets, appliances, and electronics that draw energy even when they are not "on"
4. Buy products that are made locally
5. Use mass transit, walk, or make use of some other form of "green" transportation, such as biking or rollerblading, whenever possible
6. Replace conventional light bulbs with compact fluorescent bulbs—and turn them off when you leave the room
7. Adjust your thermostats—lower in the winter and higher in the summer
8. Make your home more energy efficient with weather-stripping, double-glazed windows, insulation, and improved heating/cooling systems
9. Buy products low in petroleum

Source: American Museum of Natural History. 1998. *Biodiversity and Your Energy Use: A Guide for Green Consumers*. New York: Center for Biodiversity and Conservation. For more information, visit http://research.amnh.org.

burger served in Seattle, Washington, contains meat from Texas and Colorado, lettuce and tomatoes from California, wheat from Idaho, corn from Nebraska, and salt from Louisiana (ibid., p. 12). Not to mention the ingredients for the side order of french fries and soda!

Of course, all this consumption also creates tremendous quantities of waste. In the early 1990s, the annual global output of hazardous wastes from chemical production, mining, paper factories, energy production, and so forth was about 400 million tons, with about three-quarters of that coming from the industrialized nations.

If we are to lessen the impact that each one of us has on the earth each day, we must simultaneously reduce the amount of goods and services that we consume and develop new, appropriate technologies that create goods and services at smaller cost to the global environment. Here are two of the most important steps:

1. Redefine what is "enough" and adjust our daily lives to reflect it. The idea of living sustainably is familiar to many, though few of us can claim to live in a way that does little or no long-term damage to the environment. Moreover, all around us are the signs

that as a society we do not have a sense of how much is "enough." The billions of people living in poverty around the world have enabled the people of the industrialized world to achieve lives that are surely beyond the level of a sustainable, equitable planet. Our goal must be to achieve a more balanced, humane standard of living for people everywhere, while at the same time living within the natural bounds set by the ecological systems of the earth. This will require significant, fundamental changes in the way of life of every person everywhere, particularly in the industrialized north.

2. Implement the use of appropriate technologies that reduce the amount of resources needed to produce and dispose of each and every product we consume. It is believed that the technologies to reduce the energy consumption of every person, every industry, and every organization by 80 percent already exist. Essentially, this requires us to make things last twice as long with half the resources (Hawken, 1993, p. xiv). Driving radically more fuel-efficient vehicles, less often, with more people in them, could reduce our consumption of fossil fuels by more than half. Passenger vehicles that run for 70 miles on a gallon of gasoline are already on the market, but they constitute less than 1 percent of the vehicles on the road today. Reusing products, then reusing their materials in second or third products, dramatically reduces the energy needed in manufacturing. Products must be designed with reuse and recycling in mind. Industries and manufacturers must work together to foster recovery and exchange of waste materials that can be used elsewhere. The benefit of addressing this challenge goes beyond reducing resource consumption. In striving to meet this goal we will have to rethink how we make, consume, and dispose of every single product, and ultimately, whether we need that product at all.

Economic Reform

The third major change that we must make involves rewriting the world's economic rulebook. Whether we like it or not, the global market economy has firmly established itself as the framework within which the majority of the world's people now choose their individual and collective paths. The market economy as we know it, though, is deeply flawed, legitimizing and providing daily incentives for environmental ruin. As Al Gore clearly stated, "We make billions of economic choices every day, and the consequences are bringing us steadily closer to the brink of ecological disaster" (Gore, 1992, p. 185). Thus it truly can be said that in many ways the impending Sixth Extinction Crisis is in fact an economic crisis of global proportions.

If we have any aspirations to a future of environmental integrity, human prosperity, and a planet with a full complement of its biodiversity, then we must utterly transform the marketplace as we know it. Freely functioning markets are predicated on the principle of narrow self-interest (Pearce and Moran, 1994), yet our present market system fails in many respects to provide us, its participants, with all of the information necessary to fully evaluate where our interests lie. The true costs of our decisions are often hidden from us; they are eventually shifted onto society or the natural environment as we happily go on our way. The market also sharply insulates the individual and his or her self-interest from the interests of society. Thus the markets daily put each of us on a collision course with the world around us. It is obviously in our collective best interest to preserve the Amazon forest, if for no other reason than to maintain the oxygen-producing dynamo that some have called the "lungs of the earth." But it is equally clear to a Peruvian campesino who must feed his family, that his interests lie in cutting another hectare of the seemingly endless forest.

The net effect is a world in which "our commercial systems conflict with everything nature teaches us" (Hawken, 1993, p. 5). We are driven to consume resources as if they were endless, and we heedlessly dispose of the dross. Instead, we need to consider our most distant goals, like making sure that "biodiversity is still approximately present in 100-plus years from now" (Janzen, 1994) and embrace economic paradigms that will help us to reach those milestones.

Of course, a change of this magnitude in a structure as firmly entrenched as the global economy will require a wrenching, concerted effort by governments, businesses, and individuals everywhere. Global mechanisms including the United Nations and beyond must play a role. But the key to the solution lies in devising mechanisms that harness the power of the decisions that 6.1 billion people make every day as we spend, work, save, and consume. Here are a number of the most important changes we must strive to make:

1. Transition to a steady-state economy. Classic economic theory measures economic progress with continuous gains: gains in production, gains in consumption, gains in profits. Yet as Paul Hawken asks: "What is the logic of extracting diminishing resources in order to create capital to finance more consumption and demand on those same diminishing resources?" (Hawken, 1993, p. 5). The current economic paradigm is that the economy is isolated from the natural world, with exchanges circulating between business and consumer endlessly. The energy and materials consumed by the economy do not actually enter the system; they merely exist external to the economy. Some economists, however, have envisioned a different, open arrangement in which the economy exists together with the resources it uses and the waste it produces in a balanced steady state (Daly, 1997). Rather than growth, the steady-state economy's drive is to foster development of a better quality of life within the bounds of the ecological system of the earth.
2. Include the true costs of products in the cost to the consumer. The market economy as we currently know it fails to account for many of the costs associated with the production and consumption of most goods. For example, when you drive your car and burn gasoline, who pays the costs associated with the respiratory illnesses you are causing by polluting the air? What about the costs of a changing climate that the CO_2 and NO_x coming from your tailpipe are contributing to? These costs to the collective society—created both when a product is made and when it is consumed—are rarely included in the price paid by consumers. Alfred Pigou, an economist in the first half of the twentieth century, formalized our thinking about these "external" costs—that is, costs that are left out of the modern economy. Following this logic, biodiversity and the environment are not protected because their value (or the cost of its loss) is not included in the pricing structures that shape consumers' behavior (Meffe and Carroll, 1997). This idea of market failure has spurred much research into how the hidden costs of our consumption can be adequately included in the prices we pay. The essence of most proposed solutions is charging the producers of goods for the resources that their products degrade and the wastes that their products create. The producers, of course, would then pass on those costs to consumers, who would then be able to evaluate the true costs of the products they buy. Products that were more efficiently made, creating less waste, would be cheaper than energy-intense, polluting ones—finally reflecting their true environmental and social costs.

3. Change our measures of economic progress to include the use and degradation of resources and natural systems. Many of the most commonly used metrics of economic output continue to ignore the diminishment or degradation of the natural resources and processes that sustain human endeavor. The most basic and widely used of those indicators, the gross national product (GNP), is no exception (Gore, 1992, p. 183). As natural resources are consumed and environments' ability to support healthy ecosystems is reduced, our ability to keep using those resources is also diminished. But the current calculations of GNP do not reflect this. For example, an aging factory with outdated or broken machinery is not worth as much under current accounting schemes as a gleaming production line that promises to churn out goods for years to come. Likewise, we should be assessing the reduced ability of eroded fields and polluted groundwater to grow and irrigate future crops, and calculating the true costs and benefits of current intensive agricultural practices.

What You Can Do—Change How You Shop

What we buy not only affects how we use the earth's resources, it also influences how those products are made and discarded. Every product we buy therefore affects the environment in myriad ways, many of which are often difficult to see. Also, by choosing certain products over others, we send signals to industries and governments about how we feel about the environment. By selecting environmentally sound products, we can cast billions of "votes" per day for a world that protects biodiversity. Here are some guidelines for greener shopping:

1. Buy only what you need
2. Buy products that are made locally
3. Avoid buying disposable items
4. Choose products with minimal packaging
5. Buy products that are durable or longer-lasting
6. Avoid products made from endangered species
7. Avoid products containing toxic ingredients or petroleum derivatives
8. Buy products that were sustainably produced or farmed organically

Source: American Museum of Natural History. 1998. *Biodiversity and What You Buy: A Guide for Green Consumers*. New York: Center for Biodiversity and Conservation. For more information, visit http://research.amnh.org.

4. Abolish perverse subsidies and incentives. Governments around the world constantly try to influence the behavior of their citizens and the shape of their cultures by manipulating the economic playing field. Imposing taxes to prevent undesired actions or offering tax exemptions to engender desirable actions are among the most apparent strategies that governments employ. Often these interventions by governments wind up encouraging or even paying for environmentally destructive practices. The U.S. Forest Service, for example, in fulfilling its mandate to provide the logging industry with access to the national forests, winds up spending more on building roads than it recovers in logging concession fees—an effective windfall for the logging companies, which don't have to pay for their roads. In Brazil, a government policy designed to encourage settlement of the Amazonian frontier gave pioneers free land if they cleared more than half of the forest from their properties. It has been estimated that the global sum of all of these destructive subsidies is U.S.$2 trillion annually

(Myers and Kent, 2001). The net effect of these incentives and subsidies is to further twist the "free" market away from reflecting the environmental degradation caused by human activities.

5. Change the time horizon for economic decision making. One of the most problematic economic practices involves the discounting of future income and resource availability. Discounting allows us to compare the gains and losses that occur over time and evaluate different courses of action. For example, we might want to compare the value of clear-cutting a forest now—essentially taking all of our profits immediately and moving on to another venture (ignoring the costs of degraded lands and watersheds)—to managing the same forest sustainably, cutting a small number of trees each year, and receiving smaller profits indefinitely. Under current discounting practices, which heavily favor immediate profits over long-term profits, destructive activities like clear-cutting nearly always come out ahead on the balance sheet. In practice, then, the current discounting methods essentially make biodiversity resources worthless when projected far into the future. Several alternative methods for discounting future or present alternatives exist that favor the long-term sustainability option. We must adopt these alternative economic formulae to incorporate the long-term impacts of what we do today and make our indicators more effectively guide us toward reaching our societal goals.

Immediate Responses to the Symptoms of the Extinction Crisis

Establish and Manage Protected Areas

Conserving biodiversity where it exists, or in situ, is the centerpiece of conservation strategies. A broad spectrum of biosphere reserves, parks, wildlife reserves, forest reserves, and indigenous peoples' territories are already in place around the world. Increasingly, protected areas are being managed for sustaining complete and functioning ecosystems in order to maintain a full range of ecological processes and the habitats and species that depend on them. Many scientists and conservation organizations have suggested that protecting a targeted 10 to 12 percent of each nation's land area in this way would effectively conserve a large percentage of the world's species. However, more recent analyses are indicating that the land area necessary to conserve and protect most components of biodiversity may actually be closer to 50 percent (Soulé and Sanjayan, 1998). Barely 5 percent of tropical rain forests, the world's most diverse ecosystems, are protected; our opportunities to achieve even the earlier goal of 10 percent are fast vanishing. Twenty-nine out of sixty-three Asian, African, and Latin American countries have already lost more than 80 percent of their natural habits (ibid.). We must rapidly move to protect the remaining tracts of the world's wildlands and stitch them into an interconnected network of biodiversity reserves. Studies have suggested that such a course of action is feasible both scientifically and financially (Pimm et al., 2001), and it is essential to the near- and long-term persistence of all levels of biodiversity.

Develop Methods for Assessing the Economic Value of Biodiversity

As we have discussed above, the value of biodiversity and ecological processes and the costs of their loss are generally excluded from commercial markets. Although we know that biodiversity and the services it provides to society are crucial to human welfare, actually calculating a dollar value for processes such as nutrient cycling or pollination, to name a few, remains an elusive prospect. Yet in order to

A girl and her mother plant marsh grass to protect the bank of the Duwamish River (Washington State) from erosion, Earth Day 1995. Moving toward rapidly protecting tracts of the world's wildlands is essential to long-term protection of biodiversity. (Jay Syverson/Corbis)

capture the value of biodiversity in pricing systems, assess damages when the environment is degraded, and evaluate the worth of natural capital, we must develop techniques for appraising the economic "worth" of biodiversity. Although we are at the early stages of this effort, the results have been astonishing. Costanza et al. (1997), in a landmark paper, estimated that the global value of seventeen ecosystem services such as the provision of raw materials, climate regulation, and soil formation was in the neighborhood of U.S.$33 trillion per year. This estimate dwarfs the global gross national product total of U.S.$18 trillion per year—in effect signaling that we cannot afford to lose the subsidy that Nature provides each year (even if it were for sale). Studies like that of Costanza et al. are just the beginning, and we must continue to refine resource economics if we are to reform the way in which we value the natural world.

Monitor Biodiversity

Conserving biodiversity requires that we understand its distribution and status in space and time. Changes in the threats to biodiversity (human activities, climate shifts, disturbances, and pollution) necessitate a system that provides us with updates on where biodiversity is and how it is faring. As Noss (1990) points out, the hierarchical nature of biodiversity dictates that we monitor biodiversity at many levels: from mapping the way that animal and plant communities are distributed across landscapes to identifying the composition of those communities, tracking the increase or decrease in species' populations, and measuring the genetic structure of those populations. Designing such a comprehensive monitoring protocol continues to be a challenge that we must meet. However, only with such broadly gathered information can we design conservation strategies that reflect the most current threats to biodiversity.

Affect Legislation

Laws, and the legislative process through which they are made, are a society's means to codifying its principles, aspirations, and structures. From the standpoint of biodiversity conservation, establishing the protection of biodiversity in legal frameworks at global, national and regional levels is essential on both philosophical and practical levels. International agreements with the force of law, such as the Convention on International Trade in Endangered Species of Wild Flora and Fauna (CITES), simultaneously signal the world's commitment to end the trafficking in endangered wildlife and provide mechanisms for the convention's signatories to use in achieving that common goal. National laws like the U.S. Endangered Species Act, which very clearly articulates that species have "esthetic, ecological, educational, historical, recreational, and scientific value to the Nation and its people," are equally critical in protecting species and their habitats. Conservationists must continue to understand and involve themselves in the legislative process at all levels in order to protect the environmental laws that already exist, encourage additional legal protections for biodiversity, and foster the inclusion of conservation ethics in all laws.

Conserve Habitats and Species on Private Lands

In many areas of the world, large percentages of the land are in the hands of private owners. In countries like the United States, where government involvement in the management of private lands is strictly limited, conservation efforts must involve the local landowners if species and habitats are to be managed at all. Finding incentives and mechanisms that bring landowners into the process of planning and implementing conservation strategies is crucial to this effort. Organizations such as the Malpai Borderlands Group—a collection of landowners, scientists, and other stakeholders dedicated to maintaining the health of a million-acre region in southern Arizona and New Mexico—are leading the way in this effort. Other important initiatives on this front include the development of so-called safe harbor agreements between governments and landowners that promote current conservation efforts on private lands and ensure landowners' future options for developing their land.

Establish Pollution Permit Trading Systems

In this system, permits for discharging specific quantities of pollutants into the environment are issued or auctioned off to industry. The number of permits can be lowered over time to reduce the total amount of pollution allowed. Importantly, the permits can also be sold or traded, which provides industry with important flexibility in how it achieves compliance with pollution controls. The system also creates incentives for cleaner business: old facilities can be renovated, or newer, efficient facilities can be built, allowing their owners to sell their pollution credits and increase profits. This type of system has already been successful in greatly reducing U.S. emissions of sulfur dioxide, a product of burning coal and a main cause of acid rain. The U.S. Environmental Protection Agency presides over the exchanges of credits, phasing out some of the existing credits each time an exchange is made, as well as reducing the total number of permits.

—*Sacha Spector*

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A

Abyssal Floor

The abyssal floor is the deep part of the ocean that lies between 3,000 and 6,000 m. The continents cover 29 percent of the earth, but the abyssal floor covers 30 percent; it extends from the sides of midocean ridges to the base of the continental rise. With deep-sea exploration, principally using seismic profiling techniques, this part of the ocean floor can be divided into two sections: abyssal plains and abyssal hills. Abyssal hills vary in height from 75 to 1,000 m above the seafloor. Maps of the seafloor show that they cover 50 percent of the Atlantic and 80 percent of the Pacific Ocean floor; they are considered to be the earth's most widespread topographic feature. Circular or elliptical and 1 to 8 km in width at their base, they are probably mostly volcanic, although some could also be the result of faulting. Located on the flanks of midocean ridges and on parts of the ocean floor separated from continents by trenches, they are most abundant in the Pacific Ocean.

Abyssal plains are extremely flat features of the ocean floor that are completely covered by sediments transported from the continents by turbidity currents. In all probability these sediments also bury abyssal hills; it is most likely that the hills are found on most of the ocean floor. Where the margins of the ocean basin are ringed by trenches and intersected by rises, sediments from the continents are trapped and cannot spread over the seafloor.

—*Sidney Horenstein*

See also: Continental Slope and Rise; Oceans; Seamounts

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Adaptation

The term *adaptation* is used in two distinct, but related, ways in evolutionary biology. An adaptation is any behavioral, physiological, or anatomical feature of an organism that has been shaped by the evolutionary process to perform a specific function. Eyes, for example, are adaptations for seeing—and eyes have evolved independently in several different lineages of animals, a reflection of the importance of vision in the life of most animals.

The second sense of the term *adaptation* is the process whereby the features of organisms are modified in evolutionary history to perform new functions, or to perform functions more efficiently. For example, increase in brain size in human evolutionary history came about over time through adaptation that involved increase in cognitive capacity (thinking ability). The term *adaptation*, referring to a process, is sometimes also used in biology in a nonevolutionary, purely physiological sense. For example, when a person walks into a room and notices a distinct odor, that odor usually becomes less noticeable within a few minutes. This is an example of an internal adjustment in the person's olfactory sensory apparatus through the process of "physiological adaptation," rather than the actual disappearance of the odor itself. The remainder of this article treats adaptation only in the evolutionary sense, and it will be clear from the context in which sense—the general evolutionary process of adaptation, or the specific organismic feature—the term *adaptation* is being used.

Adaptation can be considered the central concept of evolutionary biology. Although (as discussed below) not all evolutionary change involves adaptation (that is, not all evolutionary change is adaptive), the original questions that prompted Charles Darwin, Alfred Russell Wallace, and others to develop a theory of evolution are these: Why are there so many kinds of animals, plants, fungi, and microbes? Why, in other words, is there so much diversity (see Evolutionary Biodiversity) in the world? And why are organisms that are basically very similar nonetheless different in some consistent ways—for example, why are eastern, western, and mountain bluebirds in the United States differently colored?

Darwin and other early evolutionary biologists observed the obvious functions played by anatomical and behavioral features of organisms and saw that features which differ between organisms (for example, the number, size, and shape of the digits of the front feet of vertebrate animals) correlate directly with the different functions played by those features. The human hand has five fingers including an opposable thumb, which makes it ideal for grasping and manipulating objects. The front foot of a horse, in contrast, has one digit, is covered by a hoof, and is used exclusively for support of the animal as it stands, walks, and runs. There must be, these early biologists reasoned, some process in biological history that can modify organismic features into the diverse array we see in the biological world.

That process is natural selection; Darwin and Wallace saw that not all organisms born each generation can survive and reproduce (or else the world would be quickly overrun by a single species). They also knew that organisms resemble their parents—though they were ignorant of the basic mechanisms of heredity (the modern science of genetics was not founded until around 1900, and Darwin and Wallace jointly announced their theory of evolution by natural selection nearly a half-century earlier). Finally, both men recognized that there is much variation within a population of organisms.

Both Darwin and Wallace reasoned that only those organisms best suited ("adapted") to surviving (finding food, avoiding being eaten by predators, or succumbing to disease) on average would be the ones that would reproduce—and thus pass on to their offspring what we would now call the *genetic information* that made them (the parents) more successful than other organisms in their population.

Should the environment change, perhaps other variants in the population would then be the more successful ones, and succeeding generations would inherit a different mixture of features. Finally, through a process now known as *mutation,* new forms of genetic information arise and may ultimately prove beneficial to organisms in a species by paving the way for new structures or behaviors to be selected in the general process of adaptive change.

Darwin also saw that though many adaptations influence the ways organisms survive (for example, different beak shapes and sizes in birds for capturing and eating different kinds of food—seeds, insects, rodents), some features seem to be more about the process of reproduction itself. The elaborate fantail of the male peacock, for example, is used in conjunction with his mating display in the attempt to attract females. The differences in bluebird coloration, likewise, are thought not to reflect differences in the ecology of the eastern, mountain, and western bluebird species, but rather the need for females to recognize males; the divergence in coloration between the different species arose, presumably, during periods when populations were isolated, and natural selection (actually, what Darwin called *sexual selection*) acted to maintain breeding recognition between local males and females. The populations drifted apart, developing different color patterns (and mating songs) in the process known as *speciation*—such that eastern, western, and mountain bluebirds, when they do occasionally run across one another, do not "recognize" each other as suitable mates, though eastern and mountain bluebirds are known to occasionally hybridize (interbreed).

Although reproductive adaptations are of course important—and are increasingly the focus of research by sociobiologists and others—it is the *economic* adaptations of organisms (those concerned specifically with surviving, with acquiring food) that are the most spectacular. For example:

- The golden bamboo lemur *(Hapalemur aureus*) in Madagascar eats only the tender shoots of young bamboo, which are loaded with cyanide—a substance that, for most organisms, is a deadly poison. These little animals (adults weigh only 1.35 kg) consume enough bamboo each day to kill six adult men. They are "adapted" to eating a species of bamboo that would prove fatal to anything else that ate it—thereby ensuring themselves exclusive grazing rights on this particular food source. The physiological mechanism by which these lemurs detoxify the cyanide is still unknown.
- Plants and many microorganisms have the ability to photosynthesize—in other words, to utilize sunlight to produce sugar from carbon dioxide and water. Photosynthesis is itself a spectacular adaptation, and without it life would never have diversified beyond the bacterial stage of existence. Sugars are a form of stored (solar) energy that lie at the base of the food chain in all of the world's terrestrial and aquatic ecosystems except one: the deep-sea vent faunas. In the deepest oceanic trenches, where sunlight cannot penetrate, there are nonetheless many species of crustaceans, worms, and other forms of marine life that thrive, forming complex, diverse ecosystems—all because some bacteria are able to convert the thermal (heat) energy flowing from cracks in the earth's crust (the heat is derived from radioactive decay deep within the earth). By this unique biochemical pathway, life has adapted to the sunless depths of the deepest ocean floor.
- Termites are famous for being able to digest cellulose—the stiff material that forms much of plant tissue, indigestible to humans,

cows, and virtually all other herbivores (which obtain nutrients and sugars from the plants they eat—eliminating the residue cellulose). And though termites pose a threat to the owners of wooden houses, without them, in many ecosystems (especially in drier tropical regions), there would be little or no cellular breakdown of plant material after death—and such ecosystems would quickly become clogged with dead plant life. But it turns out that it is not the termites themselves that actually perform the task of cellulose digestion. Rather, fungi and certain microbes with which they lead a commensal (mutually beneficial) existence do the work. Some termite species maintain great fungal "gardens" below ground, where the fungi are put to work breaking down the cellulose. Other termite species house the fungi (and certain microbes) in their hindgut, providing food and shelter to the fungi and microbes which, in breaking down cellulose in the termite's gut, provide the termite with nourishment. The fungi and microbes are adapted to life in the termite gut, and the termite is adapted to housing an internal "flora" that takes care of much of its nutritional needs. (The presence of the bacterium *Escherichia coli* in the human gut is an adaptation of both humans and *E. coli* along similar, digestive lines).

- The human eye was presented to Charles Darwin as an example of an anatomical structure so incredibly complex that it could not possibly have evolved by a series of adaptive stages through the action of natural selection. Darwin and later biologists were able to show, in response, that there is an entire spectrum of complexity among eyes in the animal world—with some "eyes" being simple cups lined by photoreceptor cells with a thin translucent covering that is the simplest imaginable "lens." But even though the complexity of the vertebrate eye (human and otherwise) no longer seems a credible argument against adaptation through natural selection—and hence against the very notion of evolution—nonetheless the intricate workings of all the parts that make up such eyes remain impressive. That the eyes of cephalopod mollusks, such as octopi and squids, very closely resemble the structure of vertebrate eyes, yet were evolved independently, shows how the process of adaptation frequently results in similar-looking structures—there being but a few ways that an eye can be constructed out of organismic tissues (see also Convergence and Parallelism).

Evolutionary biologists have recently become aware that the fact that a feature of an organism performs some function is not proof that the feature is an evolutionary adaptation. Biologists have come to avoid what they call "Just So Stories" (after the famous stories by Rudyard Kipling, such as "How the Elephant Got Its Trunk"). We see feathers on a bird, for example, and we perform experiments which show that birds cannot fly without feathers on their wings (indeed, most of a bird's wing consists of feathers). But that does not mean that feathers were evolved for flight. More likely, feathers served as thermoregulatory (body heat) devices, and it is now becoming clear that many Mesozoic groups of dinosaurs also had feathers—yet were not adapted to fly.

Thus the process of adaptation may well go through many phases, wherein a structure that is developed for one function is then put to use for still other functions—for which it did not originally evolve. Paleontologists Elisabeth S. Vrba and Stephen Jay Gould coined the term *exaptation* for such instances in which a struc-

Birds' wings are an example of adaptation. Wings have been shaped by the evolutionary process, but not necessarily just for flight. It's possible that feathers evolved to provide birds thermoregulatory (body heat) devices. (Academy of Natural Sciences of Philadelphia/Corbis)

ture evolved as an adaptation for one use and is then used for other functions, often with little or no further anatomical modification. The example they gave is the African black heron, a bird that hunts for frogs and fish in shallow freshwater environments, as do countless other species of herons and egrets the world over. But with the African black heron there is a difference: it folds its wings over in front of itself, forming an "umbrella" that casts a much bigger shadow than the one formed by just its body alone. Fish love the shade, and they congregate into these heron-made shadows—only to be speared by the heron as it patiently sits with its wings folded over in a way not done by any other bird. Obviously, this species of heron's wings were not evolved to cast shadows; rather, they are wings much like those in all other herons and egrets—and, in a general way, like those of all other birds. The wings were evolved for flight (in contrast to the feathers per se—see above); the new adaptation here is the use of these wings to hunt fish, a behavioral adaptation that is genetically based and so definitely an "adaptation." But the process of adaptation in this instance involved simple transfer of function of a preexisting structure: in terms of casting shadows to catch fish, the wings of the African black heron are an example of an *exaptation*.

—Niles Eldredge

See also: Convergence and Parallelism; Darwin, Charles; Ecosystems; Evolution; Evolutionary Biodiversity; Human Evolution; Natural Selection; Speciation; Wallace, Alfred Russel

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Adaptive Radiation

An adaptive radiation is a series of events in evolutionary history in which one ancestral species gives rise to many descendant species that are adapted to different ecological settings. Thus many descendant species in an adaptive radiation appear to be very different from the ancestral species. Adaptive radiations generally occur in specific geographic regions and usually occur over a relatively short span of geological time.

Adaptive radiations are informative case histories in evolution. Biologists believe that the normal evolutionary processes of adaptation through natural selection and speciation, acting on isolated species with little or no competition—and often upon arrival of the ancestor in an isolated region, such as an oceanic island chain—is sufficient to generate the richly diverse arrays of descendant species.

There is a wide spectrum of events that falls under the category of adaptive radiation. At the lower end, small bursts of speciation in a relatively constricted area commonly produce an array of adaptively divergent species. Indeed, the best example of such a "mini" adaptive radiation is provided by the famous "Darwin's finches" of the Galapagos Islands. The thirteen species currently alive have diverged into an array of small, medium, and large bill sizes, adapted for eating seeds of different sizes and toughness. Some species forage on the ground for seeds, while others hunt for insects in shrubs and trees. But others of these finch species have diverged further from the ancestral seed-cracking finches. One species, the woodpecker finch, is adapted to eating insects that it finds by using its modified beak to pry up pieces of bark. Some woodpecker finches have developed the ability to use twigs held in their beaks to pry insects out of cavities in the wood. Another highly divergent Galapagos finch species is the warbler finch; with its thin, pointed bill, this finch forages for insects on bushes, living very much like members of the New World warblers (Family Parulidae).

The Galapagos finches have diverged mainly in terms of the size and shape of their beaks, although also in their overall body size. Otherwise, they all continue to resemble each other—often to a confusing degree. In larger-scale adaptive radiations, far greater anatomical divergences commonly evolve. For example, the Hawaiian Islands provide the scene for a number of adaptive radiations among its native birds, insects, and plants. The Hawaiian honeycreepers (a subfamily of finches, as are the Galapagos finches) are considered by some to be perhaps the most famous example of an adaptive radiation. The full extent of the radiation of the Hawaiian honeycreepers will never be known, because many species have become extinct as the result of human disruption of their habitat—most notably including importation of mosquitoes. Most honeycreeper species are currently severely threatened, able to survive only in the ever-shrinking forests of native plant species in the higher elevations in remoter regions of the islands where agriculture has not yet taken over.

Ornithologists first thought that the Hawaiian honeycreepers belonged to several different families, so great has been their divergence from the common ancestor (see, for example, Pratt, Bruner, and Berrett, 1987, p. 295). Although there is a group of them that, like the Galapagos finches, remain confusingly similar (these are the "small green birds"), a group of nectar-feeding honeycreepers has evolved not only a great array of bill types but also different body sizes and, most noticeably, striking plumage. The adult iiwi, for example, has a bright scarlet body with black wings (similar to the scarlet tanager seen in summertime in North America); its bill is thin and pointed, curved downward as an adaptation for feeding on nectar from flowers of a particular size. The larger black mamo, in contrast, is all black, with a beak similar to that of the iiwi although correspondingly longer. The akohekohe, in contrast, is a large bird with a rather small beak that it uses in nectar feeding at the tops of trees. Still other honeycreepers look more like the ancestral finch and have remained seed eaters.

Yet adaptive radiations can occur on a far grander scale. Until the arrival of mankind (*Homo sapiens*) in Australia some 40,000 years ago (and perhaps earlier), the only mammals there were marsupials—mammals whose young develop in an external pouch on the mother's body. The most famous of these, of course, are the kangaroos and wallabies, which, though adapted to a form of hopping on the hind feet, nonetheless are ecologically very much like deer. Koala "bears" are also marsupials, as are the extinct thylacine "wolves" and even an extinct species of saber-toothed carnivore that looked very similar to the true saber-toothed cats of the Northern Hemisphere. Such close similarities between some of these species and their nonmarsupial counterparts are examples of *convergent evolution*. Thus marsupials evolved to play most of the roles typically played by placental mammals in North America and Eurasia.

—Niles Eldredge

See also: Convergence and Parallelism; Evolution; Galapagos Islands and Darwin's Finches; Natural Selection; Speciation

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Agricultural Ecology

The origins of agriculture can be traced back to Mesopotamia, whence it spread to the fertile crescent of southwestern Asia. In Africa, ancient climatic changes forced humans to make adaptations in their way of life. About 10,000 years ago, as drought and desertification spread from the north into central Africa, nomadic hunter-gatherers began to settle and live by fishing and planting the seeds culled from wild grains in the wet ground left behind by seasonally receding lakes. In the boundary zone between northern and central Africa, planters refined stone tools for digging and hoeing and selected those plant varieties that were most easily domesticated. Around 5000 B.C.E., a cultivated root crop, the white Guinea yam (*Dioscorea rotundata*), became the new staple food. In the northern savanna, wild millet and sorghum seeds were introduced by cereal farmers. The African agricultural revolution continued with increases in the scale of production and improvements in the food crops themselves. Nutritious oils processed from trees such as the oil palm (*Elaeis guineensis*) were an important addition to the human diet.

The resulting improvements in human health led to population growth, territorial expansion and new cultivation. Indonesian migrants settling in Madagascar, probably during the first millennium C.E., introduced bananas (*Musaceae*) and other new foods that were widely adopted in continental Africa. Like the indigenous yam tubers, bananas were propagated not by seeds but by roots and cuttings. The new staples thrived in eastern Africa, where more banana varieties were developed than in any other part of the world. In Egypt the keeping of livestock imported from the fertile crescent of southwestern Asia led to the cultivation of cereal grains such as barley, sorghum, and flax by about 5000 B.C.E. Farming in the Nile River valley made possible population growth and more complex social organization. By 2500 B.C.E., an Egyptian system was in place of overlords and land tenants working irrigated fields and orchards growing vegetables, fruits, and grains with the help of beasts of burden and improved sickles. This became the model for agriculture in the modern sense of the term.

During the era of European imperialism, colonial economic systems dependent on corvee labor in the tropics replaced small-scale local farming with large plantations and monocropping for export. France tapped rubber in southeast Asia, England planted tea in Ceylon, and the United States raised sugar cane in Hawaii. In the colonial world, much traditional subsistence farming was replaced by commercial operations that took advantage of cheap labor and abundant resources while returning little of value to indigenous laborers. The industrial revolution created a huge demand for labor and the resources on which production was based. Mid–nineteenth century textile mills in England were dependent on cotton imported from the slave labor plantations of the southern United States. Some of the most violent and turbulent upheavals of twentieth-century social movements found their popular base in land reform programs that targeted the structural inequities of colonial systems.

Traditional swidden (slash and burn) methods of shifting cultivation in the tropics allowed soils to be replenished by lying fallow for a period of years after cyclical harvesting of rotated crops. Although these time-tested methods have usually been thought to minimize biodiversity, evidence shows that shifting cultivators also preserves wild species as additional resources when economic opportunity permits. Asian forests are mostly old growth that had been cleared in earlier times, by human activity or natural causes, and reached a state of equilibrium. Swidden tracts left to go wild also support significant animal life. In the early postcolonial era, after World War II, international efforts to alleviate chronic poverty and meet the growing food demands of an exploding world population led to attempts at modernizing and rationalizing Third World agricultural production through experimentation with high-yield seed varieties bred in laboratories and new farming techniques. The Green Revolution of the1960s, which introduced genetic monocrops in proprietary seedless variants, produced spectacular short-term results but ultimately did more harm than good. The new methods both failed to produce sustainable harvests and, in the long run, depleted both soil fertility and available seed stock. As a result, once-fertile lands were left barren, and farmers were unable to replenish their crops by the traditional means of saving seeds culled from previous annual harvests. In the biotech farming of today, intellectual property issues are coming to the fore as the adoption of patented super-seed varieties enhances the structural dependency of Third World farmers and accentuates the need for agricultural reform. In technologically advanced farming of specialized high-yield varieties, as practiced by commercial agribusiness interests in the United States and Australia, maintenance of crop diversity helps in the cross-pollination of plants, the control of pests, and the decomposition of organic matter in the soil.

The existing diversity of crops worldwide, selected over 10,000 years of domestication and cultivation, is rapidly diminishing. In North America native farmers first grew Mesoamerican varieties of maize, beans, and squash; in the era of colonization they switched to domesticated European plants. Today the breadbasket of the North American plains is the most productive agricultural land in the world, providing food for millions. Nevertheless, market-driven tendencies toward reliance on massive plantations of single varieties—such as the golden russet potato, favored by fast-food outlets for french fries because of its uniform appearance—reduce the gene pool and leave crops with a dangerous lack of resistance to blight. The value and utility of extinct crops can be inferred from the fact that they were once raised domestically. Their surviving progenitors in the wild might be adaptable to increase the genetic diversity and long-term viability of domestic varieties.

European agriculture is relatively low in biodiversity. Over the past millennium, the variety of species in western and central Europe has declined, probably because of the self-contained character of farms. A wide range of crop species were introduced between the eighteenth and twentieth centuries, along with the adoption of technological advances originating in Britain and the lowland countries of western Europe. More recently, increased mechanization has combined with rising costs and falling prices, driving European farmers to seek increased efficiency and higher yields by specializing in a select few crops. According to the UN's Food and Agriculture Organization, rural livelihoods are rapidly changing, becoming far less dependent upon agriculture than is commonly supposed. In Africa south of the Sahara, farming accounts for between 50 and 70 percent of income, while in the southern part of the continent that figure is as low as 10 to 20 percent. Biodiversity of food sources remains relatively high in sub-Saharan Africa, with 60 wild grass species used for food. In Botswana, the agropastoral Tswana people obtain food from 126 plant species and 100 animal species. The maintenance of a wide variety of crops can ensure a steady if modest food supply that is reliable and resistant to the vagaries of climate change. In southern Africa, gradual mixed plantings of endemic species are proving more successful at weathering drought and erratic rainfall than many imported seeds planted according to the calendar.

The developing field known as agroecology takes a systemic ecological approach to the analysis of farming. Its practical application is to promote minimization of energy input and maximization of useful output, while avoiding the negative effects of pollution and depletion of resources. New ecological studies suggest that African rangelands are less stable, less prone to inevitable desertification, and more resilient than previously believed. Local ethnographic knowledge supports the observation that these ecosystems are subject to sudden drastic and unpredictable environmental swings in aridity, erosion, and carrying capacity, rather than slow decline. Human engineering has transformed deserts into irrigated gardens (as in Israel), developed rural agriculture through electrification (as in Egypt's Nile River valley), and dramatically modified soil fertility, the nutritional value of crops, and the gene pool of seeds.

In the Green Revolution, so-called miracle rice produced temporarily high yields, but the high amount of nutrients needed to grow it placed an untenable strain on the soil. The lack of available seed made the damage incalculably more severe. On the Indonesian island of Bali, farm lands could no longer reliably produce the sustainable harvests grown for many generations on terraced rice fields. Outside agronomists did not have a clear understanding of how the calendar of the Hindu ritual cycle, controlled by the priests of the Balinese water temples, regulated the flow of irrigation and the agricultural cycle. The religious ceremonial not only is a symbolic representation of social cooperation but also controls the timing of planting and harvesting in phase with the seasonal climatic rounds. The separation of religion and ecology, in this case, was a Western mode of conceptualization whose imposition caused material harm to the ecology of Bali and the livelihood of the Balinese. Anthropologists and other researchers were able to mediate this conflict between the guardians of traditional culture on the one hand and officials responsible for development on the other, furthering the goals of productivity and modernization as well as the continuation of customary religion and social organization. Cost-benefit analyses must take local patterns, social organization, and cultural values into account before drastic change is instituted. By not rushing to devalue and abandon traditional agricultural systems before understanding their integrative ecological functions, a balanced biocultural ecosystem was maintained in Bali.

Present efforts sponsored by the UN Food and Agricultural Organization to sustain crop biodiversity have the goal of attaining food security, defined as universal availability, stability, and access. By that standard, more than 800 million people today are food insecure. Land use and land cover analyses are the first steps to the integrated management of environmental, economic, and social functions. By combining local wisdom and resources with scientific techniques and international aid to encourage the preservation and cultivation of agricultural biodiversity, societies in the future should be able to reap the benefits of sustainable farming practices.

—*Thomas R. Miller*

See also: Agriculture and Biodiversity Loss: Industrial Agriculture; Agriculture and Biodiversity Loss: Genetic Engineering and the Second Agricultural Revolution; Agriculture, Origin of; Agriculture: Benefits of Biodiversity to; Alien Species; Biogeography; Coloniality; Conservation Biology; Cultural Survival, Revival, and Preservation; Dams; Deserts and Semiarid Scrublands; Economics; Ethnoscience; Food Webs and Food Pyramids; Industrial Revolution/Industrialization; Land Use; Organizations in Biodiversity, The Role of; Population, Human, Curbs to Growth; Sustainable Development

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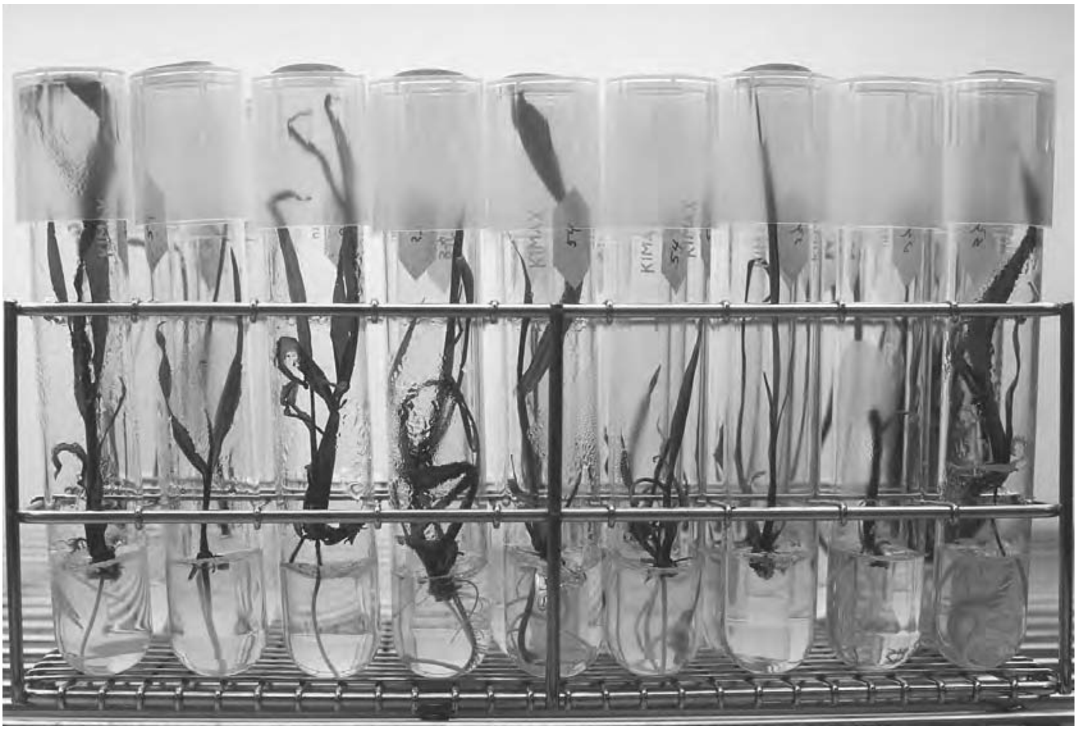
Agriculture and Biodiversity Loss: Genetic Engineering and the Second Agricultural Revolution

Genetic engineering has many and varied effects on biodiversity, but its likely long-term result will be a decrease in genetic variability of crops and other species. In a narrow sense, the large-scale deployment of genetically engineered crops that began in the mid-1990s has increased the genetic diversity of target crops by introducing wholly novel DNA segments (transgenes). When successfully introduced from another species, a transgene causes a plant to express a new trait, with little or no change in diversity among the 10,000 to 100,000 other genes native to the species. Probably more significant than the direct effect of gene insertion, however, are the indirect effects of transgenes on the biodiversity of the target crop, other crops, and other life forms. Hard data are scarce, and the direction and magnitude of biotechnology's effect on biodiversity will be evaluated accurately only after transgenes have been deployed for decades. The eventual consequences will depend on the biotechnological techniques



Genetically engineered corn plants grow in controlled conditions at the SunGene Technologies laboratory, Palo Alto, California. (Lowell Georgia/Corbis)

employed, the genes selected for manipulation, and the ways in which transgenic crops are used. Nevertheless, when viewed as an extension of industrial agriculture, genetic engineering is likely to accelerate homogenization of the biosphere.

The explicit goals of biotechnology, like those of traditional plant breeding, are to increase agricultural productivity and profitability, and often to improve human nutrition. The consequences for biodiversity are largely unplanned and indirect. Although some predictions can be made, virtually all results of research on biotechnology's environmental impact are hotly debated among scientists.

Early research suggested ways in which transgenes could expand the diversity of crops and associated species. By increasing productivity on land already under cultivation, transgenic crops could forestall expansion of agriculture and the displacement of more diverse natural vegetation. Introduced genes for pest resistance have augmented the collections of naturally occurring genes available to plant breeders, giving them more options in developing sustainable resistance. Genetic resistance, in turn, may reduce the use of broad-spectrum pesticides and the consequent loss of diversity in nontarget species. Engineering of minor crop species to produce economically valuable enzymes, vaccines, or hormones could allow farmers to diversify the range of crops they grow. Manipulation of genes that control chromosome pairing or other aspects of meiosis could allow breeders to produce fertile hybrids between previously incompatible species.

These potential contributions likely will be canceled out in the long term by genetic engineering's negative effects on biodiversity. Historically, a phenomenon known as genetic erosion has occurred when crop varieties with high yields or other traits desired by farmers have displaced more genetically diverse traditional varieties. Transgenic technology is the latest in a long line of genetic tools developed over the past century, and it will enhance the power of modern plant breeding to cause genetic erosion. In the United States, seed of nontransgenic maize, soybean, and cotton, for example, is now less available because of the wide adoption of transgenic hybrids and varieties.

Diversion of research funds from traditional plant breeding into genetic engineering can further restrict the genetic diversity of farmers' seed sources. Development of a transgenic variety can cost more than twenty times as much as the breeding of a variety through the traditional route of hybridization and selection. Given such a ratio, a breeding program could release to farmers either five transgenic varieties or 100 nontransgenics for an equivalent investment. Whatever their agronomic performance, the 100 varieties are almost certain to encompass more genetic diversity than the five transgenics.

Transgenes may cause ecological disruption and loss of biodiversity that goes well beyond genetic erosion in the farmer's field, however. Some evidence for this comes from the first transgenes to be deployed over large areas of cropland—a gene for resistance to the herbicide glyphosate in soybean and one coding for the *Bt* toxin that confers insect resistance in maize and cotton. Spraying a field with glyphosate eliminates virtually every plant of every species, except for engineered crop plants carrying the resistance gene. Evaluating the consequences for local or regional biodiversity will require many years, but some computer models have predicted reduction of plant and animal populations. Transgenic maize or cotton plants that produce the *Bt* toxin in all plant tissues at all stages of growth can dramatically reduce local populations of toxin-susceptible insects. Research has demonstrated toxicity to parasites and predators that attack insects feeding on *Bt* crops. Concern is compounded by reports that the toxin persists well after harvest, bound to soil particles where it could alter populations of soil microorganisms. However, despite such studies, the long-term effect of *Bt* on diversity is unknown. Some loss might be avoided by engineering *Bt* genes to produce the toxin only when the plant is being attacked and only in the tissue being eaten by the insect.

There is widespread evidence of gene flow through natural cross-pollination between crops and related weed or wild species, and transgenes will be transferred in the same way. There is no consensus, however, on what that will mean for biodiversity. In one catastrophic scenario, an escaped transgene might allow a wild or weed species to increase its density and range greatly, displacing other species. Evolutionary theory suggests that a randomly introduced gene has a higher probability of reducing than of increasing a weed's fitness, but whatever the average effect of a particular gene on fitness, we cannot rule out the possibility that a "superweed" may emerge once many different species are exposed to transgenes in many different ecosystems.

Monocultures lack the inherent protection against fungi, bacteria, viruses, arthropods, and weeds that comes with the genetic variability of natural ecosystems or some traditional farming practices. Genetically uniform crops must be protected against pests, and that is most often accomplished through incorporation of resistance genes through breeding, or by the use of chemical control. As illustrated by the transgenes for glyphosate resistance and the *Bt* toxin, biotechnology is an enhanced method for applying these same control strategies. Therefore its successful application can permit farmers to continue sowing monocultures, instead of turning to pest-control methods that employ genetic diversity, such as variety blends, polycultures, or crop rotation.

—Thomas S. Cox and Wes Jackson

See also: Agriculture and Biodiversity Loss: Industrial Agriculture; Agriculture: Benefits of Biodiversity to

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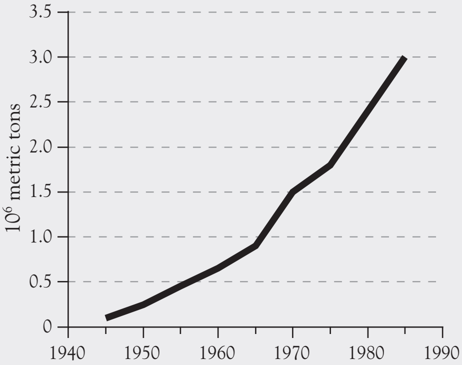
Agriculture and Biodiversity Loss: Industrial Agriculture

Over the last fifty to eighty years, most of the world's agriculture has been transformed into an "industrial agriculture." In the 1920s machines began to replace human and animal power for preparing soil, planting, weeding, and harvesting crops. Since the 1930s, newly developed, high-yielding crop varieties have been replacing traditional varieties. Most of these new varieties require inputs such as irrigation, pesticides, and fertilizers. Since the end of World War II, industrial agriculture has increasingly applied synthetic pesticides and fertilizers (Figures 1 and 2). In the 1960s, this

Figure 1

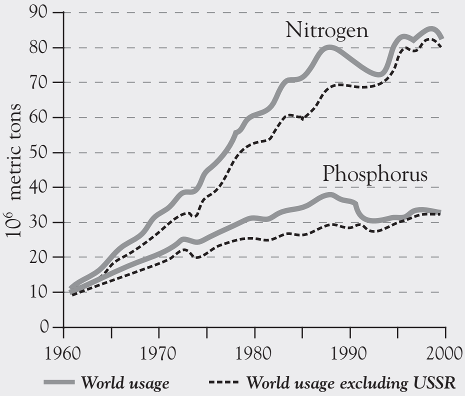
Global Pesticide Production 1945–1985



Source: Modified from Tilman, David, et al. 2001. "Forecasting Agriculturally Driven Global Environmental Change." *Science* 292–284.

Figure 2

Global Fertilizer Use 1960–2000



Source: Food and Agriculture Organization of the United Nations. http://apps.fao.org (Accessed July 17, 2002).

Note that the apparent leveling of world fertilizer use since 1990 is a result of the collapse of the Soviet Union and subsequent decreases in Soviet fertilizer use. Fertilizer use for the rest of the world has continued to increase at unsustainable rates.

agricultural revolution spread to developing countries in a process referred to as the "green revolution."

This transformation has been tremendously successful at producing food. Global grain production doubled from 1945 to 1980. Today, more food is produced per person than ever before in earth's history. This success, however, has come with costs to the sustainability of agriculture and to biodiversity.

Over the next few decades humanity must develop forms of agriculture that can meet the needs of a growing population while minimizing our impact on the environment. To do so, agriculture must be done more sustainably by protecting soil fertility; must decrease dependence on fertilizers, pesticides, fossil fuels, and irrigation; and must integrate agricultural and natural areas so farms can be reservoirs and corridors of biodiversity.

Loss of Crop and Genetic Diversity Creates More Uniform Ecosystems

Mechanization requires farms to have uniform crop types, structures, and management practices (for example, planting and harvesting dates). As a result, crop diversity has declined on most farms over the last century. For example, traditional farms, especially in the tropics, may include grains, root crops, vegetables, spices, medicinal plants, livestock, and trees for lumber, fruit, and firewood. In contrast, most modern farms are monocultures—that is, they have only one crop species planted over a large area. Farms with low crop diversity have poor "associated diversity" of species that were not assembled directly, such as insects, birds, and soil organisms.

The use of monocultures increases a farm's dependence on pesticides. Pests such as insects and pathogens (disease-causing organisms) can find their food sources more easily in monocultures than in diverse crop mixtures. Monocultures also have lower populations of the natural enemies of pests, such as spiders, wasps, dragonflies, and predatory beetles.

The genetic diversity of crops has declined with industrial agriculture. Although hundreds of edible plant species have been important in traditional crop systems, today only three crops—rice, wheat, and corn—provide 60 percent of our plant-based diet worldwide. Diversity within crops also has declined because traditional varieties, or landraces, have been replaced by a few high-yielding varieties. This process is called genetic erosion. According to the Food and Agriculture Organization of the United Nations, 75 percent of crop diversity was lost during the twentieth century. Modern varieties have supplanted traditional varieties for 70 percent of the word's corn, 75 percent of Asian rice, and half of the wheat in Africa, Latin America, and Asia. In 1950, India had 30,000 wild varieties of rice, but by 2015 only 50 are expected to remain.

The loss of genetic diversity within crops is important for plant breeding. Much of the increased yield in modern crops is owed to the genetic diversity in traditional varieties. Landraces of many crops have provided the genes needed for pest and disease resistance, or to adapt crops to poor soils, drought, and cold temperatures. By losing landraces we are undermining our ability to adapt crops to future conditions, including climate change.

Pesticides Kill Pests and Wildlife Both on and off the Farm

The U.S. Environmental Protection Agency estimates that 2 billion kg of pesticides are applied in the United States each year, and 10 billion are applied around the world. Use of synthetic pesticides increases our dependence on them in a process called the "pesticide treadmill." Insecticides and fungicides do not destroy only pests; they also kill their natural enemies.

Three combines harvest a large wheat field, Washington State. With the mechanization, chemical fertilizers and pesticides, and irrigation of industrial agriculture, more food is produced than ever before in earth's history. This success, however, carries tremendous costs to the sustainability of agriculture and to biodiversity. (W. Wayne Lockwood/Corbis)

The natural enemies of insect pests include other insects that are parasites and predators, as well as pathogenic fungi. Pest species evolve resistance to pesticides much faster than their enemies, and thus pest populations quickly recover. Loss of natural enemies also leads to outbreaks of "secondary pests"—species that are not a problem until pesticides eliminate their natural enemies. As a result of pest resistance and secondary pest outbreaks, increasing amounts of pesticides must be applied, or more toxic chemicals must be developed. This is an arms race that we are losing. Despite the constant increase in pesticide use (Figure 1), loss of crops to insect pests was greater in 1989 (13 percent loss) than in 1945 (7 percent loss).

Pesticides have impacts far beyond their target organisms. Scientists at Cornell University estimate that 67 million birds are killed each year in the United States from pesticides. Many individuals of some bird species have died after eating sprayed insects. Pesticides from agriculture flow into aquatic systems via runoff of surface water, soil erosion, and drainage into groundwater. Pesticide residues in streams, lakes, bays, and coral reefs kill aquatic plants and zooplankton (microscopic animals) that fish require for food. More directly, very low concentrations of pesticides in water have been shown to increase the mortality of young fish and amphibians.

Pesticides and other toxins have an important effect on wildlife through "bioaccumulation." Certain kinds of pesticides are persistent—that is, they do not break down as they pass through the food chain. They can be taken up by small aquatic organisms and insects and are then passed on to the fish that eat them. Those fish are eaten by larger fish, which are eaten by predators such as eagles, pelicans, seals, and bears. The toxins become increasingly concentrated in the higher levels in this food chain, so top predators accumulate dangerous concentrations. The decline in the bald eagle population in the 1900s was linked to bioaccumulation of persistent pesticides, especially DDT (dichlorodiphenyltrichloroethane). Such toxins affect the eagles' nervous systems and cause their eggshells to become fatally thin. The use of DDT was banned in the United States in the 1970s, and eagles have since recovered. Today many persistent pesticides have been replaced by alternative chemicals that are more short-lived—but more acutely toxic.

Wildlife has also been harmed by endocrine disrupters—toxins that interfere with hormones that regulate animal development. These toxins include some persistent pesticides and industrial pollutants. They appear to be linked to developmental abnormalities that have been increasingly found in wild animals, especially impaired growth of immune and sexual organs. Such deformities are appearing in many threatened species, including alligators, panthers, polar bears, and dolphins. Endocrine-disrupting insecticides have been linked in frog populations to extra limbs emerging from the stomach and neck.

Fertilizers Lead to the Depletion of Oxygen in Aquatic Ecosystems

The use of synthetic fertilizer increased seven to eight times over the last forty years (Figure 2). The major effects of fertilizer come from nitrogen (N) and phosphorus (P). Nitrogen pollution is now the single greatest source of water pollution in lakes, rivers, and bays. About half of the nitrogen and phosphorus applied is not taken up by crops; it is left in the soil or leaches into ground and surface water. In industrialized (First World) countries, about 70 percent of crops are fed to livestock, which are typically raised in confined conditions such as feedlots and "factory farms." The animal waste is concentrated in a small area and becomes a further source of nitrogen pollution.

Excess fertilizers lead to "eutrophication." As fertilizers enter water systems, they cause an explosion of growth by algae and aquatic plants. When those organisms die they are decomposed by microbes that quickly deplete the oxygen in the water, thus killing animals such as fish and shellfish.

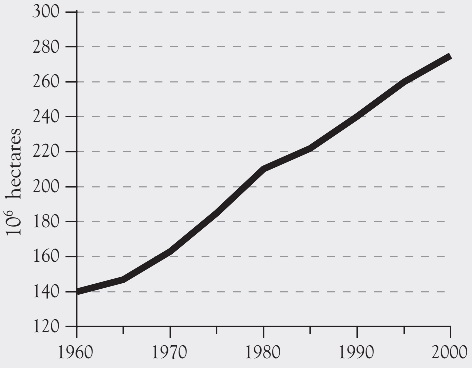
Fertilizer runoff from industrial agriculture has created forty large, oxygen-starved "dead zones" around the world. A dead zone the size of New Jersey forms at times where the Mississippi River drains into the Gulf of Mexico. This zone receives fertilizer from a tremendous agricultural area, including Kansas, the Dakotas, Iowa, and Illinois.

Irrigation Threatens Aquatic Ecosystems

Industrial agriculture consumes increasing amounts of freshwater (Figure 3). Humans now consume about half of the earth's available freshwater, and 70 percent of that goes to agriculture. When irrigation removes too much water from rivers, streams, and wetlands, habitat for fish and wildlife is depleted or destroyed. In the eighteen U.S. states that depend most on irrigation, 70 percent of the water flowing in streams and rivers has been depleted. Dams and the destruction of aquatic habitat have played a part in severely reducing populations of Pacific Coast salmon as

Figure 3

Global Irrigation 1960–2000



Source: Food and Agriculture Organization of the United Nations. http://apps.fao.org (Accessed July 17, 2002).

well as steelhead and cutthroat trout in the northwestern United States.

Conserving Biodiversity: The Solutions

Creating More Sustainable Agriculture to Protect Natural Areas

One key to conserving global biodiversity is to improve the sustainability of agriculture, especially by protecting soil fertility. If farmers maintain productive soils, fewer natural areas will have to be converted to agriculture. It is most critical to reduce soil erosion, which has destroyed one-third of the world's farmland over the last forty years. Techniques for improving soil fertility may have the greatest impact on small farmers in the tropics. Such farmers often deplete the soil after only a few years, requiring them to clear more land.

Several practices improve soil sustainability. Erosion is reduced by limiting the amount of plowing. Soil is protected and held in place by the constant presence of vegetation, such as cover crops, perennial crops, or strips of trees and native plant species. Soil fertility can be improved by interplanting or rotating food crops with plants that increase soil nutrients and organic matter.

Reducing Pollution from Agricultural Chemicals

Many studies have shown that agricultural chemicals can be replaced by alternatives that are friendlier to biodiversity. Increased crop diversity reduces the need to defend crops against diseases and pests. Mulches and cover crops can replace herbicides for weed control. Some bacteria and fungi provide nutrients to crops, and promoting them can reduce the need for synthetic fertilizers. Likewise, synthetic pesticides can be effectively replaced with biocontrol (beneficial insects, fungi, and bacteria) and biopesticides (products derived from plants, fungi, and bacteria). These agents have relatively low toxicity and do not accumulate in the food web.

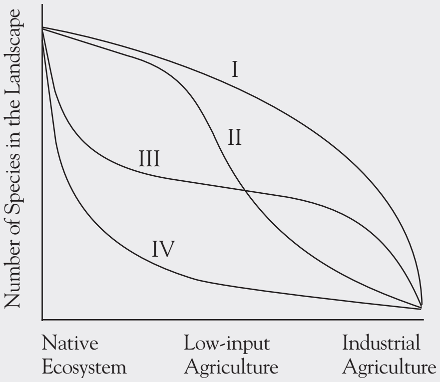
It has been argued that reducing chemical inputs would harm biodiversity. Without chemical inputs, farms may be less productive, and thus more native forests and grasslands would have to be converted to agriculture. Most evidence, however, points the other way. In the tropics, where biodiversity is the greatest, industrial agriculture has promoted export crops rather than food for local consumption. Over the last twenty years, cropland in Brazil has increased by 176 percent in order to plant export crops such as soybeans, wheat, coffee, and oranges, which are grown on large-scale, industrial farms. More important, converting to low-input agriculture does not necessarily reduce yields. Over the last fifteen years, both Indonesia and Vietnam have dramatically reduced pesticide applications—by as much as 72 percent—while rice yields have remained high or even increased. Since 1989, Cuba reduced its use of pesticides and fertilizers from 60 to 80 percent, but it produces more food now than it did in the 1980s.

Designing Agriculture That Contributes to Biodiverse Landscapes

Farms provide habitat for wildlife by increasing plant diversity and by mimicking the native ecosystems around them. Crop mixtures, hedgerows, wood lots, and strips of native vegetation attract wildlife by increasing the structural and species diversity of farms. Some types of low-input agriculture can serve as habitat for many native species (Figure 4, curves I and II). For example, traditional coffee farms have tall canopy trees mixed with the crops, while modern farms are chemical-intensive monocultures. The traditional farms maintain very high diversity of birds, bats, terrestrial mammals, and insects, and they serve as refuges for species found only in forest. In contrast, modern coffee farms have very low biodiversity.

Figure 4

The Effects of Agricultural Intensity on Biodiversity



Source: Modified from Vandermeer, John, and Ivette Perfecto. 1995. *Breakfast of Biodiversity: The Truth about Rain Forest Destruction*. Oakland, CA: Food First.

Note: How agriculture affects associated biodiversity depends on the type (intensity) of agriculture. When low-input systems mimic the native system, as shaded coffee farms do, farms can retain most biodiversity (Curves I and II). In contrast, when low-input agriculture includes more severe disturbance, such as soil tillage or extensive deforestation, it is likely to reduce biodiversity more rapidly (curves III and IV). In all cases diversity is lowest when the agricultural system is most industrialized.

At the landscape level, agriculture can best preserve biodiversity when it becomes part of a matrix connecting natural areas. Only about 10 percent of the earth's land area is protected for conservation. The choice of land uses for the other 90 percent will therefore be critical. Biodiversity cannot be preserved effectively if natural areas are isolated islands amid a sea of uniform, chemically drenched industrial agriculture. Rather, agricultural areas must serve as corridors for species to move among natural areas, and as refuges in times of stress.

Consumers concerned about biodiversity can influence agricultural practices when they purchase food. Several organizations certify and label food products that provide financial incentives to farmers who are reducing their environmental impact and preserving diversity.

—*Christopher M. Picone and David Van Tassel*

See also: Agriculture and Biodiversity Loss: Genetic Engineering and the Second Agricultural Revolution; Agriculture: Benefits of Biodiversity to

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Agriculture: Benefits of Biodiversity to

People depend on biodiversity for healthful, sustainable agricultural systems. Biodiversity is the ultimate source of all cultivated plants and domesticated animals, and it provides essential assistance in maintaining crops and pastureland. Farmers save billions of dollars each year thanks to the services of pollinators, microbes that help create productive soil, and natural predators that reduce the need for pesticides.

For thousands of years humans have used the natural diversity of plants and animals to increase the productivity of crops and livestock. Traditionally, at the end of a harvest the farmer will select seeds from the "best" plants—those that grow well in the farmer's fields (that is, those adapted to the local climate or those most resistant to prevalent pests or disease). Livestock ranchers make a similar effort, breeding animals, say, for faster growth or leaner meat. This "selective breeding" depends upon the existing genetic diversity of individuals in a species to create better strains or livestock. As agriculture has modernized over the last fifty years, new methods have developed to achieve these goals.

Genetic engineering enables scientists to create new breeds rapidly by inserting specific genes into a plant or animal to obtain a desired trait. Unlike selective breeding, however, genes can be selected from any species. For example, "Bt corn" is modified by adding a gene from the soil bacteria *Bacillus thuringiensis*, which allows it to produce Bt toxins, an insecticide against the European corn borer. Geneticists look to nature for inspiration when creating new breeds, and biodiversity is their genetic library. Despite these new techniques, existing crop strains and domesticated animals, their wild counterparts, and closely related plants or animals are still essential for breeding. Unfortunately, we are rapidly losing these sources of genetic inspiration. As agriculture has become industrialized, we are sacrificing the diverse cultivars (or landraces) and breeds that have developed around the world. Habitat loss threatens the regions where domesticated crops and animals originated. Conserving this biological heritage is critical to future agricultural production.

Biodiversity acts as insurance for agriculture. Changing climates may require drought-resistant or salt-tolerant crops, and biodiversity helps ensure that crops can adapt to future environments. Although humans have used more than 12,000 wild plants for food (Burnett, 1999), today 20 species support much of the world's population. Although there are 235 species of potatoes, only seven are cultivated. Those other species may one day become a major source of food. There are also many cases in history when a widely grown crop has failed because of disease, with devastating consequences. One famous example is the Irish potato famine, which led to the deaths of a million people. In the mid–nineteenth century, a blight (or funguslike pathogen) destroyed much of the crop. European potato crops were particularly susceptible to infection, since they had all originated from only a few sources and thus were genetically very similar. To combat the disease, a long search began to find a plant resistant to the blight. By the early twentieth century a related plant in Mexico provided the solution, and hybridizing that plant with potatoes produced a resistant strain. Unfortunately, it was not a permanent solution. Today potato blight is once again a concern, and the solution likely lies in existing biodiversity. As the world's crops become increasingly homogenized, it is important to remember the lessons we have learned: systems with higher biodiversity are more resilient, and ultimately biodiversity may solve these crises.

Biodiversity provides many services to agriculture, such as pollination, soil microbes, and natural predators. Approximately 90 percent of flowering plants depend on pollinators to reproduce, and pollination is critical to most major crops around the world (Buchmann and Nabhan, 1996). Pollinators play such a key role for crops that their loss is considered a threat to the security of the world's food supply. Insects—especially beetles, bees, and wasps—are the largest group of pollinators; however, some birds and bats are also important pollinators. Studies have shown that as pollinators disappear there is a loss in yield and harvest quality in many crops, from blueberries to pumpkins. Even crops that don't need pollination to reproduce, such as cotton, produce increased yields when pollinated. Economic losses to crop yields in the United States from the decline of honeybees alone are estimated at $5.7 billion a year (Southwick and Southwick, 1992). Replacing pollination with other methods is virtually impossible. For instance, greenhouse tomatoes were originally hand-pollinated, but that tedious process has been mostly replaced by commercially raised bees.

Successful farming depends on healthy soils, too, and it is biodiversity that helps form soil and improve it for crop production (Pimental et al., 1995). Bacteria, algae, fungi, worms, and an array of invertebrates living in soils help recycle and redistribute nutrients. They aerate soil, keep nutrients close to the surface, moderate water flow, and as a result, enhance plant productivity. Among these organisms, nitrogen-fixing bacteria are particularly important to agriculture, as nitrogen is essential to plant growth and is often a limiting factor. These bacteria are the only organisms that can convert atmospheric nitrogen into forms that plants can use. Certain plants (such as soybeans) harbor these bacteria in their roots as symbionts. During fallow periods, these plants are still used to help naturally enrich soils. Fertilizer, the human equivalent of nitrogen fixation, is highly inefficient compared with the natural process. It is expensive to produce and much of it doesn't reach its target, washing away instead and polluting aquatic systems.

Like natural fertilizers, natural pest control is important to agriculture. Pests destroy an estimated 25 to 50 percent of the world's crops each year (Pimentel 1991). Without the natural predators that control agricultural pests, these figures would be even higher (Naylor and Erlich, 1997). Natural pest control also has many advantages over chemical controls such as pesticides and herbicides. Pesticides are usually nonselective, killing both the pest and helpful organisms such as pollinators. Pesticides can create a "new problem," as pests may develop resistance over time, forcing farmers to change to another chemical to combat the same pest. Like fertilizers, application of pesticides and herbicides is inefficient. Realizing their limitations, farmers are turning to biological methods of controlling pests.

—*Melina Laverty*

See also: Agriculture and Biodiversity Loss: Industrial Agriculture; Agriculture, Origin of; Bacteria; Nitrogen Cycle; Soil; Topsoil Formation

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Agriculture, Origin of

The archeological record reveals that around 8000 B.C.E., a gradual shift took place in the nature of recovered plant and animal remains, one that directly reflects the novel emergence of large groups of sedentary humans. Such groups, by desire or necessity, consciously decided to rely on domesticating wild grasses and animals for their survival. For this reason the Fertile Crescent region has long been regarded as the cradle of civilization—that is, the place where agriculture originated. (The modern-day boundaries of the Fertile Crescent include its western edge at the Mediterranean coast, its southern edge the Negev Desert, north by the high-elevation forests of Turkey, and east at the high-elevation forests of the Zagros Mountains). But recent research now shows that agriculturally based economies emerged in seven geographically distinct regions around the world at different times in the last 10,000 years. These regions—the Levantine corridor, North and South China, Central and South America, the eastern United States, and sub-Sahara Africa—each contributed their own combination of indigenous domesticates of plants and animals.

Research into why hunter-gatherer economies changed over to a more permanent, sedentary economy based on farming lacks reliable evidence for the numerous theories currently proposed. Many believe that dramatic increases in human populations created tough ecological demands that were alleviated through agricultural techniques simply for its predictability in providing enough food for the ever-growing communities. Others argue that sea-surface temperatures indicate changes in climate between 10,000 and 5,000 years ago, changes that may have impelled farming communities to combat long-term oscillations in global weather patterns that altered the local ecological niches of plants and animals. Since each of the seven regions started domesticating and cultivating different plants and animals at different times, the explanation for why agronomy began and prospered will not likely be found in any single prime mover. Instead, the reasons behind this gradual transformation are more likely to be found in a complex host of artifacts recovered from the ecological and archaeological records for each region.

Domestication and Agriculture

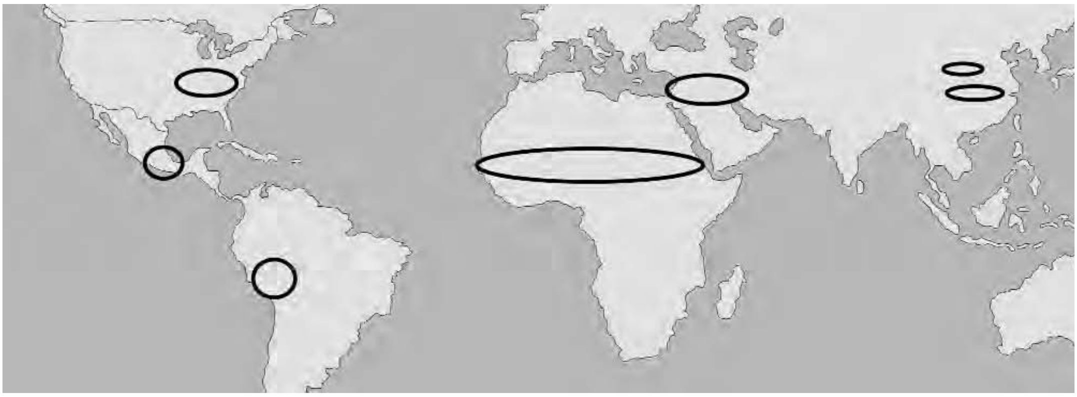
Domestication is a process through which human intervention generates novel plant and animal species that are morphologically distinct from their wild precursors. The results are not just larger seeds or smaller animals; rather, the captive populations, be they plant or animal, undergo artificial selection by their captors, as well as automatic changes that occur naturally in order for them to survive. These changes do not only occur at the phenotypic level; they also, naturally, originate at the molecular level. But more important, domestication marks an adaptive syndrome that involves significant changes in the long-term relationships between humans and the plants and animals they have domesticated.

Typically, when seed plants are domesticated—which, by the way, includes most major crop plants grown today—two automatic responses occur. Plants are selected for those that (1) retain their seeds long enough to be harvested and (2) package their seeds in convenient clusters. These plants are then continuously selected over time for those seeds that sprout more quickly, grow quickly toward the sunlight, and quickly produce shade to outcompete their neighbors. This means that domesticated seeds tend to have thinner, more permeable seed jackets and have greater developmental food reserves for quick growth than their thick-skinned wild precursors, which can survive several seasons in topsoil before sprouting. Obviously, Late Holocene humans needed plants that they could control, both in growth and yield. In the achievement of that goal, another important part of plant domestication involves soil science. Our early agronomists unknowingly altered soil texture, mineral content, and acidity by ridding the land of other indigenous plant life: plants we typically refer to as weeds. Once started, the process had to continue, or else it would end in disaster. This process probably started long before the advent of agriculture, when groups of hunter-gatherers may have burned particular areas knowing that after a fresh burn, the soil is rich and the plant foods they were familiar with grew back quickly and with higher yields.

Agriculture is defined as the practice of large-scale soil cultivation. Archaeobiologists today believe that small groups of semisedentary hunters and gatherers established home bases in regions with rich aquatic habitats, which would also have provided access to a variety of animal protein, such as fowl, fish, and reptiles. Over time, the knowledge gained of wild plant (and animal) resources allowed for the selection of seed stock for its propensity to grow quickly and produce greater yields. This enabled humans to stay in one place throughout the year. Paradoxically, having the ability to control the growth, and subsequent storage, of food resources over long periods led to major increases in the size and number of groups.

The domestication of wild grasses provided a reliable source of plant foods, which concomitantly led to the domestication of certain animals, such as goats and sheep, whose ways of life were already well known, since they had been hunted for hundreds of years. Animals were probably chosen on a trial-and-error basis, with those of interest being easy to cull, manage, and breed. Domestication of animals is easily identified in the archaeological record by comparing wild precursors to domestics. Domestic animals—sheep, pigs, and goats, for instance—become smaller in overall size. Body parts are identifiably smaller, because of the selecting for smaller, docile animals that are easier to care for. For instance, cheek teeth in wild pigs are extremely large, and their skulls are long and narrow. After domestication, teeth are half the size of that seen in the wild pig, and their skulls are much shorter. In the archaeological record, sites at which domestication first began show evidence of typical husbandry techniques, such as a predominance of older females over younger males. The skeletal evidence tells us that most male animals were killed earlier in life than females, because males typically become more difficult to handle as adults. Ultimately, the emergence of agriculture and the domestication of wild artiodactyls provided very successful periods of socioeconomic growth that obviously aided in human population explosions never before witnessed. However, the advent of agriculture also harmed regional animal and plant biodiversity, setting the stage for another major extinction event. Agricultural economies have also contributed to numerous osteological pathologies in the human skele-

Map 1



Origins of Agriculture

Seven regions around the world show evidence of independent agricultural origins.

ton that are atypical when compared with skeletons from prefarming archaeological sites.

Seven Agricultural Epicenters

The earliest evidence in the archaeological record of adaptation from a hunter-gatherer to an agriculturally based economy occurs in the Levantine corridor at approximately 8000 B.C.E. For this reason, considerably more discussion will be presented for that region than the others. The fossil record indicates that small groups of hunter-gatherers relied on a combination of wild plants and animals at the beginning of the changeover; eventually, as they became village-based societies, they relied predominately on domesticates. There are seven primary domesticates in the Fertile Crescent. These morphologically and genetically different subspecies of plants and animals are: barley, emmer wheat, einkorn wheat, sheep, goats, cattle, and pigs. There was no single event or place at which domesticates came into existence in the area, and none of the seven initial domesticates are known in any detail. However, each of the more than fifty archaeological sites in the region provides a slice of history that, when combined in total, provides for a clearer understanding of the advent of agronomy and animal husbandry.

Regarding the Levantine region, initial plant domestication was more prominent than animal domestication. First and foremost is emmer wheat. It was widely harvested within the same ranges as its wild precursor from Netive Hagdud, Jericho to Çayönü, Gritille, and Jarmo. Emmer wheat, as well as barley and einkorn wheat, changed phenotypically in the structure of the rachis, becoming tougher and more supple, while the grains became plumper with extra meat. Emmer wheat first showed up at Jericho in the Jordan Valley and Aswad at Damascus, in both places at approximately 7800 B.C.E. There is evidence that wild einkorn wheat was harvested at Çayönü long before it was domesticated. The significance of these particular cereal grains is their propensity for generating large yields. Wild barley is found the entire length of the Fertile Crescent. Although the domestication of barley overlaps with the two main types of wheat, two types of barley are domesticated for farming. One had two vertical rows of grain spikes, much like the wild progenitor, while the other subspecies had a six-row grain spike.

As for animals, the four main wild progenitors held distinct ranges. In terms of numbers, the primary animals domesticated were sheep and goats, with cattle coming in close behind. Pigs, on the other hand, seem to have had a unique history in the Fertile Crescent. It seems that wild pigs have an extremely wide range that includes Asia, but they were not found in the eastern portion of the Levantine corridor. It seems that pigs were probably domesticated in both major regions and brought into the eastern region already domesticated. What is clear is that in certain archeological sites, the number of bony elements increases significantly in each of these animal domesticates, depending on the localized region of the Fertile Crescent over time. Detailed archaeological research documents Çayönü as providing the earliest evidence of domesticated pigs, at about 6500 B.C.E. The timing of the domestication of the various animals, however, is in need of refinement. For example, wild cattle are known in the region from 7000 B.C.E., but domesticates show up between 6000 and 5000 B.C.E. A problem with comparing wild animals to domesticates relates to the difficulty in distinguishing between them, given the few elements left for examination. Often it is difficult to separate skeletal elements because they are so similar in overall morphology.

The second region to provide the earliest evidence of animal and plant domesticates is found in East Asia. Although the Fertile Crescent region generated a lot of interest in domesticating plants and animals, East Asia quickly followed independently, with two distinct agricultural ways of life. The first area to be discussed is the Yangtze River corridor (South China), dated at 6500 B.C.E. The Yangtze River valley provided a subtropical climate and temperature, which were ideal for agricultural economies based on rice. Rice is one of the most widely consumed foods in the world today. The origins of rice agriculture are thought to center in an extremely broad region, in which India was always considered a significant contributor. This theory was based on the current distribution of wild rice species. However, today, wild rice species are known from the southern region of the Yangtze River, of which the earliest evidence of domestication has been discovered. Dates from early farming communities suggest 6500 B.C.E. at the newly discovered site of Peng-tou-shan, while previously the site of Khok Phanom Di in Thailand was thought to be the earliest, at 4500 B.C.E. This indicates that Peng-tou-shan was operating and prospering at the same time that Çayönü was in the Fertile Crescent. The animals that were domesticated at this time were pigs, chickens, and water buffalo.

To the north of the Yangtze River one will find the Yellow River valley, which provides the third earliest evidence of farming-based societies. Most sites are found scattered among four different river systems associated with the Yellow River. The earliest sites are dated to around 5800 to 5200 B.C.E. and were discovered in the Hupei Basin. The settlements along the four rivers, while having their subtle differences, all are lumped under the P'eili-kang culture. The region is divided into basically two environmental zones: semidry highland steppe to the west, and temperate deciduous forests of the great plain to the east. The significance of the Yellow River valley P'eili-kang culture is their dependence on millet. In fact, this region provides the earliest evidence of domesticating that particular cereal grain. This northern region also shares their affinity for domesticated pigs, chickens, and water buffalo.

Several thousands of years pass before any evidence for the domestication of plants and animals appears in the New World. At approximately 2800 B.C.E., archaeological research uncovers evidence of squash, beans, and maize domestication in Central Mexico. There is a long history of human occupation in the Americas that is traceable back some 20,000 years before the present. It is thought that by 10,000 B.C.E., human settlements were established in South America at Monte Verde in Chile. Most likely, nomadic peoples in transit occupied Central Mexico long before that. Evidence from the Tehuacan Valley provides more than 20,000 corncobs that document in situ evolution of maize domestication. The earliest evidence of maize cultivation is dated at approximately 2500 B.C.E., taken from cob cores recovered at the Coxcatlan and San Marcos sites. Domesticated cob cores found in modern-day New Mexico were originally dated at 7,000 years before the present, but new radiocarbon dating techniques have refined the date to approximately 2,500 B.C.E. The tremendous importance of research in Central Mexico reveals that the domesticated maize discovered there lacks the ability to disperse kernels without assistance from humans, or possibly animals. In addition, it was once believed that a now extinct species of maize was the wild precursor to modern-day corn, but recent research convincingly proves that the contemporary wild teosinte grass that grows throughout Mexico is the progenitor.

Legumes are also known from this area, but recent dates indicate that the phaesolin group of beans were most likely independently domesticated in two regions at almost the same times: Mexico and the central Andes. Current accelerated mass spectrometry (AMS) dating techniques indicate that the common bean was probably domesticated around 500 B.C.E. In the south-central Andes at 2500 B.C.E., the principal crop plants were manioc and the sweet potato, and this is the first evidence of domesticating a rodent species (guinea pigs) as a food source. Although evidence of plant domestication dates to around 4,500 years ago, the earliest evidence of domestication activity comes from alpaca and llama remains dated to 5000 B.C.E. in the high-altitude puna grasslands of the Andes. Hunting of wild camelids species (guanaco is the wild precursor of the llama, and the vicuña of the alpaca) dates back 9,000 years. The earliest site of camelid domestication is located at the southern end of Lake Titicaca, at the modern-day Peru-Bolivia border. An intriguing discovery regarding animal domestication in South America focuses on rodents. The cuy, or guinea pig, was long considered an important food source for early hunter-gatherers, dating back to 12,000 years before the present and continuing for 5,500 years. The first evidence of the domestication of this rodent comes from the Ayacucho Valley, dated to 2500 B.C.E. The main inference as

A farmer transplanting rice near Dacca, Bangladesh. The origins of rice agriculture are thought to center in an extremely broad region that included South Asia. (UN photo/John Isaac)

to whether this animal was domesticated comes not from its change in overall morphology but from the significant increase in guinea pig bones recovered. It is not until much later sites that the guinea pig bones found allow for the morphological differentiation between them and their wild precursors.

There are four wild tuber species that early Andeans liked to domesticate. Of significance is the potato, which is a major food crop around the world. The wild potato is dated back 10,000 years, with Lake Titicaca the strong favorite for where domestication originated—but then again, the altered domesticate has also been dated to the same time period. More work with AMS dating techniques is obviously needed to resolve this discrepancy.

In the eastern United States at 2500 B.C.E., most evidence points to the farming of sunflowers and wild gourds. Current research points to the earliest settlements in North America having been located in what is today the eastern United States. Some of these sites have been dated to around 15,000 years before the present. Although we know that domesticated maize made its way to the region at around 100 C.E., that occurred much later than the earliest recorded evidence of plant domestication. It appears that small groups of hunter-gatherers were very much interested in varieties of goosefoot (Chenopodium, a family of widely distributed shrubs and herbs that includes the beet and spinach)—especially inasmuch as they seem to have camped and later created permanent settlements around river valley environments. Similar species of goosefoot were independently domesticated in Central and South America, where contemporary varieties still grow. These early farmers were also cultivating sunflowers. At the Higgs site in Tennessee, achenes believed to be similar to modern-day sunflowers were recovered along the Tennessee River and dated to 800 B.C.E. At another Tennessee site, in the Duck River valley, sunflower seeds were dated to 2100 B.C.E., which pushed back the date of achene domestication almost 1,300 years.

The seventh and most recent region to provide direct evidence for domestication of cereal crops and cattle is sub-Saharan Africa, dated at 2000 B.C.E. Current research indicates that hunter-gatherer communities were present in East Africa, and that they quickly turned to farming economies soon after the introduction of barley, goats, sheep, and cattle helped to ignite the development of those pseudoagricultural communities. I refer to these early farming communities as pseudoagronomists because the people living in these variable environments did not practice soil management. Rather, they employed plant and animal husbandry techniques that, when all went well, generated annual crop yields that provided food for humans and animals. The necessary skills and knowledge to manage soil over extended periods were acquired long after plants and animals were domesticated. There is some evidence to suggest that the culling and husbandry of cattle took place in the Dhar Tichitt area of West Africa around 1500 B.C.E. We do know, however, that the introduced cereals did not evolve into major subsistence crops in the African sub-Saharan region. Instead, three indigenous crops formed the basis of subsistence: millet, sorghum, and African rice.

African rice is a major crop today, and its domestication has been dated to 200 C.E. from the Jenne-Jeno site on the Niger River in West Africa. Its wild precursor has been tracked to the savanna, where it grows in watering holes during the rainy season. The other two cereals that made a change are directly related to African rice. Both pearl millet and sorghum have been traced to savanna plants adapted to arid climates. Although substantial evidence of early domestication is lacking, pottery shards from Adrar Bous dated to 2000 B.C.E. show imprints of the domesticated subspecies of sorghum grain. It seems, however, that most evidence from sub-Saharan Africa consistently tells a story of cattle herding and domestication occurring before plant domestication. It is believed by many, though, that with more research, the dates of domestication in this region will be pushed back to at least 3000 B.C.E.

Health and Farming

Skeletons recovered from these early Afro-European sites indicate that, compared with Late Paleolithic peoples, who were typically nomadic hunters and regionally sporadic gatherers, overall health was good. This deduction is based on overall stature and maximum skull base height, thought to reflect sufficient amounts of calories and protein for growth in all developmental stages. Teeth in these specimens are typically present (if not lost postmortem) and are in good shape, demonstrating access to adequate amounts of protein in later developmental stages.

When farming arrives, human skeletal profiles change. It is obvious that populations have increased twenty- to fiftyfold in some areas. Skeletons recovered indicate that stature does not seem to be affected; farmers are just as tall as their hunter-gatherer ancestors. However, the preponderance of cereal and the lack of the important amino acids provided by red meat in their diet take their toll. Dimensions of skull base height decrease; dimensions of long bone shaft decrease; and teeth are in very poor health. Endemic disease seems to be typical in farming communities. This may reflect the fact that, while overall populations might be healthy, the overwhelming numbers of individuals generate novel and numerous pathological pathways not generally encountered in hunter-gather communities. On the other hand, farming economies do provide for healthier females, mainly because they do not have to endure stressful periods during childbearing months traveling with groups as they move in search of food. Women typically maintain greater longevity in farming communities and hence, more opportunities to bear children.

Conclusion

In a variety of regions around the world, local groups of humans were experimenting with controlling the growth and yield of certain wild cereal grains and animals. Although each region is ecologically distinct, they all share one common limiting factor: reliable access to water. Ecological niches that revolve around high water tables provide access to a great variety of plants and animals. It seems that small groups of seminomadic hunter-gatherers were acutely aware of their environment, inasmuch as they had to track harvesting periods as well as local migrations. After many presumed attempts at controlling the growth of a certain few seed plants, these roaming peoples set the stage for future farming applications that would provide large amounts of cereal grains to sustain people when hunting and gathering proved unreliable. That eventually led to domesticating docile artiodactyls. Groups of people quickly turned into large communities, and eventually into huge, permanent civilizations—which was a recipe for nothing short of disaster later down the road.

It is commonly regarded that early farming economies provided a wealth of new plant and animal varieties. However, the fact is that the ramifications of changing from a hunter-gatherer society to large-scale permanent settlements are great. First, farming-based communities were already reacting to regional ecological degradation and species depletion that began with hunter-gatherers killing off large mammal animal biodiversity. After the advent of agriculture, farmers had to destroy large amounts of plant diversity to provide room for cultivating their few seed plant species. That in turn affected regional animal biodiversity. Second, farming provided predictable access to food resources, which in turn caused local population explosions. With increases in human population came endemic diseases that were easily spread throughout the communities. The host of diseases that most likely owe their success to the first agronomists include: various bone density diseases; dental attrition (caries and antemortem loss of teeth); diseases resulting from contaminated water, from both human and animal feces; and sexually transmitted diseases. One positive ramification comes in the form of fermented grains. Chuck Hilton of Grinnell College, suggests that fermenting grain into an intoxicating elixir was an ingenious way of increasing caloric intake that was not only pleasurable but also lengthened the storage life of grains. The question then: Is the glass of grog half empty or half full? Being in the midst of an extinction event with agriculture acting as a strong catalyst for ecosystem degradation, loss of species, and global warming, perhaps the glass broke a long time ago and we are now faced with picking up the pieces.

—Ken Mowbray

See also: Biogeography; Botany; Extinction, Direct Causes of; Global Climate Change; Holocene; Mass Extinction; Urbanization

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Alien Species

Alien species are species that have managed to establish breeding populations in new geographic regions, often far from their native ecosystems. Along with habitat destruction (as when farmers clear woodlots to plant crops), pollution, and overexploitation of resources (for example, when fisheries are exhausted by overfishing, or forests disappear from clear-cut logging), alien species are responsible for much of the ecosystem disruption—and extinction of native species—that is occurring in the present "Sixth Extinction." Nearly 100 percent of the importation of alien species (sometimes also called "exotic species") in recent history is the result of introduction by humans—either deliberately or accidentally.

Species change their geographic ranges under natural circumstances as well. The annual migrations of many bird species, as well as monarch butterflies and African wildebeest (whose migrations follow the rainfall), show that many species can populate very different geographic regions during different times of the year. More subtly, in the process known as habitat tracking (q.v.), climate and other kinds of environmental change can induce species to shift the boundaries of their habitat. For example, during the Pleistocene ice ages, when large sheets of continental glacial ice extended southward from the Arctic in both Eurasia and North America, the ranges of native species contracted southward as well, moving back to the north when the glaciers melted back during the warmer interglacial periods.

On an even larger scale, plate tectonic movements and other long-term geological processes have also changed the geographic distribution of species. Horses, for example, originated in Europe but spread to North America, where most of their later evolution

A notorious alien species, the brown tree snake was the primary cause of the extinction of nine of Guam's twelve native forest bird species. (Michael and Patricia Fogden/Corbis)

occurred. And, in perhaps the most famous example, when plate tectonic processes finally culminated in a complete land bridge between North and South America, when the Isthmus of Panama emerged approximately 2.5 million years ago, South American species started moving northward while North American species moved into South America. Apparently this "faunal interchange" was sufficiently abrupt that the mixing of species from the two regions resulted in extinction of some of the local species.

Such instances of faunal interchange leading to extinction are, however, relatively rare; little extinction occurs during normal habitat tracking, presumably because entire ecosystems are more or less transplanted, especially in instances of global climate change. But there is little doubt that when species are individually introduced around the globe, they sometimes cause ecological havoc—up to and including the loss of substantial numbers of local, native species. Perhaps the most notorious example of an alien species is the brown tree snake—a case that is discussed in the entry Birds of Guam and the Brown Tree Snake.

Our own species, *Homo sapiens*, responsible for spreading alien species around the globe, was the very first of the alien species. Our cultural adaptations allowed us to leave our native African tropical habitat and invade foreign terrains with very different climates and plant and animal species. (Our ancestors, *Homo ergaster* or *Homo erectus*, had also been sufficiently well advanced culturally that they had left Africa in numbers, almost a million years earlier.) The migration of *Homo sapiens* out of Africa into Eurasia—and ultimately into the Americas and across the entire world—was itself ecologically unusual. It is thought that our invasion of local ecosystems—where we encountered game animals that had never been hunted by humans—led directly to extinctions, especially of the larger game mammals. Most anthropologists now agree that perhaps the first victim of our spread around the world was the Neanderthal species—a distinct species of humans living in Ice Age Europe who, unable to cope competitively with anatomically modern *Homo sapiens*, became extinct a few thousand years after our arrival in Europe a little after 40,000 years ago.

Some scientists have pointed out that (in addition to overhunting) newly arrived humans surely must have brought with them other species—hence starting the process of introducing alien species around the globe. In addition to the possibility that humans brought pets with them as they invaded new territories, some scientists think that they and the animals with them also transmitted pathogens—disease-causing viruses and bacteria. These scientists think that, much as the measles and other diseases brought by early European explorers and settlers to the New World proved devastating to native Americans who had no immunity (because they had never been exposed prior to European contact), diseases brought by people and the animals that came with them might have had devastating effects on many native species. And it is true that many smaller species of, for example, the Ice Age biota of North America—in addition to the mastodons, mammoths, wooly rhinos, and other large and hunted mammalian species—became extinct when humans arrived in North America in significant numbers around 12,500 years ago.

There can be no question, however, that the bulk of the explosion in the introduction of alien species around the globe came during the age of exploration, the age of colonization, and now, in the postindustrial world of globalization. The Norway rat (*Rattus norvegicus*) has been hitching rides on ships at least since the days of Christopher Columbus. And rocks used as ballast for ships that have off-loaded their cargo are often dumped in foreign lands—apparently the main reason why so many species of European plants got to the United States, as their seeds were intermixed with the crushed stone. Although some of these plants may have decorative flowers, they do interfere in many places with native flowers. Indicative of their status as invaders, however, is the fact that in the eastern United States, at least, most wild-growing native European plants occur along roads and railway lines (transported originally to these already-disturbed sites by the recycling of ballast rock from ships); this is a good indication that not all invading species are able to take over undisturbed habitat.

Indeed, it is not always possible to determine why some invading alien species are wildly successful while others fail to become established at all. Periodic attempts, for example, to introduce the East Coast horseshoe crab, *Limulus polyphemus*, to San Francisco Bay have repeatedly failed (horseshoe crabs are collected to be ground into fertilizer and pig food—a practice that has gotten so out of hand that horseshoe crabs, once very abundant, are now endangered in such places as New Jersey's coastline). This failure is difficult to understand, inasmuch as horseshoe crabs are ecologically very generalized: they can withstand great fluctuations in temperature and salinity, they are not choosy about what they eat, they have few natural enemies (except man!), and they are even notoriously successful at surviving in the heavily polluted waters in the East. Yet they cannot survive in San Francisco Bay—and that remains a mystery.

Thus some alien species—perhaps most—are doomed not to survive. Others (such as the European plants already mentioned) can survive only in human-disturbed habitats, sometimes because they are already “commensal” (adapted to live in close association) with human beings. Perhaps because cities sprang up in Europe long before they did in the United States and Canada, bird species commensal with humans in Europe, such as house sparrows, starlings, and pigeons, have thrived in the United States—and, indeed, in many settled areas throughout the globe. More recently, North American human commensal species, such as the Carolina gray squirrel, have become common in Europe (and even in Cape Town, South Africa); Canada geese have recently become so common in Europe that they are considered pests.

European colonists, longing for home, often deliberately transported familiar species from their homelands—often with disastrous consequences for native species. For example, most of New Zealand’s native bird species are nowhere to be found near human settlements, where many of the birds in evidence are species transplanted from Europe. But, no matter whether deliberately or accidentally introduced, it is the alien species that unexpectedly thrive—often beyond the level seen in their native homes—that cause the most serious damage.

A very recent example of a wildly successful alien species is the European zebra mussel, now spreading throughout the Great Lakes and adjacent freshwaters in southern Canada and the eastern and central United States. This region was covered by glaciers as recently as 12,000 to 18,000 years ago, so the native freshwater mussels have only recently colonized these regions themselves. Because the shells of freshwater mussels at one time were extensively used to make buttons, and because of pollution from industrialization, native North American mussels were already in serious trouble—with at least thirteen species becoming extinct—in 1930. Now the arrival of the European zebra mussel poses an additional threat.

European zebra mussels also directly threaten human economic life. They grow so rapidly that they are continually fouling boats and wharves—and, more important, clogging the intake and outlet pipes of factories, water treatment facilities, and power plants. They have become a costly economic nuisance.

It is generally assumed that some alien species flourish in nonnative surroundings because of an absence of natural enemies—be they predators or disease-causing microbes. Sometimes, however, it is difficult to pinpoint what the reasons are, and sometimes attempts to redress the balance using “biological warfare,” by introducing native predators, backfire. A recent outbreak of a lethal form of conjunctivitis (an eye disease) has drastically cut back the number of house finches in the eastern United States. House finches (*Carpodacus mexicanus*) were brought to Long Island from the West Coast several decades ago, and their numbers have exploded up and down the East Coast and westward to the Mississippi River, displacing their close relatives the purple finch (*Carpodacus purpureus*) and other eastern bird species. It remains to be seen, but this particular, and apparently successful, invading species now has a fight on its hands. Only time will tell whether it will adapt to this disease and rebound, continue to exist in the East in diminishing numbers, or disappear completely from the regions it has so recently invaded.

—Niles Eldredge

See also: Birds of Guam and the Brown Tree Snake; Extinction, Direct Causes of; Habitat Tracking; Human Evolution; Sixth Extinction

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Amoebae

See Protoctists

Amphibians

Amphibians compose a taxon of vertebrate animals that are characterized by having legs (unless lost) and glandular skin, and by lacking the features of the other tetrapod groups: amniote eggs ("reptiles," mammals, and birds), hair (mammals), feathers (birds), or epidermal scales ("reptiles" and birds). Many of the fossil groups referred to the "Amphibia" in this sense are evolutionarily more closely related to "reptiles" and mammals than they are to living amphibians, so use of the term to include these fossil taxa promotes poor communication. In a more restricted sense, all living amphibians are generally considered to be members of the group Lissamphibia, which is considered by most systematists to be the closest living taxon to the Amniota ("reptiles," birds, and mammals). Nevertheless, the reality of the Lissamphibia remains an open question, on occasion resulting in heated discussion, with some paleontologists suggesting that salamanders and caecilians are only distantly related to frogs and other tetrapods, although the preponderance of the anatomical and molecular evidence suggested so far does support Lissamphibian monophyly. The current wisdom is that Lissamphibians were derived from dissorophoid labyrinthodonts about 280 million years ago. The Lissamphibia are composed of the three living groups, each at least 200 million years old: frogs (Anura, 4,765 species); salamanders (Urodela, 495 species); and caecilians (Gymnophiona, 161 species). Amphibians are found worldwide in temperate and tropical communities, with the exception of extremely dry areas, or most oceanic islands.

Amphibians show the greatest diversity in reproductive modes of any vertebrate group. Primitively, Lissamphibians lay eggs in water, have external fertilization, and exhibit an aquatic larval stage and a terrestrial adult (reproductive) stage. This has been highly modified through evolutionary history in many groups, and now most species of salamanders and caecilians lack aquatic larvae; most of these have internal fertilization and direct development in terrestrial eggs. (Direct development is development in which an animal after birth or emergence from an egg differs from the adult in only comparatively minor details, with no larval stage or metamorphosis.) Internal fertilization is accomplished through the use of a penis in caecilians and a male spermatophore in most salamanders, which the female salamander picks up with her cloacal lips during courtship. Similarly, a large number of frogs exhibit direct development, although the primitive reproductive mode of external fertilization, aquatic eggs, and aquatic larvae, is still the most common. The morphological diversity of amphibians is also enormous, from the legless burrowing or aquatic caecilians to tail-less hopping frogs, to the superficially mainstream but internally highly derived salamanders.

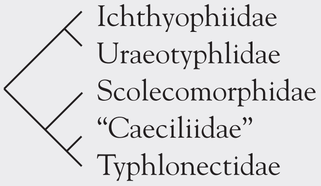
One of the most surprising things about living amphibians is that about 36 percent of all species have been named in the last sixteen years, with the rate of discovery of new species increasing each year. This growth in our knowledge is not driven by growth in the number of scientists who study this kind of diversity, but by new tools (for example, protein electrophoresis and DNA sequencing) that allow rapid discovery of species and by the fact that the extensive human modification of the planet has allowed some areas previously inaccessible to be studied with ease. Concomitant with the rapid discovery of amphibians is the realization that much of this diversity may well be at risk, with rather large numbers of species becoming very rare or extinct (for example, the gastric-brooding frog, *Rheobatrachus silus*, and the golden toad, *Bufo periglenes*) in the last few years.

Within the Lissamphibia (generally ranked as a subclass by those preoccupied by such things) the taxonomy can be characterized by the following:

Order Gymnophiona, the caecilians. The bizarre caecilians form a group of 161 recognized species of legless, eel-like amphibians, usually cast into five families, found in the wet tropics of the Americas, Africa, India, and southeastern Asia, with outliers of clear biogeographic interest in the Seychelles. They range in size from about 7 cm to 1.5 m, depending on the species. They are also seemingly generalists, eating any animal sufficiently smaller than themselves, especially earthworms, termites, and orthopterans. The number of recognized species has been stable since at least 1985, although because they are generally difficult to collect and external morphological variation is quite limited, the true number of species is likely much higher than currently appreciated. The phylogenetic relationships of the group are not well known, although careful work on this topic suggests the relationships shown in Figure 1. Caecilians are all legless burrowers in mud or leaf litter, and some are aquatic; primitively, they have aquatic larvae, but most species have direct development from eggs laid on land; some have become live-bearing. The oldest fossil caecilian is from the lower Jurassic.

Figure 1

Caecilian Relationships



Ichthyophiidae. The semiaquatic ichthyophiids (thirty-seven species in two genera) are found in the Philippines and from southern India to southern China, Thailand, and the Malayan Archipelago. They are oviparous and have free-swimming larvae.

Uraeotyphlidae. Very little is known about this taxon (four species in one genus), which is found in southern India. Because it is likely the closest relative of the Ichthyophiidae, one expects the species to be semiaquatic with aquatic larvae.

"Caeciliidae." The Caeciliidae are a poorly resolved and paraphyletic group (with respect to at least the Typhlonectidae and possibly with respect to the Scolecomorphidae as well) of 101 species found in the wet tropics of the Americas, Africa, Seychelles, and southern and eastern India. The morphological and ecological diversity in this group is, not surprisingly, large, with variation encompassing such things as bright orange body color, species whose eyes move with facial tentacles, and giant species measuring more than a meter in length. Some species are oviparous, with direct development within the egg, and other species are viviparous.

A salamander* (Oedipina grandis) *on a leaf in the 3,000-foot high Talamanca Range, Costa Rica (Michael and Patricia Fogden/Corbis)

Scolecomorphidae. The scolecomorphids are a group (six species in two genera) of live-bearing burrowing caecilians found in tropical West and East Africa.

Typhlonectidae. The typhlonectids are a group (thirteen species in five genera) of secondarily aquatic caecilians found in the Amazon, Orinoco, Magdalena, and La Plata drainages of South America, and also in places on the coast of Venezuela. On the basis of phylogenetic analysis, this group is believed to have been derived from within the Caeciliidae.

Order Urodela, the salamanders. The salamanders are an easily recognizable group of tailed and four-legged amphibians of 495 species, generally placed in ten families, found in the temperate areas of Eurasia and North America, south into the tropics of northern South America, and into the northern parts of tropical Asia. Species range in habitus from obligately aquatic giants (*Andrias*) of 1.5 m to "standard" salamanders having aquatic larvae and terrestrial adults (for example, most tiger salamanders) to tiny lungless salamanders that have direct development (for example, *Thorius*). The relationships of the nominal families are becoming clearer, with the most evidentiarily supported arrangement shown in Figure 2. All families of salamanders are monophyletic and of considerable antiquity. The oldest salamanders are from the Upper Jurassic, with evidence suggesting that at least the major extant salamander families were all present in the Cretaceous.

Sirenidae. The obligate aquatic sirens (two genera, four species), with external gills in adults, are found in the southeastern United States and extreme northeastern Mexico. Unique among salamanders, they lack hind limbs but retain well-developed forelimbs. Reproduction is not well understood in this group, but they apparently have external fertilization of eggs laid in submerged vegetation.

Cryptobranchidae. The giant salamanders (two genera, three species) are found in eastern China, southern Japan, and the eastern United States. They get enormous (*Andrias japonicus* is up to 1.4 m) and are all obligate aquatic with internal gills, external fertilization, and aquatic larvae.

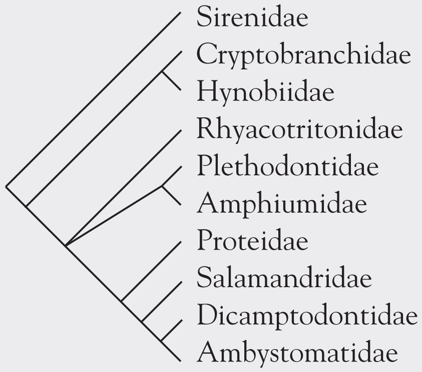
Hynobiidae. The Asiatic salamanders are a generalized group of eight genera and thirty-nine species found east of the Urals and south of the Arctic Circle to Iran, as well as in southern China and Japan. All have external fertilization and aquatic eggs, and larvae and adults of most species are terrestrial.

Rhyacotritonidae. The Olympic salamanders (one genus, four species) are found only in the Pacific Northwest of the United States and Canada. They have reduced lungs, associated with their high gradient stream habitat, aquatic larvae, internal fertilization with a male spermatophore, and semiaquatic adults that are generally found along the margins of water.

Plethodontidae. The lungless salamanders (25 genera and 342 species) predominantly have direct development within terrestrial eggs, although one tribe (Hemidactyliini of the largest subfamily, Plethodontinae) and the subfamily Desmognathinae have aquatic larvae and, except for a few examples, terrestrial adults. The Desmognathinae (two genera, eighteen species) are restricted to the eastern United States and adjacent Canada, but the Plethodontinae extend from the U.S.-Canada border region to Amazonia with large numbers of species and morphological diversity. Within the Plethodontinae, three tribes are recognized, of which evidence of monophyly is strong only for the Bolitoglossini. The Hemidactyliini represent the species that retains the primitive condition of aquatic larvae and is restricted to the eastern United States and adjacent Canada. The Plethodontini contain the speciose genus *Plethodon,* as well as *Aneides,* both in the eastern and western United States, as well as *Ensatina,* found only in the far western United States and adjacent Mexico. The Bolitoglossini is a major radiation found from California south to Amazonia, with a surprising outlier in that some of the species of *Hydromantes* (otherwise in the Sierras of California) are found in southern France, Sardinia, Corsica, and adjacent Italy.

Figure 2

Salamander Relationships



Amphiumidae. The Amphiumas (one genus, three species) are eel-like, obligately aquatic species with diminutive limbs, unpleasant dispositions, and a large size (as much as 1 m). Reproduction is via a male spermatophore, and the adults retain internal gills. The taxon is restricted to the southern coastal plain of the eastern United States.

Proteidae. The mudpuppies (two genera, six species) are aquatic salamanders found in the eastern United States and adjacent Canada, as well as one genus, one species on the Adriatic coast of northeastern Italy south to Montenegro. All species have internal fertilization (through use of a male spermatophore) and aquatic larvae, with external gills retained into adulthood.

Salamandridae. The newts and fire salamanders (fifteen genera, fifty-nine species) occur in eastern and far western North American from southern Canada to northern Mexico, but with the bulk of their diversity in Eurasia (central Siberia west to Norway, Britain, and northwestern Africa, as well as southern China and adjacent Indochina). The salamandrids are mostly aquatic as adults, although most species have adult morphologies. Reproduction is via internal fertilization and aquatic larvae, although a few species have developed viviparity.

Dicamptodontidae. The American giant salamanders (one genus, four species), like other advanced salamanders, have internal fertilization through use of a male spermatophore. Most species have terrestrial adults. Found only in the Pacific Northwest of United States and Canada.

Ambystomatidae. The tiger salamanders (one genus, thirty species) are found from southern Canada to the vicinity of Mexico City, in temperate locations in semiarid to mesic environments. The mode of reproduction is typical, inasmuch as fertilization is internal via a male spermatophore, and aquatic larvae turn into terrestrial adults; a few species, however, such as the famous axolotl (*Ambystoma mexicanum*), retain larval morphologies as aquatic reproductive adults.

Order Anura, the frogs. Frogs (one genus, 4,765 species) represent the large majority of all species of amphibians as well as the largest diversity of life histories and morphologies. These tail-less amphibians are found essentially worldwide in temperate to tropical climates, with a few species extending out to Fiji and Tonga in the Pacific Ocean. The structural diversity among frogs is broad and well known, although the species diversity and their evolutionary history are not. At present the phylogenetic history can be approximated by the tree shown in Figure 3. The nonranoid neobatrachians are referred to as the "Hyloidea," a taxon for which no evidence of monophyly has been suggested, nor its monophyly refuted. The oldest indisputable frog is from the Lower Jurassic of North America, and another arguable frog relative is known from the Lower Triassic. As one can suppose from this rather problematic tree, the received wisdom regarding the phylogeny of frogs is likely to change considerably in the next few years.

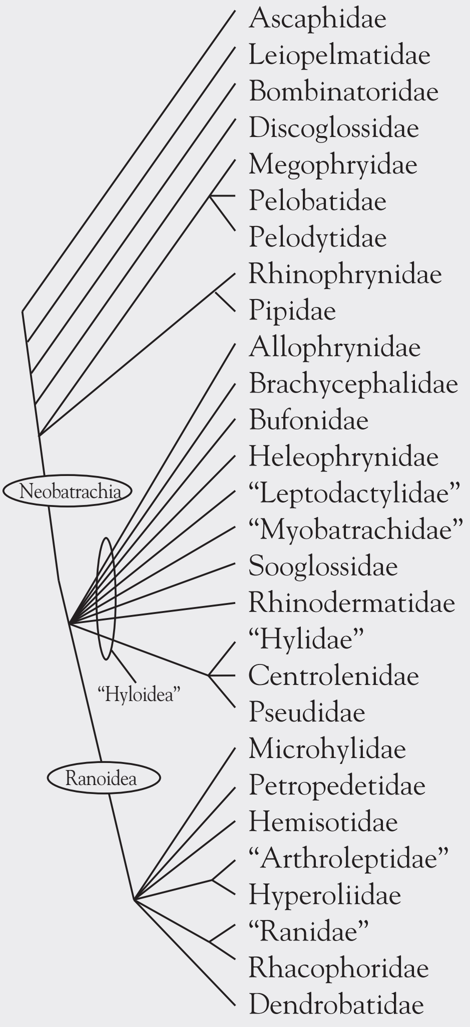
Ascaphidae. *Ascaphus* is composed of one genus, two species of small frogs found along high gradient streams in the Pacific Northwest of the United States and adjacent Canada, where their eggs are laid and their tadpoles develop. The tailed frogs are known for their peculiar intromittent organ, from whence the common name comes as well as a number of primitive characteristics that suggest their very distant relationship to other frogs.

Leiopelmatidae. *Leiopelma* (one genus, four species), like *Ascaphus*, is a relict taxon showing a number of primitive features, with only very distant relations to other frogs. This family is found solely on New Zealand. Eggs are laid on damp terrestrial locations, and the young develop directly without a larval stage outside of the egg.

Bombinatoridae. The bombinatorids (two genera, nine species) include the firebellied toads. They are found in Europe to Turkey and western Russia, and in eastern Asia, including eastern Russia, China, Korea, and

Figure 3

Frog Relationships



Vietnam. Another genus is found in the Philippines and northern Borneo. Reproduction is via aquatic eggs and larvae.

Discoglossidae. The discoglossids (three genera, ten species) include the famous midwife toad. They are found in western, eastern, and southern Europe and western Asia, as well as northwestern Africa. All species have aquatic eggs and larvae, but in *Alytes* the male carries the strings of eggs on his back and legs until they are ready to hatch.

Megophryidae. The megophryines are relatively primitive frogs of ten genera and eighty-three species, closely related to the pelobatids and pelodytids. They are found predominantly in southeastern Asian and Indonesian tropical forests and associated temperate montane habitats. All species have aquatic eggs and larvae, and in some species the tadpoles have distinctive upward-directed mouthparts that allow them to browse on the surface of the water.

Pelobatidae. The spadefoots are composed of three genera with eleven species, which are found in arid to mesic temperate North America and in Europe, western Asia, and northwestern Africa. All species have aquatic eggs and larvae and are particularly distinctive in that the rate of larval development is much higher than that of most other frogs, with some species in the western United States developing from deposited egg to froglet in less than a month.

Pelodytidae. The parsley frogs (one genus, three species) are smooth-skinned, toadlike frogs, closely related to the pelobatids, which occur in Europe and western Asia. They have typically anuran aquatic larvae.

Rhinophrynidae. The Mexican burrowing toad is a tubby, medium-size frog (one species) with a very narrow head with respect to its body; it is apparently the nearest relative of the pipids. It is found in south Texas southward to Costa Rica. Reproduction is via aquatic eggs and larvae.

Pipidae. The clawed frogs (five genera, twenty-two species) are a strictly aquatic tropical group of frogs found in tropical Central and South America and sub-Saharan Africa. Primitively, members of the group lay aquatic eggs that develop into aquatic larvae. In the South American *Pipa,* however, the eggs are gathered onto the back, which grows over them to produce imbedded individual cavities for each egg, from which free-living larvae or small froglets emerge, depending on the species involved.

Hyloids

Allophrynidae. *Allophryne* (one genus, one species) is an enigmatic treefrog of the Guianas in South America. It superficially resembles the hylids and centrolenids, but some authors have allied it with the bufonids. Its reproductive mode is unknown.

Brachycephalidae. The brachycephalids are a group of miniature frogs in coastal southeastern Brazil (two genera, five species) with reduced digits. They have direct development within terrestrial eggs, and one genus has a peculiar osseous shield on its back.

Bufonidae. The "true" toads (32 genera, 423 species) are variable, from delicate treefrog-like forms to giant toads about the size of a pie plate. Primitive bufonids lay individual eggs, but members of *Bufo* and its near allies (the large majority of the species in the family) generally lay strings of eggs. A number of taxa lack feeding tadpoles, some are direct developers, and some are ovoviviparous.

Heleophrynidae. The ghost frogs (one genus, five species) are frogs of moderate size that inhabit high gradient rocky streams. They would likely have been placed in the Leptodactylidae had they occurred in South America, or in the Myobatrachidae had they occurred in Australia. However, because they are South African endemics, most authors have treated them as a distinct family.

"Leptodactylidae." The "Leptodactylidae" are a collection of New World hyloid frogs (48 genera, 1,068 species), very likely paraphyletic with at least some of the other groups of hyloids, and characterized by lacking the derived characteristics of other groups. Leptodactylids are found from the southern United States and the Antilles to the southern tip of South America. The largest vertebrate genus, the rainfrogs of the genus *Eleutherodactylus*, are in this group (approximately 680 species), but the diversity in leptodactylids in terms of body plan and reproductive mode varies from the large-headed predatory *Ceratophrys;* to the obligately aquatic members of *Telmatobius*, which live their lives on the bottom of Andean lakes; to the rain frogs that live primarily in leaf litter in cloud forests. Primitively, the leptodactylids have aquatic eggs and larvae, but all members of the eleutherdactylines have direct development within terrestrial eggs; at least one member, *Eleutherodactylus jasperi* (likely now extinct), is viviparous.

"Myobatrachidae." The myobatrachid frogs (22 genera, 120 species) are an extremely variable collection of hyloid species found in Australia and New Guinea that lack any of the obvious derived features associated with other neobatrachian families. As such the Myobatrachidae are likely artificial. Reproductive modes are similarly variable in the group. *Rheobatrachus*, the endangered gastric-brooding frogs, are members of this nominal group, and a few exhibit nonfeeding tadpoles in nests; others have direct development in terrestrially laid eggs, although most of the species have free-living tadpoles and are otherwise similar to the "Leptodactylidae."

Sooglossidae. The Sooglossidae (two genera, three species) are a taxon of hyloid frog restricted to the Seychelles Islands of the Indian Ocean, and clearly these represent ancient relicts of the breakup of Gondwanaland. The eggs are laid on the land, and there is either direct development (*Sooglossus*) or nonfeeding tadpoles that are carried on the back of the adult (*Nesomantis*).

Rhinodermatidae. The rhinodermatids (one genus, two species) are a peculiar group of hyloid frogs found in the temperate forests of southern Chile and Argentina. They exhibit a peculiar reproductive mode in that they lay terrestrial eggs, and the hatching larvae are collected by the male, who broods them in his vocal pouches.

Hylidae. The Hylidae (treefrogs) (40 genera, 900 species) have their diversity predominantly in South America, Central America, and tropical southern North America, with other centers of diversity in the Australo-Papuan region, and with a few species found in temperate North America, Eurasia, and North Africa. The physical, physiological, and ecological diversity of the treefrogs is enormous, with arboreal and terrestrial members. Some treefrogs have bizarre helmet-shaped skulls, and some of the leaf frogs are unique in excreting uric acid like birds. Most species have aquatic eggs and larvae, but one large radiation in South America has young that develop directly in pouches on the back; in two of those the dorsal pouches penetrate through the axial musculature into the abdominal cavity.

Centrolenidae. The glass frogs (3 genera, 135 species) are another group of treefrogs in tropical Central and South America, in areas of high-gradient streams. Many species have translucent to transparent ventral skin that allows the beating heart to be seen clearly.

Pseudidae. The paradox frogs (two genera, nine species) are a small group of aquatic hyloid frogs most likely evolutionarily within the Hylidae, but the evidence so far is meager. These frogs inhabit the tropical lowlands of South America. Aquatic eggs develop into huge tadpoles ("paradox frog" from this aspect of their life history) that transform into relatively small adult frogs.

Ranoids

Microhylidae. The narrow-mouthed frogs represent an enormously diverse and speciose ranoid family (68 genera, 361 species) found worldwide in temperate and tropical locations. The group is characterized by a derived tadpole that lacks either oral denticles or a beak. The taxic diversity of the family is primarily found from tropical southeastern Asia to Australia, but other radiations are found in sub-Saharan Africa and the Americas.

Dendrobatidae. The dart-poison frogs (9 genera, 201 species) are an easily diagnosed group of small terrestrial frogs (except for one species that is aquatic) found in southern Central America and tropical South America. The common name is not particularly apt, as only a very few species were ever used for dart poison; most of the species are not particularly brightly colored or toxic, although some are highly desired in the pet trade for those reasons. The consideration of the dendrobatids within the ranoids is a continuing controversy, but the published evidence currently supports its placement here. Eggs are laid in terrestrial or arboreal locations, and either the males or females (depending on species) carry the tadpoles on their back to water.

Hemisotidae. The pig-snouted frogs are a small group (one genus, eight species) of ranoid frogs found in tropical and subtropical sub-Saharan Africa and of uncertain affinities. They burrow head-first, which is unusual for frogs, and lay eggs in subterranean nests that release the aquatic larvae when the nest floods.

"Arthroleptidae." The squeakers (7 genera, 61 species) are a composite of two groups of sub-Saharan African ranoid frogs that together have been posited to be paraphyletic to the African treefrogs, the Hyperoliidae. Direct development has been reported in most of the members of one of these groups, the Arthroleptinae, but the other group, the Astylosterninae, have aquatic eggs and larvae.

Petropedetidae. The Petropedetidae (13 genera, 101 species) are a group of sub-Saharan African ranoid frogs that are poorly studied and of dubious monophyly. Direct development has been reported in some species, but most lay aquatic eggs on vegetation overhanging water or in water and have aquatic larvae.

"Ranidae." The Ranidae (21 genera, 605 species) are a catch-all of ranoid frogs that are not members of the other ranoid families. The group is cosmopolitan, with a number of relatively closely related species (*Rana*) being found in Europe, North Africa, Eurasia, and temperate and tropical North America, south to tropical South America. The taxic diversity of the ranids is predominantly in tropical Asia, where the diversity of morphology and ecology is very large, and in sub-Saharan Africa. Arboreal tadpoles have been reported, although most species have aquatic eggs and larvae. In one group found in the Philippines and Fiji, direct development is reported.

Hyperoliidae. The African treefrogs (19 genera, 240 species) are found in sub-Saharan Africa and Madagascar. Ecologically they vary from arboreal to terrestrial. Their systematics are very poorly understood, and clearly there are many undescribed species. There are a diversity of reproductive types, with eggs being laid in the water, in arboreal foam nests, and on leaves above the water.

Rhacophoridae. The Asiatic treefrogs (12 genera, 430 species) are found in tropical and subtropical Asia, with one genus (*Chiromantis*) in sub-Saharan Africa and another radiation in Madagascar. It is reasonably clear that this taxon renders the "Ranidae" paraphyletic, although considerable work remains to be done. Most species have aquatic eggs and larvae, although a few lay their eggs in arboreal locations and some have an abbreviated nonfeeding larval stage.

—Darrel Frost

See also: Adaptive Radiation; Classification, Biological; Evolution; Evolutionary Biodiversity; Geological Time Scale; Linnaean Hierarchy; Phylogeny; Species; Zoology

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Amphineura (chitons)

See Mollusca

Angiosperms

Angiosperms, commonly known as flowering plants, are the largest and most diverse group of plants, with 275,000 species representing more than 80 percent of all green plants. As a consequence, they are the principal components of the earth's terrestrial vegetation and are the most economically important group, as the principal source of foods, fiber products, timber, medicinals, dyes, spices, and ornamentals. In terms of number and phytomass, they contribute to the food chain in many ways. The vegetative parts are consumed by and support herbivores. Shoots and roots support vast numbers of insects and other invertebrates at vari-

Grasses grow in a reclaimed coal strip mine near Westernport, Maryland. (NASA)

ous phases in their life cycles. Nectar-producing flowers support pollinating insects, birds, and small mammals such as rodents, bats, and marsupials. Fruits and seeds are an important food source for many birds, mammals, and some fish. Angiosperms are as important a food source to humans as they are to other animals, either through the consumption of grazing herbivores or through the direct consumption of fruits, seeds, and vegetables. The most important angiosperm families are the Poaceae (cereals, forage grasses, and bamboo), the Solanaceae (potato, eggplant, tomato, and chili and sweet peppers), Brassicaceae (broccoli, cabbage, cauliflower, radish, turnip, and other vegetables), Rosaceae (apples, cherries pears, plums, and many berries), Cucurbitaceae (melons, squashes, gourds, and the like), and Fabaceae (legumes and beans).

Angiosperms are a monophyletic group, and their unique features, besides the presence of flowers, are the carpel, which encloses the seeds and ripens as the fruit; the presence of a companion cell with each sieve tube element in the phloem, the photosynthate transport cells; and the presence of endosperm in the seeds that is the product of a triple fusion nucleus (that is, triploid) composed of two nuclei from the female parent and one from the male. The endosperm is generally the principal storage product (for example, the bulk of a grain of wheat) used by the developing embryo and seedling.

Growth form in the angiosperms varies from plants of less than 2 mm in watermeal (*Wolffia*, Araceae) to trees more than 100 m tall in mountain ash (*Eucalyptus regnans*, Myrtaceae). Within this range occur myriad sizes, from herbs to shrubs to trees, and forms, such as succulents in dry habitats (such as cacti), submerged aquatics both in freshwater and marine habitats (for example, sea grasses, or Zosteraceae), epiphytes (for example, most orchids and bromeliads), and insectivorous plants in bogs (such as sundews, *Drosera;* Venus's flytrap, *Dionaea;* pitcher plants, *Sarracenia;* and so forth). Life cycles also vary, ranging from herbaceous annuals that complete their life cycle within one growing season to herbaceous biennials (for example, beet, *Beta vulgaris*, and carrot, *Daucus carrota*) that grow vegetatively in the first season and then flower and fruit in the second season to herbaceous and woody perennials that grow for many years, often flowering and fruiting each year. Examples of perennial herbs are savanna grasses and lilies. In temperate areas, the aerial parts of perennials often die back, with new shoots produced the following year from underground rhizomes, bulbs, corms, tubers, or stolons.

In order to understand this diversity, it is necessary to understand the basic organization of the angiosperm plant body, which consists of three fundamental parts: stems, leaves, and roots. These organs constitute the vegetative plant body. Together the stem and its attached leaves constitute a shoot. The shoot grows from terminal buds and branches from lateral buds, which are located in the axil of each leaf, where it meets the stem. This attachment point is a node, and the area between nodes, if present, is an internode. Simply varying internode length from very long to very short can lead to vines (for example, grape, *Vitis vinifera*) versus rosette plants (for example, lettuce, *Lactuca sativa*). These positional relationships of leaf stem and axillary bud allow us to interpret the diversity of the shoot system so that we find leaves that no longer look like leaves, and stems that are so modified that they look like leaves. Thus spines are modified leaves (for example, cacti), thorns are modified shoots (for example, honey locust, *Gledistia tricanthos*), and prickles are merely epidermal proliferations (for example, roses). Stems may be flattened into cladodes that look just like leaves, as in many epiphytic cacti, or modified into tendrils as in passion flower (*Passiflora* spp.). Stems may be modified into storage organs such as bulbs, corms, rhizomes, and tubers.

Branching is of two principal types: monopodial and sympodial. In monopodial branching, there is a main terminal bud that grows as a leader shoot with lateral axillary branches remaining subordinate (for example, hickory trees, *Carya*). In sympodial branching there is no continuously growing leader shoot, because the terminal bud is determinate (that is, usually turning into a flower—inflorescence), and an axillary bud takes over as a new leader shoot, also known as a renewal shoot. Many trees combine both types of branching, with the main stem being monopodial and side branches being sympodial (for example, the pagoda tree, *Terminalia catapa*).

There are two basic types of root systems: a primary root system and an adventitious root system. The primary root system consists of a prominent tap root from which many lateral roots originate, giving rise to more lateral roots until a highly branched root system is developed. In contrast, adventitious roots arise from stems, are sparingly branched, and are often short lived. They are found mostly in the monocots (grasses, lilies, orchids, bromeliads, and so forth). Both types of roots may be modified into fleshy storage organs. Examples of these tuberous roots are the tap roots of carrots and beets and the adventitious roots of cassava (*Manihot esculenta*). The roots of most angiosperms are mycorrhizal.

Just as there is wide variation in the vegetative plant parts, there is similar variation in the reproductive parts. The reproductive unit of the angiosperms is the flower. Many vegetative shoots eventually become flower buds that have determinate growth. Flowers may occur singly or in clusters, known as an inflorescence. A basic flower consists of four sets of organs successively and alternately attached in whorls to a short receptacle. From the base upward, these are the sepals, petals, stamens (male, pollen-producing organs), and carpels (female, seed-producing organs). Collectively, the sepals are the calyx, the petals the corolla, the stamens the androecium, and the carpels the gynoecium. The calyx and corolla are known collectively as the perianth. When all sets are present, the flower is complete. In contrast, an incomplete flower is missing one of the sets. A perfect flower has both stamens and carpels; an imperfect flower is missing either stamens (a carpellate flower) or carpels (a staminate flower). Often, when the stamens are sterile, they become petaloid and are known as staminodes (for example, most rose cultivars). Species with either perfect flowers or both types of imperfect flowers are monoecious, whereas those species with only staminate or carpellate flowers are dioecious. Floral organs may be fused. When members of the same type are fused, they are connate (fused laterally) with each other (for example, the petals of bindweed, *Convolulus*). When members of different types are fused, they are adnate to one another (for example, stamens adnate to the petals in mints, Lamiaceae). When the perianth and androecium are adnate to the gynoecium, the flower is termed epigynous, and when free from the gynoecium, hypogenous. The flowers may be radially symmetrical or actinomorphic (polysymmetric), or bilaterally symmetrical or zygomorphic (monosymmetric).

The potential combinations of missing parts, symmetry, and fusions are the basis for angiosperm floral diversity. Most of this diversity appears to be in response to specialized pollination mechanisms involving the transfer of pollen from the stamens to the stigmas of the gynoecium. Wind-pollinated flowers are simple, very often unisexual, and have either reduced perianth parts or none at all. In contrast, animal-pollinated flowers are generally showy and elaborate, with varying degrees of fusion of parts and monosymmetry accompanied by nectaries. Along with this floral diversity is a range of inflorescence diversity. There are two major types of inflorescences based upon monopodial and sympodial branching. In monopodial or indeterminate inflorescences, the apex does not form a terminal flower. The first flowers to form and open are at the base of the inflorescence, and, thus, the last formed and youngest flowers are in the center. These include racemes, spikes, aments (catkins), umbels, and heads. In racemes, each flower is borne at the end of a stalk or pedicel. Spikes and aments are racemes with sessile flowers. Spikes are erect; aments are pendulous and associated with wind pollination (for example, oaks, *Quercus* spp.). Umbels have basal flowers with longer pedicels that those of the apical flowers, so that all flowers are presented collectively in one plane for pollination (for example, carrot). Heads have nonpedicellate flowers and are contracted spikes that appear spherical to flat, where the inflorescence itself may appear as a single flower (for example, sunflower, *Helianthus annus*). In sympodial or determinate inflorescences (cymes), the apex forms a terminal flower. The first flowers to form and open are those at the apex, and, thus, the last formed and youngest flowers are on the outside. Parallels to umbels and heads are formed by varying pedicel lengths but can be distinguished by the presence of older, centrally located flowers.

Fruits are a ripened carpel or, in the case of fused carpels, a ripened gynoecium. There are many types of fruits, and fruit classification is highly complex. However, there are a few common and overlying themes. When a flower has only a single carpel or several fused carpels, the fruit is a simple fruit, as in peaches and oranges. When the flower has several separate carpels, the fruit is an aggregate fruit, as in blackberries, in which each unit is a carpel. When an inflorescence ripens as a whole, the fruit is a multiple fruit, as in mulberries and pineapple. Fruits are also classified as dry or fleshy. Simple dry fruits are either dehiscent or indehiscent. Capsules are dehiscent fruits formed by several fused carpels that open either longitudinally (for example, lilies) or apically by an operculum (for example, Brazil nut, *Bertholletia excelsa*). Follicles are single carpels with a single line of dehiscence (for example, milkweed, *Asclepias* spp.), in contrast to legumes with two lines of dehiscence per single carpel. Achenes are indehiscent fruits formed by a single carpel, whereas nuts are formed by fused carpels. Winged achenes are samaras, as in ashes (*Fraxinus* spp.). Schizocarps are formed when the fused carpels separate at maturity but remain indehiscent. In maples (*Acer* spp.), the individual schizocarps are winged. Another specialized indehiscent fruit type is the caryopsis, found in the grasses, in which the single seed is fused to the fruit wall. Fleshy fruits are berries, drupes, and pomes. Berries are many-seeded fruits formed by one carpel or several fused carpels; they are found in many textures (for example, melons, oranges, tomatoes, and so forth). Drupes (stone fruits) are a single, carpelled simple fruit with a fleshy outer wall and a woody, inner wall (plums, cherries, peaches, and so forth). Druplet is used for the individual carpels of aggregate fruit (for example, raspberries). Pomes are formed from epigynous flowers in which the adnate perianth parts become fleshy (for example, apple and pears). Fruits serve as dispersal units and as agents of dispersal. They also often provide nutrients for developing seedlings.

The classification of the angiosperms is currently in a state of flux as a result of new molecular data. However, this data has yet to be widely applied and has not yet been thoroughly integrated. Consequently, the brief outline given here may well be subject to change in the near future. For example, the angiosperms have traditionally been divided into two classes: the Magnoliopsida or Dicotyledons and the Liliopsida or Monocotyledons. It is now well established that the former is artificial, because the monocots clearly are derived from within the dicots; this, however, has yet to be incorporated in the classification.

Class Magnoliopsida is the largest group, with about 200,000 species in 10,500 genera and 316 families in 65 orders. The class is divided into a minimum of six subclasses: Magnoliidae, Hamamelidae, Caryophyllidae, Dilleniidae, Rosidae, and Asteridae. The Magnoliidae have in the main perfect flowers with separate carpels and monosulcate pollen. Many members are considered archaic and are found in the Pacific Basin and particularly New Caledonia. The Magnoliidae, with about 12,000 species in 39 families and 8 orders, have been considered a basal group of angiosperms, and recent evidence supports earlier suggestions that the subclass is paraphyletic. It includes many herbaceous or semiherbaceous members that appear to form a monophyletic group, chief among which are the Piperales, Ranunculales (buttercups), Papaverales (poppies), Laurales (laurels), and Nymphaeales (water lilies). The Hamamelidae, with about 3,500 species in 26 families and 11 orders, are characterized by more or less reduced flowers with a poorly developed or missing perianth. The flowers are often unisexual and the inflorescence is an ament (catkin). The principal orders of the Hamamelidae are the Fagales (oaks and beeches), Juglandales (walnuts and hickories), and Urticales (mulberries, figs, nettles, cannabis, and so forth). The latter appears from molecular evidence to be misplaced here. The Hamamelidae are mainly temperate, with tropical members occurring at high elevations and Urticales occurring in the lowland tropics.

The Caryophyllidae, with about 11,000 species in 14 families and 3 orders, usually contains betalins instead of anthocyanins, often have the petals missing and the sepals appearing as petals, and have perisperm as the seed storage tissue instead of endosperm. The principal order is the Caryophyllales, which includes pinks, cacti, pokeweeds, and amaranths. The Dilleniidae, with about 26,000 species in 77 families and 13 orders, have a persistent calyx and style in fruit and centrifugal stamens. The principal orders are the Theales, Malvales (with kapok, cotton, okra, balsa, and so forth), Nepenthales (with pitcher plants and sundews, although the order is probably misplaced), Violales (with squashes, passion flowers, begonias, and so forth), Capparales (with capers and the mustard family), Ericales (blueberries, cranberries, and so forth), and Ebenales (with ebony, persimmons, and so forth). The Rosidae is the largest subclass, with more than 65,000 species in 116 families and 18 orders. Definitive characters are lacking, and the subclass is most likely not natural. Principal orders include the Fabales (legumes), Rosales (with roses, apples, pears and most drupaceous fruits and crassulas, gooseberries, and so forth), Myrtales (with eucalypts and pomegranates), Santalales (most families of which are parasitic), Euphorbiales (euphorbs and boxwood), Sapindales (with maples, horse chestnuts, poison ivy, mahoganies, citrus, and so forth), and Apiales (aralias, celery, rhubarb, and so forth). The latter is most certainly misplaced, based upon chemistry and molecular data and probably belongs in the Asteridae. The Asteridae, with more than 60,000 species in 49 families and 11 orders, have tubular corollas and generally only two fused carpels. Principal orders include the Solanales (potatoes, morning glories, and so forth), Lamiales (mints and borages), Scrophulariales (gesneriads, ashes, olives, scrophs, bignons, and so forth), Campanulales, and Asterales (with a single family, the Asteraceae or sunflowers, with some 20,000 species).

Class Liliopsida is characterized by flowers with the parts in threes or multiples of three, no truly woody members, one cotyledon or seed leaf, and the mature root system composed only of adventitious roots. There are approximately 7,500 species in 3,000 genera and 106 families in 23 orders. The class is divided into five subclasses: Alismatidae, Arecidae, Commelinidae, Zingiberidae, and Liliidae. Most of these are artificial, and the Zingiberidae is a subset of the Commelinidae, as is part of the Arecidae (the palms). The Arales (aroids) of the Arecidae are part of the Alismatidae. Future formal classifications of the Liliopsida will certainly reflect these changes based upon phylogenetic analyses of morphological and molecular data. Briefly, the Liliidae contains the lilies, agaves, aloes, irises, orchids, and many other commonly cultivated ornamentals. The Zingiberidae contains the gingers, bananas, strelitzias, heliconias, marantas, and cannas. The Commelinidae contains the bromeliads, water hyacinths, pondweeds, xyrises, grasses, sedges, rushes, and restios. The Alismatidae contains many freshwater aquatic monocots as well as the only marine angiosperms.

—Dennis Wm. Stevenson

See also: Biogeography; Botany; Extinction, Direct Causes of; Fungi; Gymnosperms; Phylogeny; Plate Tectonics

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Annelida—The Segmented Worms

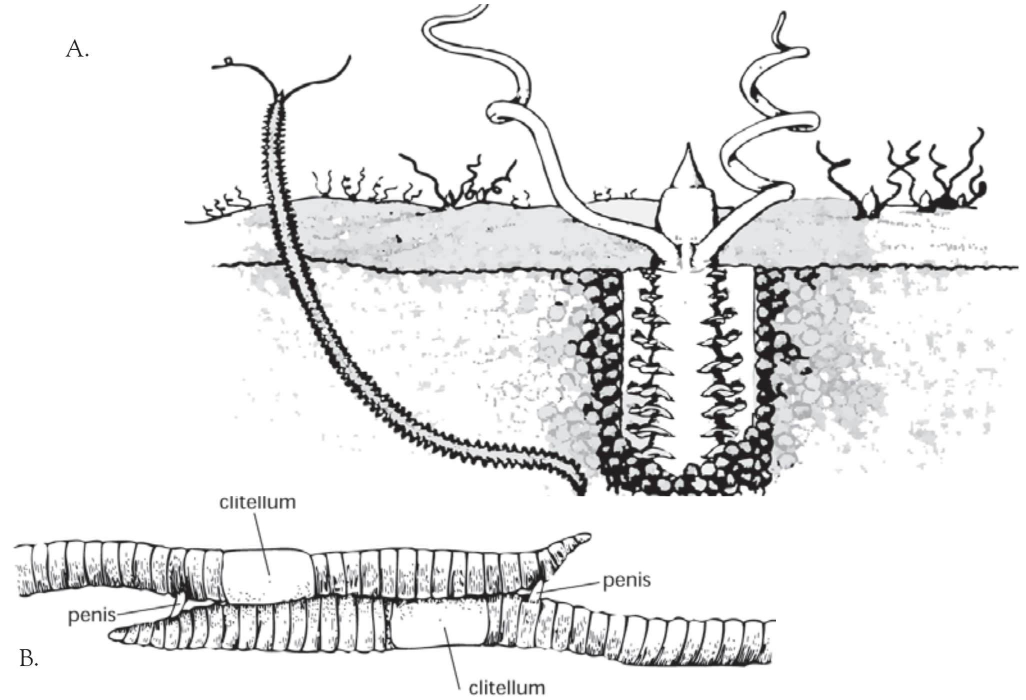
The phylum Annelida is composed of segmented, vermiform ("worm-shaped") organisms represented in nearly all terrestrial and aquatic environments. This major phylum contains more than 22,000 species distributed among two currently recognized classes, the Polychaeta and Clitellata. Annelids possess coelomate bodies divided into segments, as well as chitinous spines or chaetae (lacking in leeches). Segmentation (metamerism) appears to have evolved separately in annelids and arthropods; annelids are more closely related to mollusks and other invertebrates that produce a trochophore larvae. Annelids are represented in the fossil record dating back to the Ediacaran Period (580 million years ago), and the clitellates appear to have evolved from the polychaetes. The phylum Annelida may also contain the Echiura, a group of nonsegmented worms, and the Myzostomida, a group of echinoderm parasites.

Polychaeta—A Multitude of Many-Bristled Worms

The polychaete worms represent the greatest diversity within the annelids, with more than 15,000 species divided among approximately eighty families, and estimates of over 5,000 species remaining to be discovered. Polychaetes display a wide range of morphologies and are found in nearly all marine habitats, including deep-sea hydrothermal vents and methane ice seeps. Fewer polychaetes are known from freshwater areas, and fewer than ten terrestrial species have been described. The previously distinct phyla containing the pogonophoran and vestimentiferan worms (important members of hydrothermal vent communities) are now placed within the polychaete family Siboglinidae.

Polychaetes typically undergo sexual reproduction and produce trochophore larvae, but asexual reproduction is also exhibited. During development, addition of segments occurs at a growth zone in front of the postsegmental region of the worms (pygidium) surrounding the anus. The presegmental region of the worm (prostomium) contains the cerebral ganglia and sensory structures; the mouth is positioned immediately posterior, surrounded by the first body segment (peristomium). Segments often display exterior projections (parapodia) with bundles of chaetae, although many species exhibit highly modified segmentation.

Divergence in body form among polychaetes



A. *Scolelepis squamata*, a polychaete found on sandy beaches where the worm suspension feeds by extending two palps from burrows. B. Two earthworms exchanging sperm during reproduction.

is based largely on the type of habitat and feeding biology of the species. The Nereididae (with more than 450 species) are common mobile predators of marine sand and mud habitats, feeding on invertebrates with the use of chitinized jaws. In contrast, members of the Capitellidae (with more than 140 species), Glyceridae (more than 75 species), Lumbrineridae (more than 200 species), and related families exhibit streamlined bodies (reduced parapodia) that aid in their burrowing way of life. These benthic worms are ecologically important deposit feeders and are often the dominant species in continental shelf and slope communities. Capitellids and other infaunal species are documented as pollution indicator species, revealing organically enriched areas.

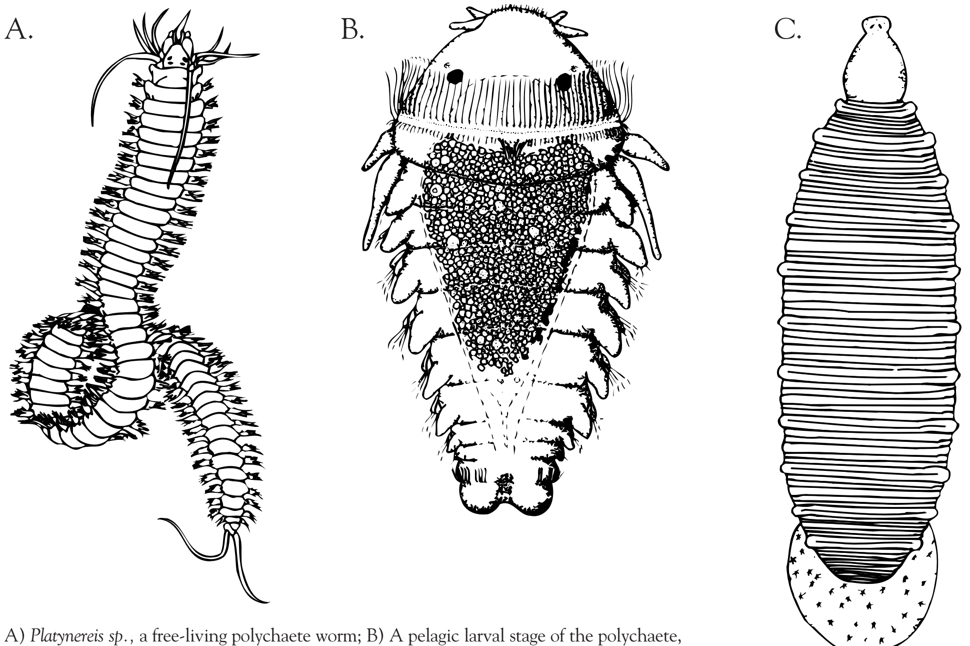
Many additional families contain members that are sedentary. The Sabellidae (with more than 300 species) and Serpulidae (more than 525 species) produce tubes by cementing sand grains together with mucus or secreting calcium carbonate, respectively. The feeding appendages of these worms are modified into a crown of tentacles that is used to filter food from the water; although common inhabitants of coral reef areas, few casual observers would recognize their colorful tentacular crowns as belonging to polychaetes. The Terebellidae (with more than 375 species) inhabit tubes or crevices and feed on deposited materials by means of numerous prehensile tentacles. Members of the Spionidae (more than 320 species) possess only two tentacles used for deposit or suspension feeding. Within this family, the genus *Polydora* and related genera bore into calcareous substrates. The worms can destroy commercially harvested mollusks (such as clams and scallops) and are therefore economically important pests. These and other polychaetes have affected marine ecosystems as invasive species introduced through ballast water or aquacultural shipments.

In addition to free-living and sedentary polychaetes, at least seven families contain pelagic species. More than 350 polychaetes have formed parasitic or commensal relationships with other phyla. For example, many of the symbiotic Polynoidae are found associated with echinoderms, and certain Syllidae are found associated with sponges, cnidarians, or other invertebrates.

Clitellata—Oligochaetes and Leeches

Unlike polychaetes, the clitellates exhibit a relatively uniform body plan with homogeneous segmentation. The oligochaetes and leeches are united in this class by the clitellum, a reproductive structure that produces mucous cocoons. Clitellates are hermaphroditic, with single individuals capable of producing sperm and eggs. Development is direct (no trochophore larvae) from eggs deposited in cocoons.

The subclass Oligochaeta contains more than 6,000 species distributed among at least twenty-five families. Oligochaetes are found mostly in freshwater and terrestrial habitats, although approximately 500 species have invaded marine areas. They range in size from interstitial species (of less than 1 mm) to giant Australian earthworms that reach lengths of more than 3 m and are considered one of the most endangered animal species. The Lumbricidae (with more than 300 species) contains those earthworms, which are perhaps the most familiar representatives of the Annelida. Most oligochaetes are detritivores, feeding on dead organic material. These worms have simple, conical prostomiums without head structures, and chaetae are present but in reduced numbers from polychaetes. The stout chaetae aid



A) *Platynereis sp.*, a free-living polychaete worm; B) A pelagic larval stage of the polychaete, *Eteone dilatae;* C) *Cystobranchus verrilli*, a leech parasite of fish in burrowing, and earthworms are thus able to perform the ecologically important functions of aeration and decomposition in soils. The Euhirudinea, or true leeches, are carnivores that derive nutrition from blood-feeding on vertebrate or invertebrate hosts or by ingesting small invertebrates. They are closely related to the Branchiobdellida (a group found only attached to the gills of freshwater crayfish) and the Acanthobdellida (represented by a single species of Arctic worm). Presently there are more than 600 recognized species of Euhirudinea placed into two orders, the Arhynchobdellida and Rhynchobdellida. Leeches lack chaetae and exhibit a fixed number of segments with reduced internal divisions. Further modifications include a caudal sucker and posterior sucker for attachment; the caudal sucker is also utilized in feeding. Leeches are generally restricted to freshwater environments, but some inhabit marine waters; a few are found in terrestrial areas of the tropics.

Among the Arhynchobdellida, the families Haemopidae and Hirudinidae possess serrated jaws used to pierce the body of hosts. The Rhynchobdellidae contain the Glossiphoniidae and Piscicolidae, members of which bore into the tissue of hosts through the use of a muscular proboscis. Many blood-feeding leeches have formed specific host-parasite relationships, and some species act as vectors for blood parasites of vertebrates. The benefits to man from leeches include the detection of polluted habitats as well as their use in microsurgery and in the development of anticoagulants.

—*Jason D. Williams*

See also: Alien Species; Benthos; Deep-Sea Hydrothermal Vent Faunas; Estuaries; Freshwater; Topsoil Formation

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Anthropology

Anthropology is a scholarly discipline that aspires to be the study of humankind, broadly defined. It has been classified at different times with the social sciences, the natural sciences, and the humanities. Any aspect of humanity may come under anthropological scrutiny. Although the discipline thus overlaps with many others, including sociology, psychology, and biology, the anthropological perspective remains unique by virtue of its methodology and approach. In its early days, anthropology emphasized the study of non-Western or preliterate peoples (the so-called primitive) and comparative sociological description. Contemporary anthropology finds its subjects in all corners of society and all walks of life, including the urban, Western, and postmodern. There are currently five major subfields of anthropology: sociocultural anthropology, archaeology, physical or biological anthropology, linguistic anthropology, and applied anthropology. These subdisciplines, while remaining more or less separate, have innumerable tendencies or currents within them. Anthropological research methods and techniques vary widely by subdiscipline and intellectual orientation, ranging from quantitative to qualitative, from statistical analysis to participant-observation. For most of its history, anthropology has distinguished itself from other disciplines through its focus on humans not as individuals but as members of groups.

The concept of culture as an organizing principle sets anthropology apart from other social sciences such as psychology (which seeks to understand individual motivation and behavior rather than group identity). The enormous variety in human languages, customs, modes of socioeconomic life, beliefs, and ecological adaptation is subsumed under the general concept of culture. Sociocultural anthropology, the largest of the subfields, is a compound term incorporating the British stream of social anthropology, the American stream of cultural anthropology, and French structuralism. In the trajectory of American cultural anthropology, the twentieth-century Boasian school was linked to the nineteenth-century German intellectual tradition. Alternatively, for much of the twentieth century, a rival school, based in British social anthropology and known variously as structural-functionalism, increasingly held sway. Other schools have had considerable influence on Western anthropological thought as well, in particular the French lineage originating with the sociology of Durkheim and Mauss, extending to the structural anthropology of Levi-Strauss, and the poststructuralism of the late twentieth century.

Physical anthropology is the study of humans as biological organisms. Evolutionary anthropologists and primatologists compare human beings to their hominid predecessors and to other primates, including apes and lemurs. In the nineteenth century, the main school of physical anthropology was concerned with anthropometry, the measurement of skeletal and anatomical features, in order to classify people into racial categories called physical types. This method of categorizing relationships among people was gradually shown to be scientifically invalid. Forensic anthropologists assist in legal proceedings and humanitarian work by identifying human skeletal remains. Medical anthropology is an interdisciplinary branch of anthropology that studies cultural, physiological, and environmental factors in illness, disease, and healing.

Archaeology is the study of antiquity and the past through the excavation and analysis of buried settlements, graves, artifacts, and remains. The division between prehistory and history was not applied in Europe itself, where the past has been studied as a continuous epoch. The establishment of the Smithsonian Institution in 1846 accelerated the formation of American archaeology. Nineteenth-century archaeologists read cultural patterns from excavated artifacts in a kind of prehistoric ethnology. Geology has had a strong influence on archaeology, sharing techniques of surveying, mapping, excavation, dating finds, and reconstructing prehistory. In the twentieth century, stratigraphic techniques increased knowledge of cultural change in prehistory. After 1950, American archaeologists shifted their focus from reconstructing patterns of diffusion and migration to examining internal processes as a source of cultural change. Environmental factors and transformations within individual societies could be read through the distribution patterns of artifacts, houses, and settlements. Spatial archaeology focuses less on artifacts and more on habitation patterns as keys to ethnohistory and the ecological interactions of humans with their environment, with an emphasis on reconstructing household organization and social structure.

Linguistic anthropology focuses on the social aspects of language systems, speech acts, and communication behavior. Its forms include descriptive constituent analysis of language sound and structure, reconstructive historical linguistics and glottochronology, the sociolinguistics of speech communities, language planning and policy, and the ethnography of communication. Applied anthropology investigates human relations and their application to practical matters. Applied anthropologists utilize methods of participant observation and ethnographic interviewing in projects that seek to assist clients and interest groups.

The human quest for self-awareness is documented at least as far back as the inscription "Know thyself," carved over the entrance to the Oracle of Apollo at Delphi in the 6th century B.C.E. The Delphic ideal has proved to be an elusive one, in both the realms of individual psychology and group sociology. The reportage of Greek historians are counted among the earliest chronicles of a comparative or cross-cultural character. Tales of Africans in the Roman Pliny the Elder's *Natural History* blended observed ethnographic fact with fantastic fables drawn from voyagers' chronicles. During the eighteenth century, Enlightenment thinker Alexander Pope's *Essay on Man* modified the ancient injunction to individual self-knowledge, broadening its aspect to humanity in general with these words:

> Know then thyself, presume not God to scan,
> The proper study of mankind is Man.

According to Boas, Magnus Kunst in 1501 was probably the first to use the term *anthropology* to mean the study of man from the psychological point of view, as did Immanuel Kant in the late eighteenth century. Blumenbach first used the term *anthropology* to describe the study of man from a physical point of view. These two branches of anthropology in the modern sense were first brought together by W. Edwards in 1839. In France anthropology was defined as a branch of the natural sciences studying the human family in itself and in relation to nature. In Germany the term *anthropology* usually referred to physical anthropology only, while ethnology denoted the psychological side of the field. In the United States eighteenth-century philosophy had primarily meant practical science. Thomas Jefferson became the first anthropologist in the United States when he published *Notes on the State of Virginia,* detailing American Indian botany and languages, to prove to Europeans that the New World had a history and a civilization worthy of the name. Native America was the classic subject of U.S. anthropology in its formative years of the late nineteenth and early twentieth centuries.

Social Darwinism and racial anthropologies developed in Germany around the same time. The principal challenge to social evolutionism came in the form of diffusionism, as exemplified by the German *kulturkreislehre*, or culture-circle school. Diffusionists reasoned that similar traits found in widely dispersed societies—including material culture forms—could be traced back to earlier dispersal from centers of civilization. Objects, traditions, languages, and religions moved outward in radiating concentric circles from classical centers like Java and China into surrounding areas and ultimately to remote outposts. As fashions changed in the center, they sent out ripples of change in a wave effect that grew weaker toward the periphery. The most remote forms thus represented the oldest survivals and the earliest layers of culture. But no people is marginal to itself. The extreme form of diffusionism ruled out independent invention as an explanation for the resemblance of widely dispersed phenomena or material forms, attributing innovation to the so-called high civilizations such as China and India, and their colonizing missions to other parts of the world. In his studies of Northwest Coast material culture, however, Boas found that like effects often sprang from unlike causes, and that the meaning of an object lies in its function, not its form.

At the end of the nineteenth century, Boas was among the first to use the term *cultures* in the plural to signify the lifeways of specific groups rather than *culture* in the abstract, which at the time carried connotations of universal development along an evolutionary scale. His anthropometric studies of growth among European immigrants to the United States showed the inherited characteristics of biology and physical adaptations to environment and nutrition as interdependent variables that could influence each other over time (Boas, 1940). Boas's inductive method meant that grand theories could be built up only from a proliferation of fact and artifact, not derived from universal hypotheses. The background of this battle was rooted in two conflicting worldviews driving nineteenth-century scholarship: evolutionism and diffusionism. Cultural evolutionists, reasoning that Darwin's natural selection extended into the social realm, held that all societies went through comparable stages of development. So-called primitive peoples occupied a lower rung on the ladder of evolutionary progress, while Northern Europeans and Americans were at the top. Social evolutionists considered the cultures and social institutions of preliterate societies to reflect earlier stages of European history. Although the influence of Victorian British anthropologists such as Frazer and Tylor remained strong, U.S. scholar Lewis Henry Morgan, who studied the Iroquois in the 1870s, created a particularly influential evolutionary model according to which human societies passed through three stages: "savagery," characterized by hunter-gatherer subsistence and band-level organization; "barbarism," in which settled communities based on cultivation arose; and "civilization," marked by the introduction of writing. The inherent racism and ethnocentrism of this view suited the imperial aspirations of European colonial powers administering native subjects about whose ways they knew little and understood less.

Any measurement of physiological difference within racial or cultural groupings was found consistently to be at least as great as that between groups, demonstrating that racial categories conceived as such are not fixed biological barriers but exist as socially defined boundaries on a continuum of characteristics, impressions, or measurements imposed by an observer rather than on strict divisions inherent in nature. In place of either an evolutionary ladder of social development or the none-too-human theories of polygenesis, Boas posited that physiological variation was the result of long and complex tribal histories of migration, intermarriage, and other events that could be reconstructed by careful collection of material and analysis of data ranging from human bones to pottery shards to folklore. Language and culture were shown to be acquired independently of racial "type" or national origin. Although the underlying psychic unity of mankind remained the wellspring of our most fundamentally human institutions, the social and psychological particularities of our customs, values, and behavior owe more to nurture than nature. Environmental constraints, climate and topography, energy and resources became increasingly important to anthropologists through the twentieth century, as fieldwork became the hallmark of the discipline and as successive generations of scholars developed empirically based theories of the forces shaping human cultures.

An ardent opponent of the pseudoscientific reductionism of social Darwinism, Boas was influenced by the German diffusionist school. Adolf Bastian was alone at the time in occupying a middle-ground position. Bastian, who traveled and collected widely, believed that similarities in the form of objects and customs reflected a basic underlying psychic unity of mankind. This theory partially agreed with evolutionists insofar as it posited monogenesis, the idea that humanity is a single species with a single origin. The opposing view, polygenesis, contended that nonwhite peoples were descended from different primeval ancestors and were actually members of a species different from and inferior to Northern Europeans—a widely held view among scientists in the nineteenth century. Boas and others, collecting anthropometric data, helped to disprove the pseudoscientific racism of polygenesis and the eugenics movement and to turn anthropology away from the rigid racial categorization of physical types toward a more complex and realistic understanding of human differences.

Anthropology was distilled by Boas into the tripartite model of race, language, and culture seen as independent, interrelated variables. Boas, generally regarded as the "father of American anthropology," devoted considerable attention to physical anthropology and linguistic studies but considered the psychological aspects of the field to be of paramount interest. He emphasized that anthropology was distinct from other fields in its concern with the study of man in society, not as an individual. Material culture of the sort collected and displayed in museums was taken as evidence, either of historical patterns or of evolutionary stages of development, depending on the worldview of the investigator. Boas was instrumental in shifting the discipline from a museum-based approach to a university-centered one, paralleling his gradual shift from a search for universal laws of human behavior to the historical particularism that considered each culture to be a unique product of complex combinations of circumstances. At the same time, anthropological methodology moved away from the armchair approach of nineteenth-century scholars to the fieldwork model exemplified by Bronislaw Malinowski's participant-observation studies in the Trobriand Islands during World War I. At the close of his classic *Argonauts of the Western Pacific* (1922), Malinowski added a comparativist corollary to the ancient Delphic wisdom and defined the fieldwork paradigm that would be the distinguishing characteristic of anthropology. We cannot know ourselves, he wrote, "if we never leave the narrow confinement of the customs, beliefs and prejudices into which every man is born. Nothing can teach us a better lesson in this matter of ultimate importance than the habit of mind which allows us to treat the beliefs and values of another man from his point of view." Malinowski's treatise was a call for mutual understanding and tolerance issued in the context of the urgency of World War I. The perspective of self and other pertained to the West and the colonial world; cultural relativism was a lens through which to correct the habits of ethnocentric vision. As pragmatist philosopher Henry David Thoreau had advocated, the perhaps impossible precept "Know thyself" was translated into the more possible "Know what thou canst work at."

Much of modern anthropology was a reaction to and rejection of Boasian methodology. The schools of cultural evolution and cultural materialism, which had their heyday in the 1960s and 1970s, were derived from Marx's axiom that the mode of production determines a society's structure and superstructure. The principle of "infrastructural determinism" seeks first causes of human behavior and the social phenomena of consciousness in environmental circumstances. The basic model was borrowed from the earlier ethnographic works of Lowie, Kroeber, Wissler, and Steward, as in the ecological adaptation of Plains Indian cultures following the introduction of the horse to North America. One problem with the cultural materialist paradigm is its disavowal of the role of thought, human agency being reduced to its interplay with the environment and divorced from the abstract reasoning, conceptual thinking, and ideational creativity that have enabled the human species to profoundly alter its own environment.

Postwar anthropology expanded its subject matter to include industrial and postindustrial societies and Western cultures. In the postcolonial era, anthropology critically examined its own colonial roots and underwent a radical self-evaluation. This reflexive turn, beginning in the 1960s, has become increasingly prominent since 1980. The fragmentation of the discipline has increased, as biological and culturalist orientations move further apart. Many anthropologists serve as activists for the interests of the people they study, as in the political struggle over land claims in the Amazon between the Yanamamo Indians and centralized state governments. Anthropologists remain in the center of controversies surrounding the origins of the first Americans—as in the struggle among scientists, Indians, and the Army Corps of Engineers over the proper disposition of early human remains found in Washington state and known as Kennewick Man.

Anthropology continues to make contributions toward mutual human understanding, equality, and tolerance in a multicultural world. Anthropological knowledge and technique are increasingly used as tools in the assertion of territorial and human rights, as well as the politics and poetics of identity. The preservation and study of biological and cultural diversity is a disciplinary descendant of salvage ethnology, environmental studies, and ethnoscience. The emergence of new biocultural paradigms recalls Ralph Waldo Emerson's assessment of the evolution of the Delphic exhortation to knowledge: "And in fine, the ancient precept, 'Know thyself,' and the modern precept, 'Study nature,' become at last one maxim."

—*Thomas R. Miller*

See also: Archaeology and Sustainable Development; Ethnology; Ethnoscience; Linguistic Diversity; Physical Anthropology

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Ants

See Arthropods, Terrestrial

Archaebacteria

Archaebacteria ("old bacteria") are one of two fundamentally different kinds of bacteria, the other being eubacteria ("true bacteria"). Archaebacteria, made of prokaryotic cells, are distinguished by several biochemical features that include characteristic 5S and 16S ribosomal RNAs, lipids linked with ethers (R-O-R) rather than esters (R-C-OH), and a lack of peptidoglycan in their cell walls. They may be an ancient life form, little changed from their original ancestors, primarily because of the similarities among their long-chain RNA molecules; since these are found in the ribosomes of all organisms, they probably have not changed much over evolutionary time.

Although bacteria do not fossilize well and thus have historically proved difficult organisms to classify on the basis of evolutionary history, advances in molecular biology and its study of the macromolecules making up life have clarified the ancestral relationships among these organisms. In the latter part of the twentieth century, American biologist Carl Woese and German biologists Otto Kandler and Wolfram Zillig led the charge to reclassify living things based on this genetic revolution. It is not surprising to learn that, reminiscent of what are thought to be the earliest life forms, these bacteria contain some of the most resistant beings on earth, the so-called extremophiles. Many are able to withstand temperatures and conditions quite inhospitable to the majority of modern surface dwellers, including many other bacteria, all plants, animals, fungi, and protoctists. Among the archaebacteria are the methanogenic bacteria that are poisoned by oxygen. Other archaebacteria are halophils, salt lovers that thrive in high concentrations of sodium chloride (salt like that prevailing in Great Salt Lake near Salt Lake City, Utah). Still others are thermoacidophils that are able not only to live but also to reproduce in boiling hot springs under sulfuric acid conditions. Some (Koreabacteria) are detected in moderate marine waters solely on the basis of their ribosomal RNA sequences. That the archaebacteria can grow in dry salty oceansides, in boiling muds, in and around erupting volcanoes, in Old Faithful at Yellowstone National Park, and under the water at ocean bottom in submarine vents pouring forth sulfide-rich fumes speaks to their ancient heritage: although scarce and inhospitable to the majority of life forms today, such environments were no doubt much more common on the early earth during the Archean Eon. Geologist Jack Corliss argues that deep sea vents, full not only of sea creatures such as giant tube worms (pogonophorans) but also of methanogenic archaebacteria, are those ecosystems most like the environments of life during its beginnings, more than three and a half billion years ago. The chemistry of these zones is less dependent on sunlight and oxygen than modern surface ecosystems, thus agreeing with paleobiological reconstructions of the ancient planet.

The very name archaebacteria, in conjunction with an emphasis on the antiquity of these organisms (rather than on their molecular biological features), seems to argue against Woese and others who would divide life into three kingdoms: one eubacterial, another archaebacterial, and the last composed of all the nucleated or eukaryotic organisms. Because of our vantage point as humans, we cannot help be the measure of all the things we observe, and thus, important as it is, molecular biological comparisons of organisms is not the only criterion for comprehensive classification. Recombination mode, presence or absence of embryos, of absorptive, heterotrophic, or photosynthetic nutrition, behavior, and morphology must also be taken into account. Thus in the five-kingdom classification system, archaebacteria are not given their own kingdom (or "domain," as Woese calls Archaea) but considered one of two great bacterial subkingdoms. We prefer the term Archaebacteria to Archaea, because the latter downplays the undeniable fact that these microscopic beings share the structural details, much of the physiology, and the genetics of the rest of the bacteria.

—Lynn Margulis and Dorion Sagan

See also: Bacteria; Benthos; Classification, Biological; Evolution; Evolutionary Genetics; Five Kingdoms of Nature; Microbiology; Oxygen, History of Presence in the Atmosphere

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Archaeology and Sustainable Development

One of the greatest threats to natural biodiversity arises from the growing imbalance between human populations and the availability of food, which is especially acute in many of the world's least prosperous nations. Food scarcity lies behind the encroachment of extensive slash-and-burn agriculture upon natural tropical forests, a major cause of biodiversity loss. How can the needs of poor, hungry people be reconciled with the laudable goal of preserving natural biodiversity? To find a solution, we will have to devise effective strategies of sustainable development; these are policies and programs that not only stimulate progressive economic growth but also are socially and environmentally sustainable. The UN World Commission on Environment and Development has defined sustainable development as "development that meets the needs of the present without compromising the ability of future generations to meet their own needs" (WCED, 1987, p. 43).

Designing and implementing sustainable development strategies will be neither quick nor easy. For example, while it seems obvious that reducing human population growth should be a high priority, birth control programs will not succeed on the global level without fundamental reforms in education, health care, and the status of women; such reforms, unfortunately, will probably take many years. A more promising, though more complex, approach is to seek environmentally and socially sustainable ways of increasing food production while simultaneously applying the brakes to human population growth.

One potentially sustainable strategy for enhancing food production involves agricultural intensification, the purpose of which is to increase agricultural yields without expanding the overall area under cultivation. What forms of agricultural intensification might be most effective in less-developed nations? Although it is true that agricultural yields can be increased through "green revolution" programs (usually involving high-yielding crop strains, mechanization, chemical fertilizers, and pesticides), researchers have found that such approaches are costly and tend to favor wealthy farmers over poorer ones, giving the latter no choice but to pursue the more extensive kinds of cultivation that are so damaging to natural biodiversity. Canal irrigation and other water management techniques are forms of agricultural intensification that tend to be more widely available. Yet such methods can enhance food production over the long term only if water is employed efficiently, with maximal benefit to crops and with minimal waste.

Researchers have found that water-use efficiency is often hindered by bureaucratic incompetence, water-access disputes, wasteful applications, and, increasingly, human-induced climate changes that are altering the global distribution of water. Among the likely effects of global warming will be a climatic regime in which some areas receive far less rain and others far more than is currently the case. Future water management projects will have to be flexible enough to deal with such climatic perturbations, along with an array of political and technological challenges. One outstanding question in this regard is whether small-scale strategies, low in cost and tailored to local conditions, might actually be more sustainable over the long run than large-scale projects run by centralized bureaucracies. Of course, such a question cannot really be answered without long-term information on the successes and failures of various kinds of agricultural systems. Archaeology is one field that is especially qualified to provide such long-term data on strategies of water management and agricultural intensification in other times and places. Let us look at some examples.

In Mexico and Venezuela, archaeologists have studied the remains of small-scale agricultural systems that, in pre-Hispanic times, actually sustained larger human populations than do the modern systems now in use in those same localities (Spencer 2000). One example involves human settlements associated with the Purrón Dam, an ancient dam and irrigation system in the Arroyo Lencho Diego locality of the Tehuacán Valley, Mexico. Only 260 people lived at San Rafael in the Lencho Diego region in 1990, sustained by water from a long and costly irrigation canal built by the federal government to transport water from a distant source. By contrast, the ancient agricultural system used water from the local arroyo and yet managed to support a population of 975 to 1,190 (based on the number of archaeological households) during the Early Palo Blanco phase (150 B.C.E.–250 C.E.). A second case is the archaeological site of La Coyotera, near Santiago Dominguillo in the Cañada de Cuicatlán, Mexico; this site is also associated with a pre-Hispanic irrigation system. In 1990 the Dominguillo locality had a population of 477, but one thousand years ago some 1,345 to 1,675 people were sustained by irrigation agriculture there, even though the ancient system was less centralized and much smaller in scale than the irrigation systems recently built by the federal government. A third example is from the western Venezuelan state of Barinas, where archaeologists have surveyed and excavated the La Tigra drained-field agricultural site, in the alluvial zone of the Gaván Locality. The drained-field technique involved the digging of multiple canals, and it required a moderate investment of labor; yet it allowed for the cultivation of two crops per year (instead of just one). The canals served to collect scarce rainwater at the onset of the rainy season, and they also promoted proper drainage in the alluvial zone during the peak of the rainy season; the result was a lengthening of the growing season and a doubling of productive output. At present the economy of the Gaván Locality is oriented toward large-scale ranching, and the area is home to hundreds of cattle but only some fifty people. Yet during the Late Gaván phase (550–1000 C.E.) the human population here totaled between 925 and 1,375, supported in part by the drained-field system.

These cases suggest that archaeological data on traditional agricultural systems could be put to good use by contemporary planners who are trying to find low-cost, sustainable ways to increase agricultural production in tropical countries. These three systems were all relatively small in scale; they required only modest amounts of local labor for their initial construction and drew strictly upon local sources for their water supply. The operation of these systems did not cause any detectable biodiversity loss in their natural settings. Nor is there evidence that an elaborate bureaucracy was required to build or manage any of them. Yet they worked well for hundreds of years, and their success provides support for the argument that small-scale, local solutions are potentially more sustainable than large-scale, centralized strategies of agricultural intensification (see Mabry 1996).

From archaeology we can learn which strategies have worked in the past, under what conditions, and for how long. We can draw upon such data as we try to plan wisely for what lies ahead.

—*Charles S. Spencer*

See also: Agriculture and Biodiversity Loss: Industrial Agriculture; Population Growth, Human; Subsistence; Sustainable Development

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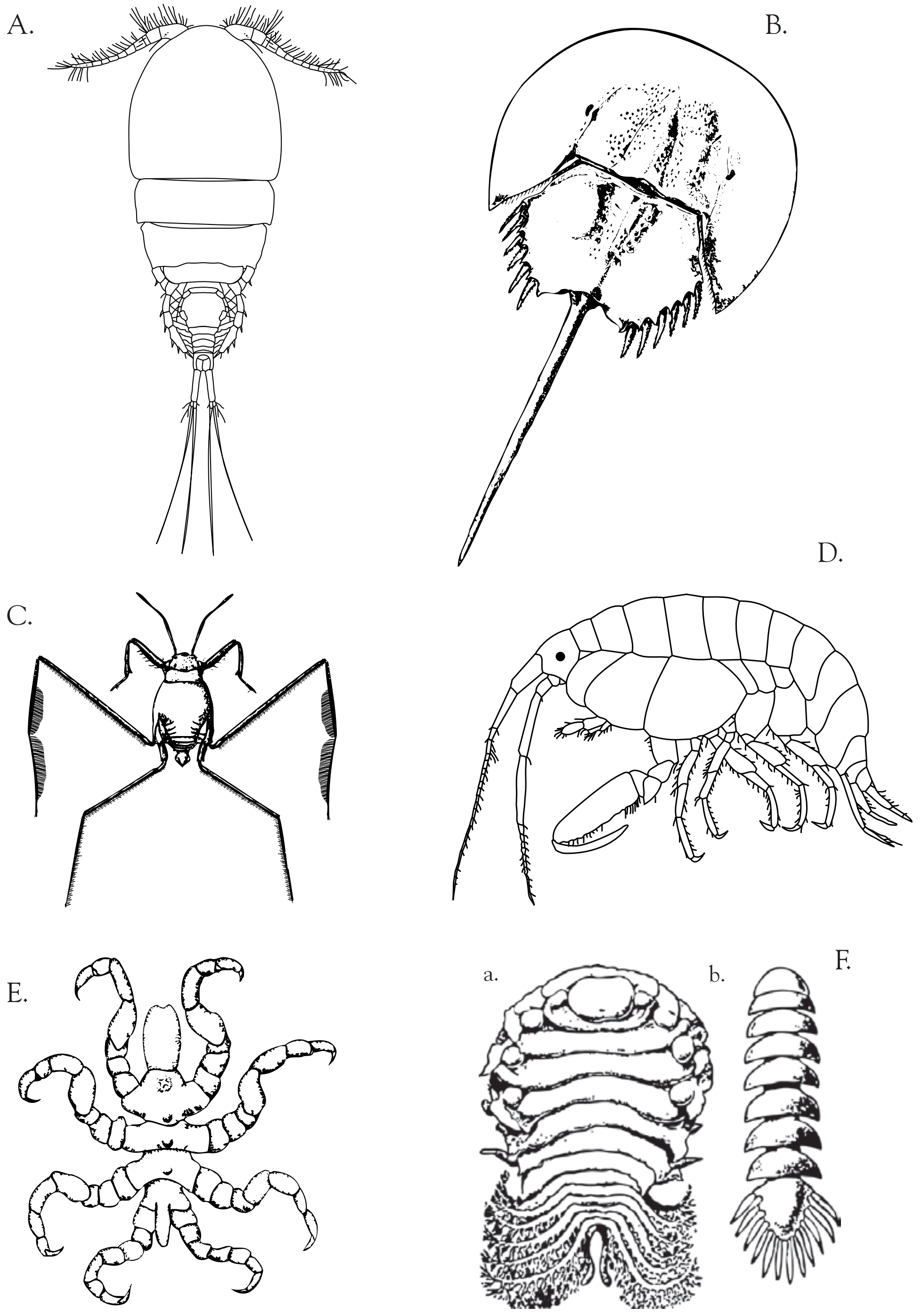
Arthropods, Marine

Arthropods are the most numerous animals on earth in terms of described species, with approximately 1.25 million taxa. However, that probably represents only a portion of the total number of arthropod species in the world, with estimates of diversity (including undescribed species) starting at 2 million. People are perhaps most familiar with members of the Insecta, and indeed they constitute the bulk of arthropod species whose successful colonization of land led to their rapid radiation in form and function and their habitation of nearly all terrestrial regions, with many species occurring in freshwater as well. Insects, however, represent only a portion of the morphological diversity present in the arthropods and are not the dominant arthropods of the seas.

The organisms that are grouped together under Arthropoda are those that possess metamerism (that is, segmentation) and a pair of appendages on each segment (although these may be lost on some segments in the more derived taxa). Arthropods also possess such synapomorphies (shared characters) as a chitinous exoskeleton that is molted at intervals (controlled by the hormone ecdysone) and an absence of cilia on or in the body. Many scientists consider the velvet worms (Onychophora) and water bears (Tardigrada) to be the two phyla most closely related to the arthropods.

Of all described arthropods on the planet, only a small percentage, perhaps 3 to 5 percent, are adapted to an exclusively marine life. This includes the majority of Crustacea (approximately 50,000 species); all of the Pycnogonida, or sea spiders (with more than 1,000 species), and Xiphosura, or horseshoe crabs (4 species); and a few Arachnida (approximately 1,000 species). The Insecta, with more than 1.1 million described species, are extremely poorly represented in the marine environment, with only a few hundred species in the intertidal zones and near-shore environments, and a mere five species of water-striders (*Halobates*) and perhaps a few midges (Diptera) being found on the open ocean. The myriapods (millipedes, centipedes, and so forth) have no marine representatives. In keeping with the fact that the oceans constitute a semicontinuous worldwide habitat, almost all the marine arthropod higher taxa (except the horseshoe crabs) today have an essentially worldwide distribution, at least within a broad latitudinal range.

The small percentage of arthropods found in the marine environment stands in sharp contrast to the fact that the seas were home to the earliest arthropods. Early representatives, such as the chelicerate horseshoe crabs (Xiphosura) and sea scorpions (Eurypterida), as well as primitive crustaceans such as those found in the Burgess Shale deposits in Canada, shared the seas with the now-extinct trilobites. Although the trilobites were a moderately



A) Copepod (Copepoda) *Aphotopontius forcipatus;* B) Horseshoe crab (Xiphosura) *Limulus polyphemus;* C) Water-strider (Insecta) *Halobates micans;* D) Amphipod (Amphipoda) *Stenothoe marina;* E) Sea spider (Pycnogonida) *Pycnogonum stearnsi;* F) Parasitic isopod (Isopoda) *Ione cornuta*, a: female, b: male successful group of wholly marine animals (approximately 4,000 species), they were, for reasons unknown, unable to survive the climatic changes at the end of the Permian and left no descendants. Although their basic body plan did not vary as widely as in some other arthropod groups, which may have contributed to their extinction, they did exhibit a remarkable array of variation in form and armature.

Chelicerata: Horseshoe Crabs, Sea Spiders, and Marine Mites

There are about 94,000 described chelicerates, those arthropods that lack antennae, possess chelicerae (feeding appendages), and have the body divided into a cephalothorax and abdomen. Most chelicerates are arachnids (spiders and their kin; approximately 93,000 species), but only about 2,000 chelicerate species are found in purely marine habitats. The majority of these marine taxa fall into two groups: the sea spiders (Pycnogonida) and the mites (Acari). In contrast to the sea spiders, which are exclusively marine (with more than 1,000 species), only about 1,000 of the 45,000 described mites are known from truly marine habitats. Many mites have adapted to life in mildly halophilic (salt-loving) habitats, such as beaches and salt marshes, but relatively few species have secondarily adapted to a truly marine environment, making them the only arachnids to do so. Most marine mites are shallowly subtidal, but some species have been taken from abyssal depths as deep as 7,000 m. Mites are difficult to define morphologically as a group, and the synapomorphies (that is, shared evolutionary characters) for uniting them are unclear. In fact, the term *mite* is used for three distinct orders of chelicerate arthropods: Opiloacariformes, Parasitiformes, and Acariformes; the last two orders have only marine representatives. Marine mites contain both free-living species and parasites of both marine reptiles and invertebrates.

Unlike mites, the pycnogonids all share a fairly homogeneous body plan. They are perhaps the most poorly known arthropods, both in terms of biodiversity and biology. As a group they are defined by the presence of a piercing proboscis and a pair of parapalps behind the chelicerae. Many species are known only from single specimens, and the distributions and biology of most taxa are unknown. Most pycnogonids are small and subtidal, but some are large (for example, *Dodecolopoda*, with a legspan of up to 60 cm); a few species are known from depths down to 6,800 m. All are free-living as adults, but some species develop within hydroids and are thus parasitic in part of their lifecycle.

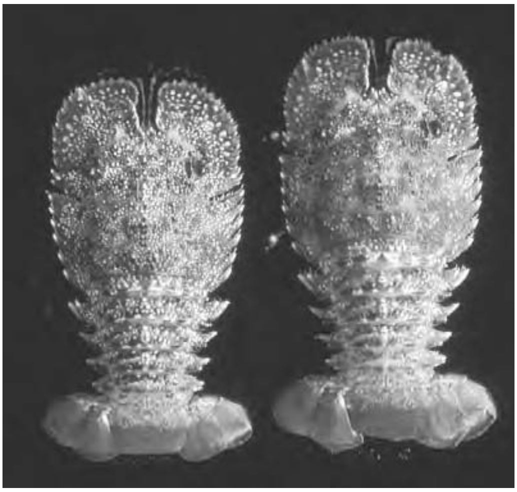
The horseshoe crabs are the best known marine chelicerates, despite the fact that there are only four extant species in three genera (*Limulus*, *Carcinoscorpius*, and *Tachypleus*). These animals have fused thoracic segments and reduced/fused abdominal segments. They resemble the primitive chelicerates of the Cambrian and are close relatives of the extinct sea scorpions. Three of the four extant species live in the Indo-Pacific ocean, while the fourth occurs in the western Atlantic, from Nova Scotia to the Yucatan Peninsula; all are free-living. All of these species have been heavily impacted by overfishing for use as bait (for example, for lobster and whelk fisheries in the United States), and all have received some measure of protection in at least part of their ranges, especially in Japan and the mid-Atlantic United States. They are unique among marine arthropods in coming ashore on sandy beaches to breed; their eggs, as a food source, are intimately involved in the lifecycles of numerous species of terrestrial animals, principally migratory birds.

Marine Insecta: Water-Striders and Midges

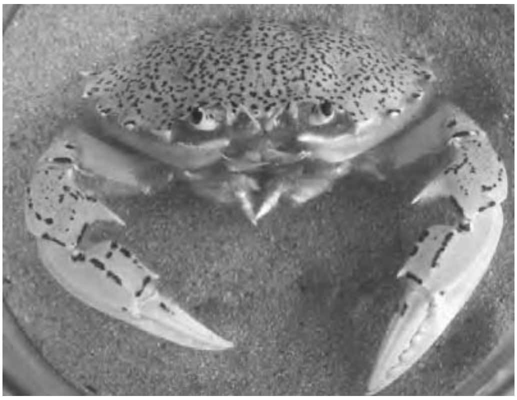
Insects evolved from a marine ancestor in the distant past (fossil insects are known from the Devonian). However, only a limited number of taxa have reinvaded the marine environment, and all are adapted to living on the ocean surface rather than at depth and are air-breathers; none can survive lengthy immersion in seawater. This limitation is reflected in many of the synapomorphies of the insects, such as the presence of tracheae and malpighian tubules, which are direct adaptations for terrestriality and do not function properly underwater. A number of insect orders (for example, Hemiptera, Diptera, and Coleoptera) contain taxa that have some degree of halophilic tendencies, but, like the arachnids, these are almost all confined to salt marsh and intertidal habitats. The only insects that live out their lives wholly on the ocean are the five species of *Halobates* (water-striders) and a small number of midges, whose larvae are found free-living at or near the surface. It appears that the insect body plan, so successful on land and in freshwater, is not only unable to cope with a highly saline environment but, in addition, has not been able to adapt secondarily and reinvade the oceans. Even insect parasites of marine birds and seals, such as lice, are not truly marine, inasmuch as they cannot stand lengthy exposure to sea water; there are no insects parasitic on whales.

Crustacea: Masters of Marine Arthropod Diversity

There are approximately 52,000 described species of crustaceans, and many of those have successfully colonized freshwater habitats (for example, crayfish, conchostracans) and terrestrial habitats (for example, land crabs, pillbugs). But the majority of the species occur today in the same marine environment as their ancestors in the Cambrian Era. Unlike the case of insects or other invertebrate phyla, it is difficult to speak of a “typical” crustacean form, or bauplan. All crustaceans possess two pairs of antennae, one pair of mandibles, and two pairs of maxillae on a five-segmented head-shield (cephalon), but two or more of these segments are typically fused, depending on the crustacean group. Likewise, the body segments tend toward fusion and a corresponding reduction in appendages. This variation has resulted in a wide diversity of basic forms within the Crustacea, perhaps more than in any other phylum. Many crustaceans possess forms that, although distinctly unalike, are immediately recognizable and familiar: this includes the crabs, shrimp, and lobsters (Decapoda, with more than 10,000 species, 90 percent marine); bivalved ostracods (Ostracoda, 5,500 species, mostly marine); copepods (Copepoda, with more than 8,000 species, mostly marine); and barnacles (Cirripedia, with more than 1,000 species, all marine). The importance of these groups in the marine food web, and as direct or indirect food sources



Lobster (Decapoda)* Parribacus perlatus *(Courtesy Christopher B. Boyko)



Crab (Decapoda) **Ovalipes** *sp. (Courtesy Christopher B. Boyko)*

for humans, is well documented. However, many other crustacean groups are equally numerous, either in numbers of individuals or species. An example of the former is the pelagic euphausids (Euphausiacea) with only 85 species, all marine, but in population size large enough to form a major food resource for whales.

Members of the Peracarida exemplify taxa with low numbers of individuals (many species are still known from only a single specimen) but with a high diversity of species. Peracarids include isopods (Isopoda, with more than 4,000 species, about two-thirds marine); amphipods (Amphipoda, more than 6,000 species, mostly marine); cumaceans (Cumacea, more than 800 species, all marine); and tanaids (Tanaidacea, 500 species, all marine). All peracarid groups occur worldwide and at various depths, but they are perhaps most important in that they make up a substantial portion of the deep-sea benthos and may well play important roles in deep-sea ecological processes about which we currently know very little.

The diversity of form that runs through the Crustacea is also likely to have impacted the ability of these animals to exploit almost every type of habitat. Marine Crustacea occur in all oceans and at all latitudes and depths. They also occur in large numbers at some of the most inhospitable regions of the planet, such as at black smoker vents and hydrothermal seeps at abyssal depths. Most marine crustaceans are free-living and tend to be predators, scavengers, or detritivores (for example, shrimp, crabs, cirolanid isopods) or filter feeders (for example, nonrhizocephalan barnacles, porcelain crabs). However, both the Copepoda and Isopoda have numerous parasitic species on a variety of other animals. The amphipods, with the Cyamidae (whale-lice), and the barnacles, with the Rhizocephala, each have one lineage that is exclusively parasitic. Only the Branchiura, or fish-lice, are wholly parasitic and found only on cold-blooded vertebrates; this group is found mostly in freshwater, but there are a few marine species.

Some crustaceans have evolved mechanisms that allow them to colonize both land and freshwater environments (for example, pillbugs, land crabs), and these are considered the most derived taxa within their respective groups. This, coupled with the example of the insects, suggests that the evolution of terrestriality is one-way and that once fully adapted to land, a given lineage cannot return to the sea. However, some Crustacea are more tied to the land than others. Some species, such as all the so-called land crabs (Gecarcinidae), must return to the ocean to release their progeny, as their larval stages require development in the marine environment and thus tie these species to the sea.

Conservation

No marine arthropods are presently listed as endangered, although some, such as horseshoe crabs and certain commercial crustacean species (such as lobsters) are considered threatened in at least part of their range and are protected by collecting restrictions. This is probably more a function of our lack of knowledge regarding the biodiversity of marine organisms at the species level and higher than a true representation of the health of marine arthropod populations. Special care should therefore be taken to protect such commercially valuable species until thorough assessments can be made on the impact of fishing practices on these marine arthropods and the habitats in which they live.

—*Christopher B. Boyko*

See also: Arthropods, Terrestrial; Biogeography; Oceans; Phylogeny

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Arthropods, Terrestrial

Arthropods, a large phylum of jointed animals with an exoskeleton, had marine origins more than 550 million years ago. The first records of animal life on land were other arthropods, which appeared approximately 100 million years later. This eventually led to a modern diversity of more than 1.5 million known species, most of which are winged hexapods, the insects. Arthropods are pivotal for terrestrial ecosystems, as phytophages, pollinators, parasites, predators, and detritivores. Some species are vectors of epidemic diseases; others live in the most complex societies in the natural world. A combination of small size and exoskeletal structure allowed arthropods to invade various terrestrial niches. Generally short generation time and, for winged insects, excellent dispersal ability has also made most species genetically highly adaptable. These factors probably led to the unparalleled success of terrestrial arthropods in the 4 billion years of life on earth.

The Major Groups of Terrestrial Arthropods

SUBPHYLUM CHELICERATA: Arthropods with two pairs of head appendages used for feeding (chelicerae) and modified for various functions (pedipalps). All terrestrial species are predatory, with exception of the highly diverse mites.

CLASS ARACHNIDA:

Acarina (mites). The Acarina constitute the largest group of arthropods besides insects, with approximately 50,000 species known, and an exceptional diversity of forms and habits. Because of their obscure size, most still need to be described. They include species that feed on fungi and plant tissues, and those that cause plant galls; they are predators and parasites of a great range of arthropods and other animals. Typical acarine parasites of vertebrates include mange (Psoroptidae), chiggers (Trombiculidae), and the blood-feeding ticks (Ixodida).

Araneae (spiders). The Araneae are an ancient group, known first from the Devonian, approximately 400 million years ago. Most spin silk for aerial webs, snag lines, or drag-lines on the ground, to either snare or detect arthropod prey. Some, such as wolf spiders (Lycosidae), fishing spiders (Pisauridae), crab spiders (Thomisidae), lynx spiders (Oxyopidae), and jumping spiders (Salticidae) stalk prey and spin little or no silk. *Scytodes* "spits" a poisonous "glue" to subdue its prey. Some 40,000 species of spiders range in size from barely a millimeter in length to the "bird spider" tarantulas of South America, 20 cm (8 inches) in leg spread. All spiders secrete venom for killing prey, among the most toxic being *Lactrodectus* (black widows, red backs) and *Loxosceles* (brown recluses), which occur in warm temperate and tropical regions. Less well known are the funnel-web spider of Australia (*Atrax*), and probably the most venomous and aggressive of all, the Ctenidae of South America. The bite of one ctenid, *Phoneutria fera*, secretes a poison that can kill 300 mice. Despite their reputation and even the common phobias about them, spiders are important as among the most notable predators of terrestrial arthropods.

Pseudoscorpionida (pseudoscorpions). Resembling miniature, tail-less versions of true scorpions, generally only 4 mm in length or less, pseudoscorpions are predatory on small organisms such as nematodes and mites. They live in forested habitats among leaf litter and under bark and are much more diverse than scorpions, with approximately 3,000 known species. Some disperse via phoresy—attaching to another, more mobile animal, generally a winged insect.

Desert hairy scorpion on gravel (William Dow/Corbis)

Scorpionida (Scorpions). A well-known group of predatory arachnids that inhabits xeric and tropical environments, scorpions are perhaps 400 million years old and closely related to extinct eurypterids (all of which were marine); the modern fauna of only 1,500 species appears to be a remnant of past diversity. As with spider venoms, toxicity of the sting varies greatly. Species with lethal venom include *Centruroides sculpturatus* of the American Southwest.

Opilionida (harvestmen, daddy-longlegs). Opilionida are familiar arachnids with eight stiltlike legs, though some tropical species have armored bodies with short legs.

Palpigrada, **Ricinuleida**, **Schizomida**, **Uropygida, Solpugida, and Amblygygida.** These are relatively minor orders of arachnids, with only a few dozen to several hundred species each. The first three orders are small, obscure, and rather generalized in structure. The last three contain some very impressive, swift predators with large, fearsome-looking pedipalps.

SUBPHYLUM CRUSTACEA:

Isopoda and Amphipoda ("pillbugs," beach "fleas"). Most species of these orders are marine; terrestrial species are detritivores. They include the familiar pill bugs, some of which roll into a tight ball when disturbed (for example, *Armadillium*). Terrestrial amphipods occur among leaves of some wet, tropical forests.

SUBPHYLUM TRACHEATA: This subphylum includes those arthropods that respire via tracheae, and that have uniramous (unbranched) appendages. They are also called Atelocerata, in reference to the single pair of antennae.

CLASS DIPLOPODA (millipedes): Most millipedes have thirty or more segments, with most segments bearing two pairs of legs, though newly hatched millipedes have three pairs and gradually add more segments with each molt. Polyxenid millipedes are unusual in having only thirteen pairs of legs in adults and a body covered with tufts of fine scales. Openings to the reproductive organs are near the head in millipedes, not the posterior end. Most species are detritivores or phytophagous; a few are predatory. Many secrete noxious or even toxic substances for defense, and some are warningly colored (aposematic).

CLASS CHILOPODA (centipedes): Centipedes are elongate, flattened forms with fifteen or more pairs of legs, and only one pair per segment. Reproductive openings are at the posterior end of the body. All species are active predators, killing prey with a pair of highly modified first pair of legs, the poison "jaws." Most species are innocuous, but larger ones (up to 25 cm, approximately 12 inches) can inflict bites that are very painful or even deadly to humans.

CLASSES PAUROPODA, SYMPHYLA: These classes consist of small (1–8 mm in length), whitish arthropods that live under rocks and among leaves, with ten to twelve pairs of legs. Unlike millipedes they have only pair of legs per segment, but like millipedes they have the genital openings near the head. All are detritivores.

CLASS HEXAPODA (INSECTA): Insecta are terrestrial arthropods with three pairs of legs. Primitive forms have no wings, though some species of pterygotes (winged insects) have wings that are highly reduced or entirely lost (these generally live in habitats with severe climates, or burrow, or are parasites).

Orders **Diplura, Protura,** and **Collembola** (springtails): These three orders comprise approximately 10,000 species of usually small (1–5 mm), obscure hexapods living among stones, logs, and leaf litter. Proturans have lost antennae, with forelegs instead modified for that function. Collembola usually have a furcula that allows them to spring into the air. Both Collembola and Protura have mouthparts recessed into a pocket in the head. All are detritivores. Diplurans have a pair of pincerlike forceps that they use for preying on small arthropods.

Orders **Microcoryphia** (bristletails) and **Thysanura** (silverfish). These are flat, scaled, wingless insects that look superficially similar, though the thysanurans are actually more closely related to the winged insects. Some are inquilines in the nests of social insects.

Order **Ephemeroptera** (mayflies): Mayflies are the most primitive living winged insects, and the only insects in which a molt occurs in the winged stage. Nymphs are detritivores in freshwater. Adults typically emerge en masse ("hatches," to fishermen) to live for a day or less; they have vestigial mouthparts and do not feed, and they form mating swarms that are sometimes of immense size. Dying mayflies from huge swarms have been known to fall to the ground several feet thick. They form an exceptionally important base of aquatic food chains, particularly as food for fish. There are approximately 3,000 species.

Order **Odonata** (dragonflies, damselflies): This order consists of approximately 5,000 species of predatory insects with large compound eyes; sharp, toothed mandibles; a long, rudderlike abdomen; and strong, maneuvered flight. Dense spines on the legs are used to seine midges and other small insect prey in air, or they pluck insects from plant stems. Very long, thin pseudostigmatine damselflies of the American tropics pluck insect prey from spider webs. Nymphs are aquatic predators.

Order **Plecoptera** (stoneflies): There are approximately 2,000 species of Plecoptera, with an aquatic nymph stage that is often found clinging to stones in cold, clear streams and lakes. Most nymphs graze on films of algae, though some are predaceous. Adults are flattened and rather generalized in structure. Some males attract females by drumming their abdomen on a branch with a frequency characteristic of the species.

Order **Orthoptera** (crickets, grasshoppers, katydids): These are primarily herbivorous insects, with enlarged hind femora used for jumping, though some do not jump (mole crickets and analogs) but have molelike forelegs for burrowing. Some, such as a few katydids (Tettigoniidae) and eumastacid grasshoppers, are predatory. Pseudophylline ("false leafed") katydids are exceptional mimics of leaves, complete with leaf veins, splotches, and even chew marks. Orthopterans are probably best known for their songs, produced to attract mates. The sounds are produced by stridulation—generally rubbing a "file" structure against a scraper, either on the wings, the legs, or even the mandibles.

Order **Phasmida** (stick insects): These are all cryptic mimics of the leaves and branches on which they feed; they also protect themselves with noxious secretions. The longest insects are some phasmids that reach well over a foot in length.

Orders **Grylloblattodea** (rock crawlers), **Zoraptera, Dermaptera** (earwigs), and **Embiidina** (web spinners): The first two orders are the smallest insect orders, with only 20 and 40 species, respectively; there are 1,200 species of Dermaptera and 400 species of Embiidina. Most are very generalized in structure, though earwigs typically have a pair of strong, terminal forceps and short, leathery forewings (hemelytra). Web spinners have bulging, glandular foretarsi that secrete silk for housing their colonies. Dermaptera are worldwide; Zoraptera and Embiidina are primarily tropical; and rock crawlers, which are wingless, are considered a highly relict order that occurs only near or among glaciers in northern North America and Asia. All are detritivorous.

Dictyoptera: Orders Blattodea (cockroaches), Mantodea (mantises), Isoptera (termites). Although biologically very different, termites and mantises appear to have evolved from cockroaches approximately 150 million years ago. All 2,200 species of termites are highly social, living in colonies with specialized castes, including individuals who reproduce, tend the nest and young, or defend the colony. All termites feed on plant cellulose (some on fungi), which they digest via symbiotic protists or bacteria in their gut. All 1,500 species of mantises are cryptic for ambushing prey; those that mimic flowers feed on pollinating insects. Early "roachoids" possessed ovipositors some 100 to 300 million years ago; true roaches (approximately 5,000 species) have lost an ovipositor and usually lay their eggs in a hardened egg sac, the ootheca.

Orders **Psocoptera** (bark/book "lice"), **Phthiraptera** (lice), **Thysanoptera** (thrips): These are all small insects with cryptic habits. Most of the 3,000 species of Psocoptera are winged and live in leaf litter, under bark, or stones, where they are detritivorous. Thrips probably evolved from primitive Psocopterans approximately 250 million years ago. They have distinctive, narrow wings with a fringe of long hairs. Some feed on fungi, others are predatory, and many feed on plants. The Liposcelidae include the common "book lice" (*Liposcelis*) psocopterans, which are wingless and also found in mammal nests. This family probably gave rise to the true lice, the Phthiraptera (6,000 species), all of which are wingless ectoparasites of birds and mammals. Some lice species have chewing mouthparts that they use for feeding on keratin, which composes hair, feathers, and skin. Sucking lice have piercing mouthparts and feed on blood. Groups and species of lice are usually very host specific. Human lice are *Pediculus humanus* (Pediculidae) and *Pthirus pubis* (Pthiridae), the former of which is more slender. The only other species of *Pthirus* is one occurring on gorillas.

Hemiptera: The Hemiptera are a group comprising the orders Heteroptera (predatory and plant bugs), Auchenorrhyncha (tree hoppers, plant hoppers), Sternorrhyncha (aphids, whiteflies, scale insects), and the tiny order Coleorrhyncha. All 100,000 species have mouthparts modified into a thin tube for piercing and sucking fluids from plants, other insects, or vertebrate blood. All auchenorrhynchans and sternorrhynchans feed on plant fluids; only some of the so-called higher heteropterans feed on plants, such as the stink bugs (Pentatomidae) and the plant and seed bugs (Miridae and Lygaeidae), among others. Most of the primitive Heteroptera are predatory, including water boatmen (Corixidae), backswimmers (Notonectidae), and water striders and their relatives (Gerridae and others). Some Belostomatidae (giant water bugs) can reach 10 cm (nearly 4 inches) in length and feed on small fish and tadpoles. Bedbugs (family Cimicidae) feed on the blood of birds and mammals. The ones that attack humans, *Cimex lectularius* and *C. hemipterus*, do not transmit diseases, though the bites are very irritating.

Order **Neuropterida** (snakeflies, dobsonflies, lacewings, antlions). Most of the 5,000 species composing the Neuropterida are predators as adults and larvae; some are larval ectoparasites of spiders (Mantispidae). The larvae of many have long mandibles with a groove through which seeps poison and enzymes that kill and liquefy the contents of prey. Antlions are larval myrmeleontids that trap ants in conical pits. "Owlfly" larvae (Ascalaphidae) are similar to antlions but are cryptic on bark and in leaf litter and ambush prey with huge, sickle-shaped mandibles.

Order **Coleoptera** (beetles): The most diverse group of insects or any arthropod, the Coleoptera contain 350,000 known species. They are morphologically conservative, the main feature being the pair of elytra, or hardened forewings. Most of the diversity in the group is due to several huge families, particularly the so-called Phytophaga or the leaf beetles (Chrysomelidae), long horns (Cerambycidae), and weevils (Curculionoidea), all of which account for 150,000 species alone. Several predatory families are also very diverse, especially the Carabidae and Staphylinidae, comprising nearly 100,000 species. The order has some of the smallest adult insects (Ptiliidae, to 0.2 mm length) as well as ones with the most body mass (African *Goliathus* scarabs). The plethora of beetle species bore in wood and stems; feed on leaves, fungi, fruit, and carrion; and are predatory. Only a few families have larvae that are parasitic on other arthropods. Only one species has evolved into an ectoparasite of vertebrates: *Platypsylla castoris*, on the American beaver.

Orders **Mecoptera** (hangingflies, scorpionflies) and **Siphonaptera** (fleas): All 2,500 species of fleas are wingless, blood-sucking ectoparasites of birds and mammals. Recent studies indicate their close relationship to the Boreidae, a family of Mecoptera. Boreids, or snow scorpionflies, have rudimentary wings. They are found in cold, mossy habitats in the Northern Hemisphere, where they are often seen walking on the snow in late winter and early spring. Most of the other 500 species of scorpionflies have a more generalized morphology with a long face. Male Panorpidae have large genitalia curled over the abdomen, scorpionlike, hence the common name. They are predaceous and scavengers.

Order **Strepsiptera** (twisted-winged parasites): This is an extremely unusual order of 500 species with very controversial relationships,

A worker bee builds a wax comb. (Frank Lane Picture Agency/Corbis)

perhaps related to Coleoptera or to Diptera. The eyes and facets are large, like clusters of grapes; males have hind wings with very reduced venation and forewings reduced into small clubs, or halters. Females are wingless and resemble larvae; they live inside the host insect that they parasitize.

Order **Diptera** (true flies): Most adult flies have one pair of wings, the hind pair reduced to halters (a few species have lost all wings). This is an order of exceptional ecological and morphological diversity, with 100,000 known species and probably more "unknown" species than any other group of insect. Of prime medical importance, the group contains many blood-sucking species: phlebotomine sandflies, mosquitoes (Culicidae), blackflies (Simuliidae), horseflies and deerflies (Tabanidae), and tsetse (Glossinidae), among others. Many primitive flies (nematocerans) have aquatic larval stages. Some are parasitoids of other insects (for example, Tachinidae); decomposers of carrion (blowflies and fleshflies, Calliphoridae and Sarcophagidae); predators (Asilidae); and pollinators (Bombyliidae, Syrphidae). The small fruitfly *Drosophila melanogaster* is used extensively in genetic research and is the best known complex eukaryote.

Order **Hymenoptera** (wasps, bees, ants): The Hymenoptera are renowned for the great societies constructed by ants (family Formicidae), which can number millions of individuals for some species of army ants and leafcutter ants. All 12,000 species of ants have advanced sociality (eusociality), meaning that there are specialized castes. In Hymenoptera, the workers, soldiers, foragers, and nurses are all sisters. Eusociality also occurs in some bees (honeybees [*Apis, Bombus*] and meliponine stingless bees), as well as in vespid wasps (paper wasps/yellow jackets, potter wasps). Sociality in Hymenoptera probably evolved because of the genetic mechanism that determines sex (haplodiploidy), which makes sisters more closely related to each other than to any offspring they could bear themselves. Thus, their genetic fitness is maximized by raising sisters, not their own offspring. Bees (Apoidea), of approximately 20,000 species, are probably the most ecologically important group of insects, since they are the most important group of angiosperm pollinators (see Pollination). Pollen and nectar are collected to provision their larvae. Bees and ants belong to a group of families (the Aculeata) that has an ovipositor modified into a sting for defense. All Hymenoptera have an ovipositor, but in many other forms it is used to lay eggs into host insects within which the larvae develop, consuming the host. These parasitoid wasps are extremely important in regulating the populations of other insects, such as defoliating caterpillars.

Order **Trichoptera** (caddisflies): This order is closely related to the order **Lepidoptera** (moths and butterflies), but biologically they are very different. Larval caddisflies live in freshwater, where most construct cases from sand grains, pebbles, or bits of vegetation. Lepidoptera are terrestrial, and the great majority of them have larvae that feed on angiosperms. This order is the largest lineage of plant-feeding organisms (with approximately 110,000 species), and it also appears to be one of the youngest orders. The earliest Lepidoptera appeared approximately 150 million years ago, but they showed little evolution until the angiosperms radiated 100 million years ago. Butterflies (Papilionoidea) are a group of five families of active, day-flying moths that advertise themselves with broad wings having warning or sexual coloration. Lepidoptera are extremely significant ecologically as pollinators and phytophages.

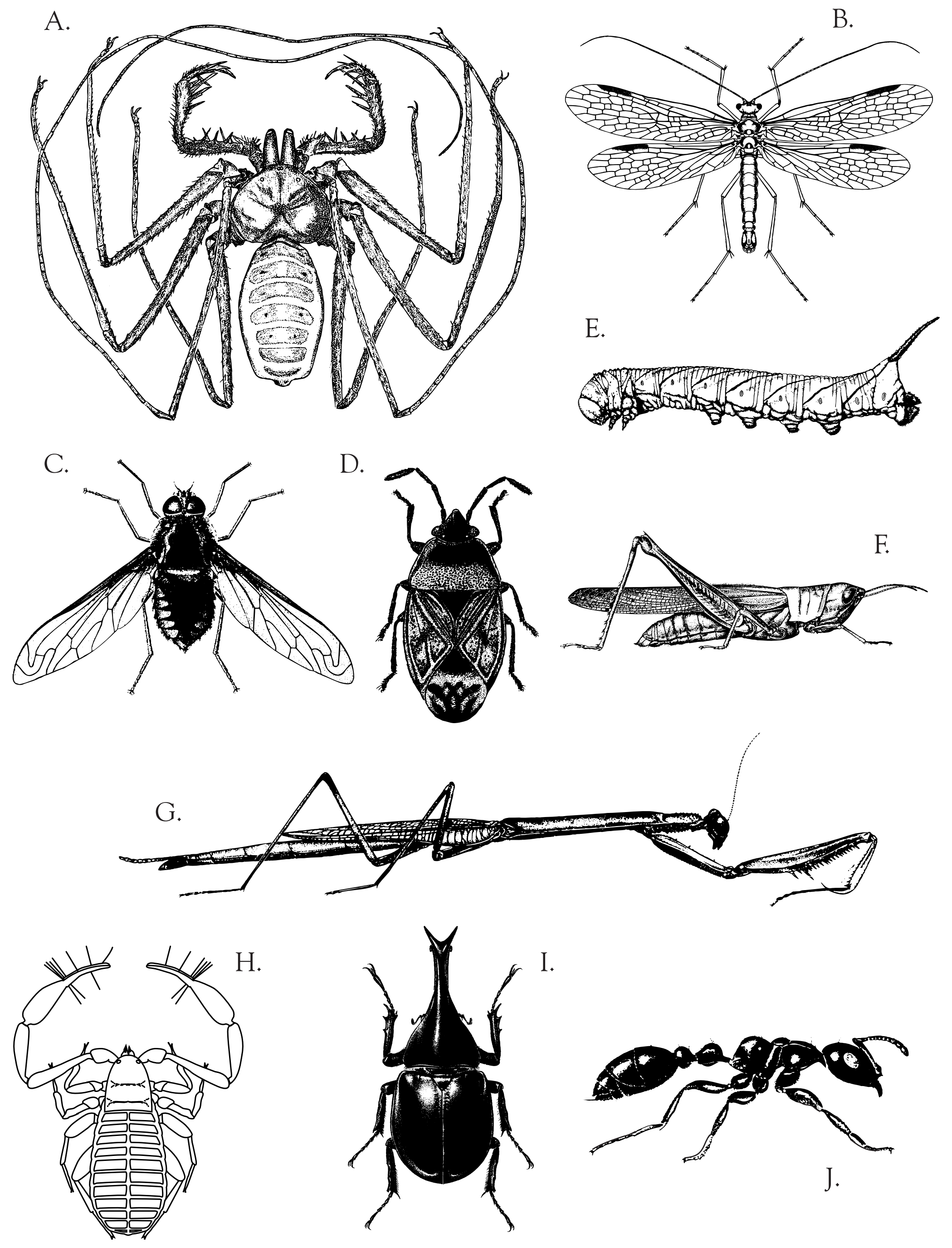
Ecological and Economic Significance

Certain arachnids, such as mites and spiders, and many insects have profound effects on terrestrial ecosystems. No species of plant or fungus is known without at least one arthropod that feeds on it, and there are usually many more. Insects are the predominant herbivores in forests, and in most grasslands and savannas they consume more than herds of ungulates. Some introduced species have produced devastating effects, such as the gypsy moths (*Lymantria dispar,* introduced from Europe) on oak forests in eastern North America, and the so-called Colorado potato beetle (*Leptinotarsa,* introduced from North America) on potatoes in Europe. Predatory and parasitic arachnids and insects also are among the most significant selective agents in the control of such outbreaks. Without pollinating insects, approximately 90 percent of the world's flowering plants could not reproduce. Bees are the most important group of pollinators, but many flies, wasps, Lepidoptera, beetles, and thrips are also significant.

Insects have had dramatic impact even on human demographics, as vectors of plagues and other devastating diseases. Most such diseases are tropical to warm temperate, among the most significant being those caused by biting flies such as mosquitoes: malaria (caused by *Plasmodium* sporozoans), yellow fever and encephalitis viruses, and elephantiasis and other kinds of filiariasis (caused by nematode worms). Other important fly-transmitted diseases include leishmaniasis or "kala azar"(from phlebotomine sandflies), onchocerciasis or

Figure 1

Assorted Terrestrial Arthropods



A. Order Amblypygi; B. Order Mecoptera; C. Order Diptera; D. Order Heteroptera; E. Order Lepidoptera; F. Order Orthoptera; G. Order Mantodea; H. Order Pseudoscorpiones; I. Order Coleoptera; J. Order Hymenoptera "river blindness" (a nematode transmitted by blackflies), and sleeping sickness (a trypanosome, transmitted by tsetse). Tens, perhaps hundreds of millions of people have died from these diseases over the past millennium alone. In South America, as many as 50,000 people die each year from Chagas's disease, another type of trypanosome, but one transmitted by blood-feeding triatomine assassin bugs. In areas of heavy infestation, the louse *Pediculus humanus* is a major vector of epidemic typhus. Ticks are important vectors of Rocky Mountain spotted fever (caused by a *Rickettsia*), Lyme disease (a *Borellia* spirochaete), Tularemia (a bacterium, *Francisella*), and others. Epidemics have not been entirely tropical: one of the most devastating plagues in history was the bubonic plague, or "black death" of medieval Europe, caused by a bacterium (*Yersinia pestis*) transmitted by *Xenopsylla* fleas from rats. Despite intensive efforts to control these diseases through vaccines or extermination of the vectors, none have been extinguished. Some diseases, including malaria, are becoming notoriously difficult to control, because of rapid evolution of the parasites and insecticide resistance in the insect vectors.

In their 400 million years, insects have proven to be more enduring than many other groups of organisms. Mass extinctions that have dramatically affected or even exterminated other groups, such as the K/T extinction that marks the end of dinosaurs and ammonites, had little effect on insects. Despite this resilience, many insects are becoming extinct as a result of human activities. Best known are various butterflies, since these are most easily monitored in the field. Some birdwing butterflies of the Asian tropics (*Ornithoptera*) have become extinct or highly endangered as a result of zealous collecting. Populations of others, such as the Karner Blue (a lycaenid butterfly), became endangered because of habitat loss. The caterpillar feeds on a lupine in pine barrens of the northeast United States, which are being lost to housing developments. Like many vertebrates endemic to islands, species of large, flightless insects have fallen easy prey to introduced rats and mongoose, such as the phasmid *Dryococelus australis* on Lord Howe Island, some large-headed stenopelmatid crickets (wetas) on New Zealand, and the giant earwig of St. Helena Island, all probably extinct. Most endangered and extinct insects were either narrowly specialized or distributed, like those in fragile ecosystems on distant islands.

—David Grimaldi

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Artiodactyls

Order Artiodactyla is composed of hoofed mammals that have two, or sometimes four, functional toes on each foot. The diversity and abundance of this group is of major economic importance to humans. Through hunting and domestication, most artiodactyl families have been utilized by humans either for transportation or as important sources of meat,

A pig, one of the domesticated artiodactyls with econmic importance to humans. (Henry Horenstein/ Corbis)

milk, and hides. Some species, such as the giant wild ox (*Bos primigenius*), are extinct in the wild and are represented today only by their domesticated descendants. Artiodactyls evolved from condylarths, an extinct group of herbivorous placental mammals that originated in the Late Cretaceous. The earliest artiodactyls, such as the rabbit-size *Diacodexis*, are known from the Early Eocene. Artiodactyls reached their greatest diversity in the Miocene; twenty-one families were represented, including the ten extant families. The more than 220 living species of artiodactyls are arranged in eighty-one genera, ten families, and three suborders: Suidae (pigs), Tayassuidae (peccaries), and Hippopotamidae (hippopotamuses) in Suborder Suiformes; Camelidae (llamas, vicunas, camels) in Suborder Tylopoda; and Tragulidae (mouse deer), Giraffidae (giraffes, okapi), Moschidae (musk deer), Cervidae (deer, muntjacs), Antilocapridae (pronghorns), and Bovidae (antelopes, cattle, goats, sheep, bison, buffalo, anoas) in suborder Ruminantia. Their natural distributions included most worldwide land masses except Antarctica, New Zealand, the Australia–New Guinea region, the West Indies, and the oceanic islands, but a few species have been introduced by humans into some of those places.

There is an impressive range in body size among living artiodactyls. The rabbit-size lesser Malay mouse-deer (*Tragulus javanicus*) is the smallest, with a head and body up to 75 cm, shoulder height up to 35 cm, and weight up to 8 kg. The hippopotamus (*Hippopotamus amphibius*) is the most massive, with a body up to 500 cm long, shoulder height up to 165 cm high, and weighing up to 4,500 kg. The giraffe (*Giraffa camelopardalis*) is the tallest artiodactyl, reaching a height of up to 5.8 m; it is also the tallest living terrestrial animal.

All artiodactyls are herbivorous, but pigs and peccaries also eat carrion, invertebrates, and small vertebrates. They occur in nearly all terrestrial habitats: tropical and temperate forests, woodlands, savannas, steppes, deserts, and the polar latitudes. Species are terrestrial and active either during the day or night. Hippopotamuses are amphibious, immersed in rivers and lakes during the day, but emerging at night to forage on land. Some species are solitary (anoas, for example), but most live in herds. The wildebeest (*Connochaetes taurinus*) is a keystone species that significantly affects the structure and stability of its local community and environment.

The diagnostic anatomical feature shared by all artiodactyls is the paraxonic feet: the primary weight-bearing axis of each foot (plane of symmetry) passes between the third and fourth digits. The first digit is absent in all living species, and the lateral digits (two and five) are reduced in size. The Suidae, Hippopotamidae, Tragulidae, and forelimb of the Tayassuidae have four digits (collared and white-lipped peccaries have three digits on each hind foot); species in the other families are characterized by two complete digits, with the lateral toes either absent or rudimentary. In the Camelidae, Cervidae, Giraffidae, Antilocapridae, and Bovidae, the third and fourth wrist and ankle bones (metapodials) fuse in each foot to form a single cannon bone to which are attached the two toes. The anklebone (astragalus) has pulleylike articular surfaces above and below that restrict lateral movement of the hind feet but allow for significant flexion and extension. The digits are encased in hooves in all artiodactyls except camels and their relatives, which bear digits with nails. Most artiodactyls lack a clavicle (shoulder bone), and most species in suborder Ruminantia bear horns or antlers. Upper incisors are reduced in number or absent. Canines are absent or very small in most species but form prominent tusks in pigs and hippopotamuses. Pigs and hippopotamuses have low-crowned molars with chewing surfaces formed by cusps; all the other artiodactyls have high-crowned molars sculptured by crescent-shaped ridges.

Added to these diagnostic traits are the distinctive structure and function of the artiodactyl stomach. In most mammals the stomach is a single chamber, but it consists of two chambers in pigs and hippopotamuses, three in camels and mouse deer, and four in all the other artiodactyls. All species in suborder Ruminantia consume a huge amount of vegetation and recycle and reconstitute it in their enlarged and complex stomachs, a process called ruminating (pigs, hippopotamuses, and members of Camelidae are nonruminants). Ruminants graze or browse vegetation (grasses, leaves, the woody parts of trees and shrubs), swallow it after only slightly chewing, then rest in places protected from predators to digest it. The food is high in cellulose but low in nutritional content. The slightly chewed (masticated) vegetation passes into the first chamber, the large rumen, where it is stored and fermented as the animal feeds. During rest, the food is regurgitated from the rumen into the mouth and remasticated (chewing the cud). After a long period of remastication, the vegetation (or cud) is swallowed a second time, bypasses the rumen, and proceeds to the second chamber, the reticulum. From there the food is drawn into a third chamber, the omasum, from where it passes into the fourth chamber, the abomasum, which is lined with glandular tissue and is the counterpart of the single stomach chamber of most other mammals. The stomach chambers contain a diverse bacterial fauna that breaks down cellulose and is crucial to the digestive process. In most other mammals, microbial fermentation of ingested food takes place only in the intestines. Microbial fermentation in the stomach releases proteins, carbohydrates, and lipids, which are more efficiently absorbed by the intestines. Remastication allows more thorough breakdown of the cellulose in plant cell walls, and the bacterial fauna maintains itself by feeding on nitrogen released by digestion of cellulose.

Most artiodactyls were described in the eighteenth and nineteenth centuries, but new species are still being discovered, such as the sao la (*Pseudoryx nghetinhensis*) and the giant muntjac (*Muntiacus vuquangensis*), described in the 1990s; both live in tropical forests of Vietnam and Laos.

—Mary Ellen Holden

See also: Bluebuck; Endangered Species; Mammalia; Paleontology; Preservation of Species

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Atmosphere

The mixture of gases that surrounds the solid earth is called the atmosphere. Although it represents a very small fraction of the weight of the earth, it is very important because it is essential to life and is highly reactive, circulates, and plays an important role in the evolution of landscapes. Carbon dioxide plays an important role by trapping heat, causing the greenhouse effect, which keeps the earth warm and livable, for the most part.

The atmosphere is dominated by nitrogen (78.08 percent); oxygen (20.95 percent) and argon (0.93 percent) are next in abundance. Carbon dioxide, which is essential to all plant life, makes up only 0.32 percent of atmosphere.

Oxygen is chemically reactive and important in the weathering of rocks, the decay of organic matter, and combustion. Nitrogen is relatively inert and unavailable to plants directly; therefore it must undergo chemical changes to make it useful to vegetation. Water vapor plays an extremely important role in the hydrological cycle. Unlike most of the gases in the atmosphere, which are fairly constant or vary within limits, water vapor is highly variable. Air in desert areas may contain only 1 percent vapor by volume; in tropical areas, however, where the air is warm and moist, the content can be as high as 4 percent. Water vapor is most abundant near the surface, although it amounts to less than 1 percent of the total atmosphere volume. The source of water on earth has traditionally been explained by degassing from within the planet, released through volcanic eruptions; a few researchers, however, have suggested that at least some water came from cometary impacts.

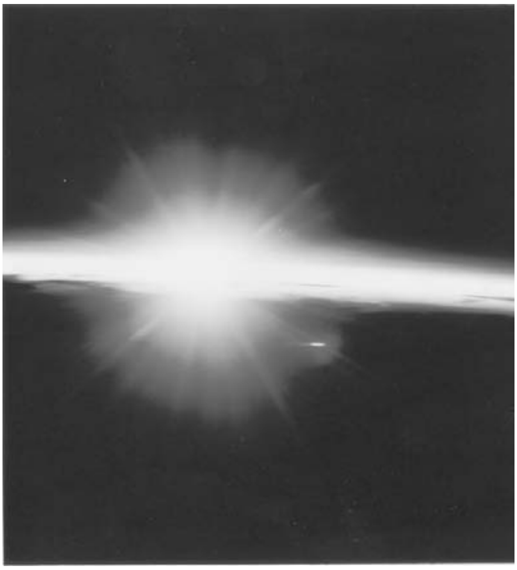
The temperature of the atmosphere varies considerably, reflecting—like the solid earth—its subdivision into several layers. Vertically, each layer has different properties and is found at specific elevations.

The troposphere is the layer closest to the surface, containing 75 percent of the atmosphere's weight, all of the water vapor, and most of the particulate matter; it is 8 to 18 km high. Its upper boundary, called the tropopause, is closer to the surface at the poles than at the equator. The temperature gradient of the troposphere is about 6.5 degrees centigrade per km of rise from the surface to the tropopause. It is where most of the solar radiation striking the surface is converted to thermal energy and the resulting heat is exchanged by direct contact with surface of the earth. Because the air at the surface expands, it rises and subsequently cools, thus creating a pattern of thermal convection not unlike the process that takes place within the earth at the asthenosphere. By this process the troposphere is kept in motion and is part of the process that drives the hydrological cycle. It is where almost all the clouds are and where the earth's weather takes place.

The stratosphere, the next higher layer, has a constant lapse rate at lower levels, where it reverses forming a temperature inversion, as cold, denser air is trapped by warm air above, reducing the vertical movement of air and making the stratosphere a cap over the troposphere. The air is almost cloud free and without turbulence—ideal for jet aircraft to fly through—except that occasionally the tops of a few giant thunderstorms extend into the bottom of the stratosphere. Because there is little vertical movement, the air forms horizontal layers and moves within those layers and not across them. Although very dry, the stratosphere does have trace amounts of water, producing faint, pearly clouds at about 30 km. The stratosphere contains 24 percent of the atmosphere by weight, reaches to 45 km above the surface, and contains the ozone layer, which is created when ultraviolet light strikes an oxygen molecule (O_2) and breaks it into two individual atoms that then combine with normal oxygen to form ozone (O_3). The ozone layer intercepts nearly 100 percent of ultraviolet light from the sun and, as a result, shields the earth's surface against radiation that causes severe sunburn, skin cancer, and genetic mutations.

Above the stratosphere are the mesosphere and the thermosphere, both of which contain the remaining 1 percent of the air by weight. The mesosphere lies between 45 and 92 km, and its temperature decreases with altitude until it reaches the mesopause, where the air is –93 degrees centigrade, the coldest expanse of the atmosphere. The outer layer, the thermosphere, has extremely high temperatures, as high as 1,300 degrees centigrade. But because the air density is so low and the hot molecules are so far apart, an object such as a satellite is unlikely to intersect many of them.

The outermost zone, the magnetosphere, traps particles entering the atmosphere and protects the earth from damaging radiation from the sun. The sun is the source of almost all of the energy that drives the oceans and atmosphere, the controlling entities that produce weather and climate. Of the solar radiation that the earth receives from the sun, almost 30 percent is reflected back into space by clouds, dust, and the atmosphere itself. The remaining 70 percent heats up the continents, islands, oceans, and atmosphere; drives the winds and ocean currents; evaporates water; and supplies energy for life through photosynthesis. Some of the radiation is scattered and diffused, but about 50 percent of what strikes the surface is absorbed, causing the surface temperature to rise. This heat is then radiated as infrared radiation back into the atmosphere, where water vapor, carbon dioxide, and other greenhouse gases absorb most of it. About 18 percent of the sun's energy evaporates water from the land and oceans; as the vapor condenses, the energy is returned to the air.



Earth's atmosphere photographed by astronauts. (NASA)

When the earth's average temperature

remains the same, the amount of energy received equals the amount of energy radiated and reflected back into space. However, if the two do not balance, a change in climate results. Changes can also occur if the sun's output increases or diminishes, or if some parameter on earth changes, such as a period of intense volcanism. On a daily basis, however, the amount of solar radiation that earth receives varies from place to place, day to day, and season to season. Rotation of the earth on its axis causes the change between night and day, and inclination of its axis causes seasonal change. Other factors that influence the amount of solar radiation the atmosphere receives are the presence of clouds and the distance between the earth and the sun.

Earth's orbit around the sun is elliptical (averaging a distance of 150 million km); thus the distance varies throughout the year. The Northern Hemisphere is closest to the sun in winter (January 3) and farthest in summer (July 4), indicating that seasonal temperature changes and distance have only a minor correlation. Because there are more land masses in the northern latitudes, there is rapid seasonal heating and cooling there, making the summers warmer and the winters colder than in the areas south of the equator, where there is much more water.

—Sidney Horenstein

See also: Atmospheric Cycles; Climatology; Hole in the Ozone Layer; Nitrogen Cycle; Oxygen, History of Presence in the Atmosphere

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Atmospheric Cycles

The term *atmospheric cycles* refers to the movement and circulation of gases and particles in the atmosphere, how they are utilized, and how long they remain there. Much is known about oxygen, and it is probably the gas that has the simplest cycle. Plants on the land and in the seas produce oxygen during photosynthesis, releasing it directly into the atmosphere or the water. Some of the oxygen is removed by animals during breathing and is incorporated into cellular materials or released in the form of carbon dioxide. Oxygen is also absorbed into fresh and marine water at the air-water interface, where it is utilized by organisms or involved in chemical reactions with materials within the water column or on the bed of the water body. Oxygen is also removed from the atmosphere during the weathering of rocks on the surface as it combines with the rock, forming minerals.

Fires of all kinds, whether cook fires, burning forests, or the result of warfare, remove oxygen from the atmosphere. About 23 percent of the atmosphere is oxygen, and the residence time has been estimated at about 7 million years.

Nitrogen, the most abundant gaseous component, making up 76 percent of the atmosphere, circulates slowly and has an estimated residence time of 44 million years and a complex cycle because it also combines in complex ways with other gases of the atmosphere. While it takes a great deal of energy to break apart a molecule of nitrogen gas, many species of bacteria take nitrogen from the atmosphere and transform it into an important component of soil. Some bacteria also release nitrogen back into the atmosphere as they break down organic material.

Particles in the atmosphere come from natural and anthropogenic sources. Natural sources include volcanic eruption, dust kicked up during windstorms, and salt from the evaporation of ocean spray. The residence time for these particles is measured in days and weeks, but in the case of volcanic eruptions, in which the particles are blasted high into the atmosphere, particles can remain for years before settling down on the land or sea.

Anthropogenic sources of particles come from a variety of activities, such as the burning of fossil fuels, industrial processes, forest fires, smoking cigarettes, and the wearing away of automobile brake linings. The residence time of these particles, as well as of those from natural sources, varies according to such factors as wind speed, precipitation timing, and height in the atmosphere. Although the concern regarding airborne particles whether anthropogenic or natural is usually related to health, successive volcanic eruptions over a long period of time can produce a shield to solar radiation, reducing the temperature of the earth's surface and thus altering the climate. Concern about gases, however, revolves around their role in global warming, discussed elsewhere in this work.

—Sidney Horenstein

See also: Atmosphere; Climatology; Global Climate Change; Hole in the Ozone Layer; Nitrogen Cycle; Oxygen, History and Presence in the Atmosphere

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Atolls

An atoll is a ring of coral encircling a shallow lagoon. The coral rises from great depths to just below high-tide level. The surface of the reef may extend above sea level as a series of low, flat islands containing wave-tossed and eroded coral debris. In the Pacific Ocean, Polynesians and Micronesians settled many of these islands. Because corals require sunlight, only the upper portion of the coral is living, to depths of 150 m in the Indian and Pacific oceans and 50 m in the Caribbean Sea. In addition, almost all corals need warm water and do best when the temperature is between 23 and 25 degrees centigrade, which keeps them from growing in cold-water currents and cold water at depth.

That reefs extend to great depths provided a puzzle to early geologists and naturalists. For example, modern drilling in Enewetok Atoll passed through 1,400 m of coral before coming to volcanic rock. Many theories were proposed to explain these observations, but it was Charles Darwin, in 1837, who presented the explanation that coral reefs and volcanic islands were connected. He recognized that there are three types of islands in the sea: volcanic islands, corals reefs, and a combination of the two; he proposed that they represent stages in a single sequence of development. After a volcanic island is formed and activity ceases, corals begin to grow in the shallow water on the edge of the volcano, forming a fringing reef. As the oceanic plates move and slowly subside, carrying the volcanic edifice downward with them, the reef builds upward and outward continually, to maintain its position within the zone of light. When subsidence is too rapid, the reef is brought into sunless depths where it dies, never forming an atoll unless uplift brings the mass close to the surface and new coral builds upon it.

As subsidence continues, a barrier reef forms adjacent to the partially submerged volcano and is separated from it by a lagoon. Eventually the volcano subsides completely, leaving

Small atoll off Bora Bora, French Polynesia. (Owen Franken/Corbis)

an atoll continually growing upward as sinking continues. Reefs are among the most diverse environments on earth and have complex assemblages of plants and animals that are intensely competitive with one another. The atoll surfaces, on the other hand, are not diverse but are usually home to unique species, as are many oceanic islands.

—Sidney Horenstein

See also: Coral Reefs; Lagoons; Oceans

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Avian Malaria and the Extinction of Hawaiian Birds

The beautiful birds of Hawaii have weathered many storms of invasions. The usual culprits—humans, dogs, pigs, cats, and rats—have all left their footprints on the Hawaiian ecosystem. But in this fragile paradise, the smallest invaders—mosquitoes, protozoa, and viruses—have had an impact disproportionate to their size. In fact, these tiny invasives may have dealt the final blow to several extinct species, such as the 'O'o (*Moho nobilis*) and the grosbeak finch (*Psittirostra kona*). Other species are teetering on the verge of extinction under the continued threat of invasive species.

When the first humans, voyagers from Polynesia, arrived in Hawaii around 300 C.E., they found lush tropical forests. There were no terrestrial predators; in fact, there were no mammals (except one species of bat), no snakes, and (as befitting a paradise) no mosquitoes. There were, however, an abundance of birds, demonstrating the fabulous species radiation that often occurs in isolated populations.

Like all settlers, the Hawaiians modified and exploited their new home to suit their needs. Trees were harvested for wood, and land was cleared for settlements. The native birds were hunted for food as well as for their colorful feathers. The Hawaiians brought some domesticated animals with them, including Asian pigs, dogs, and fowl. The Polynesian rat (*Rattus exulans*) most likely arrived as a stowaway and quickly became established as an invasive species. When the first Europeans arrived in Hawaii at the end of the eighteenth century, the islands' biota had already changed dramatically: most of the lowland forest had been cleared, the human population was burgeoning, and many species of flightless and ground nesting birds had already become extinct.

The arrival of Europeans brought new dangers for the native forest birds. Cattle, goats, sheep, and English pigs were introduced, and these free-ranging animals wreaked havoc upon the native vegetation. More aggressive species of rats (*Rattus rattus*, and *R. norvegicus*) arrived with the Europeans, and mongooses (*Herpestes auropunctatus*), introduced in an attempt to control the rats, turned out to have a taste for eggs and nestlings. A variety of songbirds, such as the Japanese white-eye (*Zosterops japonica*), and gamefowl were released for pleasure and sport. These birds, or perhaps domestic poultry, brought with them some passengers of their own: the avian pox virus and the blood parasite (*Plasmodium relictum*), which causes avian malaria.

We do not know exactly when introduced diseases began to affect Hawaii's native birds, but naturalists noticed forest birds with lesions attributable to avian pox at the end of the nineteenth century. Avian malaria probably went undetected at first, because it does not produce externally visible lesions and because the *P. relictum* parasite was not recognized as the cause of the disease until the twentieth century (van Riper et al., 1986). These diseases probably did not begin to spread among the native birds until after 1826, when a ship arriving from Mexico dumped barrels of fetid water containing mosquito larvae (*Culex quinquefasciatus*)—a vector for *P. relictum*. The Hawaiian birds, which had evolved in isolated safety, were immunologically naive to these diseases and therefore particularly susceptible to them. For some species, already burdened by the stresses of habitat loss, invasive predators, and competitors, introduced disease may have been the final straw. By the beginning of the twentieth century, an absence of birds, even in seemingly undisturbed parts of the forest, had become apparent (Warner, 1968).

Introduced diseases have most significantly affected the lowland forest birds. Mosquitoes breed in pools of standing water, especially those commonly found near human habitations. In the forest, feral pigs make wallows and break open logs in which water collects, creating prime locations for mosquito reproduction. At present mosquitoes are restricted to the warmer, lower altitudes, but if global climate change leads to warming, the range of the mosquitoes may expand into higher elevations. Likewise, the introduction of new mosquito species adapted to more temperate climates might provide a vector to carry avian malaria to high altitudes. In the meantime, remnant populations of some species are now found only outside of their original range and faced with the added stress of coping with a new habitat.

Like all ecosystems, the Hawaiian forests are dynamic. A single change results in a cascade of effects. The extinction of one species may lead to geographical and ecological shifts for other species. The extinction of the 'O'o opened the flowers of the ohia tree (*Metrosideros polymorpha*) as a food source for another nectivorous bird, the i'iwi (*Vestiaria coccinea*). It was fortunate for the i'iwi that this niche became available, because the lobelioid flowers that had been its primary food source were undergoing a wave of extinctions as well. In some cases, introduced species may step in to fill a gap left by the disappearance of native species. The ie'ie vine (*Freycinetia arborea*) was rescued by the Japanese white-eye when its native pollinators went extinct or became too scarce to perform their duties (Cox, 1983).

Assaults upon native birds by hunters, habitat destruction, introduced predators, competitors, and disease have all contributed to the demise of several species. One biologist, Jack Jeffrey of the U.S. Fish and Wildlife Service, has aptly described this as "negative synergism." To date, half of the recorded Hawaiian bird species have become extinct since the arrival of humans on the islands, and 40 percent of the remaining species are endangered (Youth, 1995). We may never know how many species succumbed to avian malaria and avian pox. Disease ecology along with habitat protection and predator control must all be taken into consideration in order to save other species from the same fate.

—Julie Pomerantz

See also: Adaptive Radiation

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B

Bacteria

Discovery of Bacteria

When one thinks of biodiversity, it may be tempting to ignore bacteria. But bacteria, also known as prokaryotes—a name that derives from the lack of nuclei in their cells—in many ways hold the richest reserves of planetary diversity. All other life forms on the planet are eukaryotes—that is, they are composed of cells with nuclei. That is not entirely surprising. Bacteria are the oldest life forms on the planet; with an evolutionary history stretching back almost 4 billion years, they have had more time to evolve than more familiar, visible, and recent organisms. As macroscopic beings, experiencing life at our own size, human beings did not merely ignore bacteria for centuries: we did not even know of their existence. Smelly cheeses and feet, diseases, and the smells of fresh forest air: while today we know that they are made possible by, or even directly caused by, the growth and release of chemicals by bacteria, for most of human history they were interpreted to stem from other sources, such as evil spirits or God. With the innovation of the microscope, however, the vast scope of the bacterial world began to be gleaned. The early use of this device by Anton van Leeuwenhoek, a Dutch draper from Delft, suggested the depth and breadth of the alien and wonderful realms not visible to the unaided eye: van Leeuwenhoek explored the subvisible realm everywhere it might be, from the teeth scrapings of alcoholics to frogs' rectal fluid. But if van Leeuwenhoek had already by the 1600s inferred the vast scope of our once unsuspected planetmates, the bacteria, it was not until the invention of more powerful microscopes, evolutionary theory, and modern cell biology that we have begun to realize the true contribution of these beings to global biodiversity.

Metabolic Diversity

Bacterial cells show some obvious diversity. They vary in length from less than 0.1 micrometer to more than 100 micrometers. Furthermore, most bacteria in nature are multicellular. Some are shaped like trees, and others are long filaments or berry shaped. But the most striking contributions of bacteria to biodiversity are not visible even with the most powerful modern scanning electron and transmission microscopes: they are, rather, genetic and metabolic. It turns out that all of the vast seeming diversity of visible animals—from grazing deer in the woods to luminous

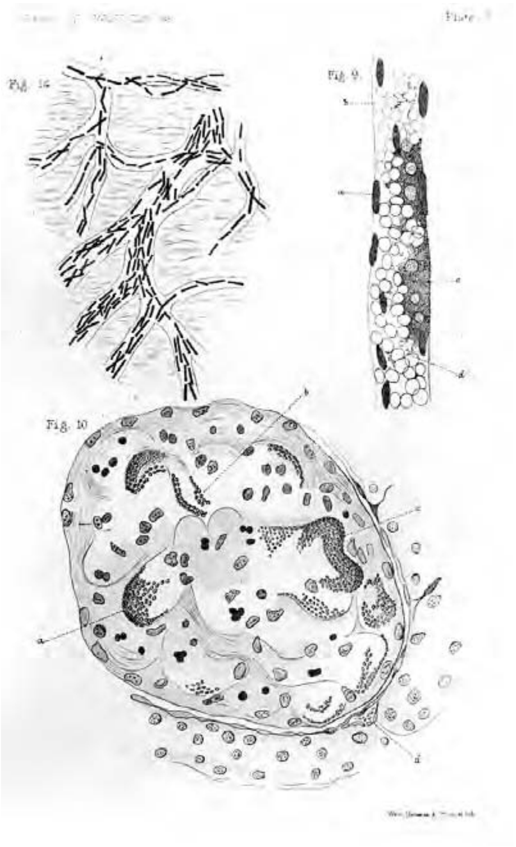

Illustration of bacteria found in wounds, from* Investigations into the Etiology of Traumatic Infectious Diseases *by Robert Koch, 1880. (Library of Congress)

fish in the oceans to the myriad insects, flowering trees, and still uncataloged species of the tropical forests—is basically a set of variations on a single theme. The theme is that of aerobic life. For a biologist, *aerobic* doesn't mean working out to a Jane Fonda video but rather refers to the intake of oxygen at the cell level to procure energy for intracellular metabolism. All plants, animals, fungi, and most all of the larger, nonbacterial (that is, eukaryotic) microbes known as protoctists are aerobic. Metabolically, virtually every "normal" or familiar organism with which you are acquainted shows virtually no change in metabolic diversity as you look from species to species.

The reason is that the surface of the earth has been propagated by the offspring of a very specific type of bacterium—the so-called respiring or oxygen-breathing bacteria, which must be counted as one of the two or three most successful genomes ever in evolutionary history. But like a Microsoft Word program stifling other word processing programs, however successful they are, the prevalent oxygen-breathing form of cell metabolism represents only a tiny fraction of the many ways of doing things. From the perspective of cell numbers, bacteria are still the majority shareholders of the planetary surface. And despite the seeming omnipresence of familiar, macroscopic, oxygen-breathing forms of life, the biochemical diversity of this planet remains largely bacterial. Except for a few esoteric compounds, such as the structural materials of trees and esoteric hallucinogenic alkaloids, all of life's major structural and functional compounds were developed in nature's bacterial crucible, whose innovations result, as we discuss below, from the natural tendency of bacteria to exchange genes, to "genetically engineer," across what would be species borders. And you do not have to know the details of their chemistry to get a feeling of how metabolically diverse are the bacteria or prokaryotes. They thrive in places that would kill aerobic life forms: hundreds of meters beneath earth's surface in rock, on the sides of nuclear reactors, in salt flats and scalding hot springs up to 113 degrees centigrade, in Antarctic ice patches under conditions similar, according to some scientists, to those found on Mars.

Seemingly simple bacteria use DNA to reproduce themselves and to perform an extensive arsenal of environmentally important metabolic tricks, including but not limited to oxygenic photosynthesis, nitrogen fixation, ammonia oxidation, amonification, manganese reduction, iron reduction, sulfide oxidation, sulfur reduction, methanogenesis, fermentation, proton reduction, and nitrate respiration. Some of these processes are still beyond our industrial capabilities. Their chemical and informational skills still exceed those of many human manufacturing and computing processes. Indeed, Canadian biologists Sorin Sonea and Maurice Panisett in their book *Prokaryotology: A Coherent View* note that if bacteria had been discovered not on the Earth but on Mars, they would have been considered alien life forms.

Origin and Evolution of Bacteria

The first bacteria may have come from meteorites in space, been directed here by alien life forms, or, most likely, evolved from complex chemical reactions on the surface of the Earth. Many sorts of material systems are known to become more complex when exposed to flows of energy; energy flows are also known to cause cycles, both chemical and physical, to arise. A flow of energy represents complexity pre-existing in the environment that reaches thermodynamic equilibrium, sometimes by forming complex structures. Beyond the actively researched details of the origins of life from nonlife, one can assume that the first living beings were chemical cycles becoming more complex. Energy from the environment, such as geothermal energy from the earth, solar energy, and energy stored in chemical compounds, funneled through cell membranes. Cell membranes are amphiphilic, meaning that they tend to keep the oily compounds of life inside them and the water of the environment outside. Any form that began actively to seek energy sources, such as the first faithfully reproducing bacteria with DNA, would have quickly spread to oust other energy-driven complex systems. Researchers today, by looking at the details of modern cyclical cell metabolism, may be able to discover the ancient steps leading from thermodynamic systems to the first bacteria.

Viruses are smaller than bacteria, and they are composed of relatively few genes and proteins. They are not true organisms or cells, however, because they can reproduce only by using the genetic and protein-making apparatus of living cells. And truly functioning cells, today, are all bacteria. The smallest bacterium known is Mycoplasma, one form of which causes venereal diseases in human beings. Like viruses, however, Mycoplasma must be considered a derivative or degenerate form: it appears to be the evolutionary result of earlier, more self-sufficient cells that reproduced on their own. When cells team up, as occurs often in evolution (the phenomenon is known as symbiosis), organisms may be taken care of, even sometimes inhabiting the insides of other cells, and thus lose parts of themselves; viruses and Mycoplasma, although small, do not represent the oldest life forms.

The oldest known life forms are microfossils of bacteria from Australia and South Africa. Radioactively dated at some 3.5 billion years, these microfossils show evidence of bacteria being already widespread on the planetary surface. Indeed, because the early Hadean geological eon during earth's formation was so hot, older microfossils of bacteria would not have survived in the rock record. Thus, as soon as there could be evidence of fossil bacteria, there is.

Genetically, the earliest bacteria are thought to have been archaebacteria, a classification that includes methane-producing bacteria, halophiles that survive conditions too hypersaline (salt-rich) for most other organisms, and sulfur bacteria able to tolerate the extreme heat radiating from earth's interior. What ties these diverse sorts of bacteria together is their

RNA, which exhibits a long stretch of similar base pairs, one that is substantially different from the rest of bacteria, sometimes known as eubacteria. Such bacteria, able to inhabit extreme conditions inhospitable to other living beings, are known as extremophiles. Geological evidence from the earth's crust provides strong evidence that free atmospheric oxygen did not exist early on in the earth's history; breathable oxygen in the air, it turns out, was probably put there by life—bacterial life. The change from an early oxygen-poor (anoxic) planetary environment to a modern planetary surface rich in oxygen (oxic) was one of the most dramatic events in the history of the biosphere. The presence of extremely hardy extremophiles able to tolerate conditions no longer prevalent on the earth's surface points to a past in which bacteria not only dominated the biosphere but were also its sole inhabitants.

Obviously, we cannot know exactly what happened during the course of evolutionary history. However, it is clear that bacteria played, and continue to play, a key role both in early evolution and in present global ecology. It is impossible to appreciate the importance of bacterial diversity fully without an understanding of the major impact that they have made on evolutionary history.

The first bacterial cells may have been fermenters, gaining energy from hydrocarbon compounds produced naturally before life by the rays of the sun. Like modern fermenting cells, they would not have required atmospheric oxygen, which had not yet accumulated in the atmosphere. Alternatively, the first life may have been photosynthetic anaerobes, such as the purple bacteria that today use the energy of sunlight and the hydrogen of hydrogen sulfide (H_2S) rather than water (H_2O) to make the hydrogen-rich compounds of their bodies. Biologist Jack Corliss, one of the first to go down into the ocean abyss in the submersible *Alvin*, was part of the team that discovered thriving ecosystems beneath the Galapagos Islands. He proposes that similar thermal upwellings were the site of first life. Here, at the bottom of the ocean, pogonophoran tubeworms are internally fed by symbiotic bacteria who themselves feed not on sunlight or other organisms. Instead, they take their energy directly from the oxidation of hydrogen sulfide gas seeping up from deep within the earth's crust. Such sulfide bacteria, which are genetically classified with the most ancestral types, could have been among the first life forms. Corliss argues that the first life forms fed off similar sulfide redox gradients, which would have been more prevalent on the earth's surface during the earliest eons (the Hadean and Archean) of planetary history.

Gene Trading and Cell Symbiosis

Although the evolution of bacteria contains, as previously suggested, the seeds of all biological diversity, it cannot, of course, be detailed here. However, one fact especially stands out. That is the role of symbiosis—living together—in producing all the other life forms. Without immune systems or reproduction dependent upon mate recognition, bacteria are supremely promiscuous beings—indeed, beings in which infection and sex is virtually the same thing. Unlike animals, which must recognize and breed with mates of the opposite sex by donating an equal apportionment of genes from each of two parents, new bacteria can be produced directly, whenever one injects genes in the other. And such injections need not be 50 percent; they range from 2 or 3 percent of the parent's genetic endowment to nearly all of it. The result is that genetic engineering, although for us new, is an ancient bacterial "technology." The sexual proclivities of bacteria include a rampant exchange of genes next to which our species' most Bacchanalian orgies look like rather subdued affairs. Characteristic bacterial genes can be found in plants, animals, and fungi.

Yet symbiosis dwarfs even this bacterial sexuality or genetic engineering in its ability to bring together different genomes. Feeding on, with, and within other cells, invading and destroying or entering and living with other cells, bacteria propagated major transitions in evolution—the transitions that were to lead to protoctists (such as amoebae and paramecia), fungi, animals, and plants. The most striking of these symbioses, for which there is much evidence (morphological, behavioral, and genetic), are those of the green parts of plant cells and algae—the plastids—and the previously mentioned respiring bacteria that evolved to become the oxygen-using parts of all familiar life from mushrooms to elephants—the mitochondria. In the case of plastids, the best evolutionary conjecture is that green-colored cyanobacteria (the first bacteria to use water for hydrogen) were eaten by other cells—but not digested. As time went by, they continued to photosynthesize: in return for a warm, sometimes mobile environment, they produced food from little more than sunlight, water, and air, feeding the cells in which they found themselves along the way. The ancestors to mitochondria, DNA-containing parts found outside the nucleus in all animal and plant cells, were probably bacteria that invaded larger cells. Again, however, instead of killing the cells in which they found themselves, or being killed by them, a partnership evolved. Over time, the genomes merged and multiple beings became one. That the host cells in these alliances came from the same stock is suggested by the genetic likeness of cells with nuclei, eukaryotic cells, to the presumably ancestral archaebacteria. In summary, then, the biodiversity we see today depended for its existence on metabolically diverse bacteria coming together in sex and symbiosis, and evolving in new, long-living unions. And, whatever we do to ourselves, we may take philosophical solace, at least, in the knowledge that the diverse bacterial underlayer that gave rise to all plants and animals, as well as us, was around for billions of years before we got here, and will likely survive for billions of years more after we are gone.

—Lynn Margulis and Dorion Sagan

See also: Benthos; Coevolution; Communities; Ecosystems; Oxygen, History of Presence in the Atmosphere; Protoctists; Speciation; Viruses

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Barrier Islands

Barrier islands are long, straight, or curved, narrow strips of clastic particles (that is, sands and silts) adjacent to coasts that have been built up by waves. They are located where land and sea come together. Between the barrier islands and the coast are usually lagoons, bays, and marshes. Tidal inlets cross the islands and

Aerial view of a barrier island that keeps pack ice from Ushakovsky village, Russia (Wolfgang Kaehler/Corbis)

connect these bodies of quiet water with the ocean. Barrier islands and their adjacent lagoons account for more than 10 percent of the world's shorelines. They are typically found adjacent to broad and low coastal plains like those found in the eastern United States. Cross-sections of barrier islands typically have a profile, starting from the sea, that consists of the shore face, beach, dune, back-island flats or marshes, coastal bay or lagoon, and mainland. The shore face extends from the place where storm waves affect bottom sediment to the low-tide zone. The exposed part of the island begins at low tide, the outer limit of the beach, and continues to the base of the dunes.

The beach is composed of two parts, an inner section with a uniform slope that extends to a drop-off or berm, and an outer section where the slope begins a steeper angle to low water. Many beaches are within the intertidal zone, but the inner sections may be affected by wave action only during storms. The ocean side of the island is constantly changing as a result of the interplay between waves, currents, and wind. The highest elevation of the island is occupied by one or more rows of dunes that are constantly reshaped by wind. The dunes are low and occur only if there is a supply of sand and if the wind blows from the same direction most of the time. Behind the dunes are low areas composed of sediments that have been washed through or over the dunes during storms and fine material carried in by the wind.

Some barrier islands are only beaches. Between the barrier islands and the mainland are lagoons, bays, and estuaries, where tidal currents are important processes. Barrier islands provide protection and defense for the mainland from high surf and storms. Barrier islands along the East Coast from Long Island to Cape Canaveral are composed of clastic deposits derived from the erosion of headlands and from the seafloor, but farther south in more tropical regions barrier islands are composed, in part or entirely, of carbonate sediment derived from shells of organisms.

Barrier islands are frequently broken by channels that form after storms. Where they occur, tides usually rush through them carrying sand and silt to form deltaic deposits in the lagoon behind the island. Severe storms and hurricanes can alter the shape of barrier islands, which becomes evident when lighthouses have to be moved as a result of the disappearance of the island. Overuse of the islands, including real estate development, often leads to the destruction of vegetation that binds the loose sand together, eventually subjecting them to increased erosion and in some cases disappearance.

Barrier islands are also very sensitive to changes in sea level. Subject to higher energy forces on the seaward side than on the landward side, barrier islands retreat landward over time, generally 0.5 to 2 m, but up to 20 m in some places. All around the world they have been repeatedly exposed and drowned during the Ice Age as sea level rose and fell during the retreat and advance of the glaciers, resulting in their shifting of position in response to the changes. In northern Canada, where glacial rebound has raised the land upward, barrier islands can be found as much as 100 m above the adjacent sea.

—Sidney Horenstein

See also: Atolls; Beaches; Coastal Wetlands; Coral Reefs; Estuaries; Lagoons; Oceans; Tides

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Beaches

Beaches are shores built of unconsolidated sediment, most commonly sand. But you can also find beaches composed of cobbles and boulders and clay and silt. Located between land and sea, from low water to highest elevations subjected to waves, they are among the most dynamic of environments. Waves and currents constantly move beach material, and wind also plays an important role, blowing finer material away from the beach, where

Muir Beach, California (Courtesy of Scott Horst)

it accumulates as sand dunes. Over time, beaches change their width and thickness as sources of sediment, the rise and fall of sea level, and uplift and subsidence affect the area. Typically, beach sediments come from the land through stream transport or erosion of adjacent cliffs.

Along the southern part of coastal United States, where the coastal area is low and sandy, long, straight beaches are typical. Along shorelines adjacent to mountainous regions, or where bedrock is adjacent to the sea (as along the coast of southern Maine), curved beaches are more common.

Barrier beaches are long strips of sand that are separated from the mainland by a body of water. Spits are beaches that extend from the land and terminate in open water. Tombolos are beaches that connect an island to the mainland or another island.

Because the beach environment is so dynamic, large plants are absent, and the animals are typically burrowers. They have mechanisms for utilizing the minute particles of food that are entrapped in the spaces between the sand grains.

As the beach slopes upward, away from the sea, it is subject to less wave action—creating a rough parallelism on the types of animals found. Beaches usually contain a small variety of species, but they tend to abundant.

—Sidney Horenstein

See also: Atolls; Barrier Islands; Coastal Wetlands; Coral Reefs; Estuaries; Lagoons; Oceans; Tides

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Beauty of Nature, Biophilia and Ethics

There are three basic reasons why we should value biodiversity—and be concerned that it is being lost at such a rapid rate (see Sixth Extinction). Two reasons lie in the direct benefits humans receive from living species: humans rely on at least 40,000 species of plants, animals, fungi, and microbes in their daily lives—especially for food, shelter, clothing, fuel, and medicinal purposes. In addition, "ecosystem services," including the ongoing production of essentials such as nitrogen and oxygen, the water cycle, replenishment of fisheries and so forth—all essential to the quality of human life as well—depend on the health of the world's ecosystems. These two aspects of "why we should care" about biodiversity are thus utilitarian, in the sense that human life depends upon biodiversity. This entry concerns the third category of reasons why biodiversity is important to human life: a combination of esthetic and ethical concerns that have convinced a growing number of people that it is morally wrong to destroy the world in which we live—that is, that there are moral as well as utilitarian values at stake.

Nearly all of the six billion people alive at the start of the new millennium live in complex societies in which most of their food is produced by agriculture and fishing. Moreover, many people live in cities—and often have little or no contact with the natural world: cities basically grow by destroying the physical and biological environment, and even the parks that preserve a bit of open space and greenery are often filled with formal gardens—with many of their plants (and even animals) not native to that region. Agriculture has enabled the human population to explode over the past 10,000 years—and that is the root cause for the rampant destruction of ecosystems over the globe. But at the same time, agriculture, in removing people from life in local ecosystems, has caused many of us to think that we are above and beyond nature. In a sense, we feel that way for good reason, as humanity has almost entirely stopped living inside local ecosystems. It is difficult for a city-dweller to see the connections we still have with the natural world: our continued dependence on the species and ecosystems of the natural world.

At the same time, however, nearly everyone responds to the bright clear air on a sunny day. And though few studies have been performed, there are many stories about inner-city children taken on field trips to the countryside—and their delight in such simple things as rolling in a pile of leaves, walking through a woodland, or even running around in a grassy field. It is as if all humans still have within them a sense of familiarity with—even a love for—the natural world, no matter where they live their daily lives. The great national parks of the United States—places of scenic wonder such as the Adirondacks, the Blue Ridge and Smokey Mountains of the East, Yellowstone and Yosemite in the West—had their beginnings in the nineteenth century. These lands were set aside, it is true, in part because their remoteness and often rugged terrain precluded early settlement and farming. In addition, the emerging railroad business of the nineteenth century enthusiastically backed the creation of national parks simply as destinations for tourists. But clearly there was something else as well, for if people did not respond to the beauty of such places, and also to the solitude, away from the hustle and bustle of city life, they would not have visited them. Indeed, one of the major complaints in modern American life is that destinations such as Yellowstone National Park have become so popular that traffic jams occur whenever bear and elk are spotted, and campsites are so crowded with people watching portable television sets that the original allure of such places is threatened.

Tourists watching the eruption of the Old Faithful geyser in Yellowstone National Park. (Gunter Marx Photography/Corbis)

The sense of pleasure and well-being—the sense of being *at home*—in wild surroundings has struck some observers as evidence that, though we humans essentially forsook life in the natural world with the invention of agriculture some 10,000 years ago, and though culturally we have become divorced from the natural world, we nevertheless retain deep within us a true bond with the natural world. Indeed, famed evolutionary biologist Edward O. Wilson—the man who coined the term *biodiversity*, and someone who cares deeply about the fate of the ecosystems and species of the world—believes that we actually retain a love of nature in our genetic makeup. Wilson calls this "biophilia." Along with many modern evolutionary biologists, Wilson believes that much of human behavior is rooted in our genes—and that aspect of his work remains controversial. Biophilia, its proponents contend, is a retention from our earlier evolutionary history—from the days when proto-humans, as well as early members of our own species, *Homo sapiens*, were living on the African savannas and later elsewhere around the world. And whether or not there are genes in the human genome that govern a delight in the living world, virtually everyone agrees that children as a rule do not have to be taught to love nature.

As evidence for his position, Wilson also points to the negative feelings people seem to have instinctively toward certain components of nature. Fear of snakes ranks high here, as does fear of fire. Our sense of fascination—largely based on dread—while watching television films about large carnivorous mammals (lions, tigers, leopards, wolves, and bears, for the most part), birds of prey (hawks, eagles, and vultures), crocodiles, sharks, and, of course, snakes reflects this underlying unease. These are dangerous animals today—and obviously were to our ancestors in our deep evolutionary past. Monkeys, for example, instinctively fear birds of prey, leopards, snakes, and fire—and it seems almost certain that we share pretty much the same basic fears.

When ancestral species of our human lineage evolved the capacity to walk upright, and adopted life on the open savannas (though there is some thought that members of these early species, 3 to 4 million years ago, in all likelihood still spent the night in trees, for safety's sake), they began a relationship with the other animals of the African ecosystem that still echoes today. For the most part, human beings—whether armed or not—can, if they exercise the proper caution, walk about unmolested in the African plains—*but only in daylight*. Certainly there are dangers, but herds of zebra and antelope melt away at the sight of humans walking single-file across the savanna; even lions rarely attack humans in daylight. At night it is a totally different story—and people are instantly transformed from being one of the most feared, to one of the most fearful, of species. Indeed, Mark Twain once observed that the human species seems to have a collective propensity for irrational fears (even downright madness) at night; that state of affairs also probably comes down to us from the early days in our evolutionary history on the African plains.

If such fears are retentions from our evolutionary past, reason biologists like Wilson, why can't the positive side, the love of nature and a feeling of being safely at home within it, also be retentions of our evolutionary past? Thus Wilson feels that, given the chance, a natural human love for the natural world will blossom—and help us stem the tide of the Sixth Extinction. What needs to be done, in this view, is simply to rekindle the flame that has been dampened by so much human existence in cities and other nonlocal-ecosystem environments since the invention of agriculture.

But there are other, parallel arguments about what people ought to do. Much of the teachings of the world's religions are codifications of how people ought to behave, generally referred to as morality. In addition, there is a rich history in nonreligious philosophy that seeks to derive, on general principles, how people should behave—the general area of ethics. In other words, apart from selfish motivations (that is, the first two reasons why people should care about biodiversity), and regardless of how "innate" our desire to maintain the living world may be (despite the fact that we are relentlessly destroying it), are there moral or ethical reasons why people should care about the fate of the world's natural environment? Scholars and thinkers in philosophy and religion are increasingly answering "yes!"

As an example, consider the Judaeo-Christian tradition. When conservation emerged as a serious concern in the 1950s and 1960s, some scholars pointed a finger of blame at religions such as Christianity. They said that the concept of dominion over "every creeping thing"—lines from Genesis, the first book of the Bible—amounted to a license to exploit all resources (including biological resources) to the hilt, as everything on earth was said in the Bible to have been put there by God for the use of mankind. And this tendency to regard not only mineral resources but all living things as ours, to do with what we please, was patently getting out of control.

And there is no doubt that, whatever the reason, human beings have indeed acted as if everything else on earth (even indeed, other human beings—witness the pernicious practice of slavery, which, contrary to popular belief, is still practiced in some societies) was put there for our own use, profit, and pleasure. Human beings, at least in Western societies, are notorious for not caring much about what will happen in the future—beyond, say, a half-generation away (long enough for their own children to grow up). There is, many would say, a natural penchant in humans to reap the benefits in the short term and not care what lies in store for generations ahead.

But we are, clearly, living in a finite world. There is a finite amount of habitable space, and, though we have yet to reach it, surely a finite capacity for us, no matter how sophisticated our technologies, to produce food. Already there are far too many people on earth to be able to support them all at the average middle-class standards of a U.S. family. Right now there is a dire shortage of safe drinking water for perhaps as many as a third (maybe more) of the world's people.

Thus, whatever our line of thought—be it a selfish regard to preserve useful resources; be it a sense that we must, for our own sake, preserve the natural environment from which we so recently sprang; be it the purely ethical consideration that we ought, on simple ethical grounds, to pass the world along to future generations more or less in the condition we found it; or be it the religious position currently becoming popular on many college campuses around the United States, that the "dominion" passage of Genesis can easily be seen as a sense of *stewardship,* that humans have the duty to preserve and conserve God's creation—there is a surge of thinking that the earth and all its inhabitants are in peril and we must do something about it.

—Niles Eldredge

See also: Agriculture, Origin of; Economics; Ecosystems; Population Growth, Human; Sixth Extinction; Sustainable Development

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Bees

See Arthropods, Terrestrial

Beetles

See Arthropods, Terrestrial

Benthos

The term *benthos* indicates the collective set or assemblage of organisms at or near the bottom of seas, lakes, and rivers. Many of these organisms are relatively or completely sedentary, moving very slowly or being fixed to the bottom. These assemblages can be further divided into those that live either on the bottom itself or on other organisms—the epifauna (animals) and epiflora (plants)—and animal assemblages that live just below the surface—the infauna. Fishes and other more motile organisms that are habitually part of the benthic system but that maintain the capacity to swim from place to place are described as being demersal.

The benthos contrasts with pelagic organisms in marine and freshwater environments (also called limnetic in freshwater systems). Many organisms spend parts of their life cycles inhabiting both the benthos and the pelagic environments. For example, many types of organisms have a larval stage that disperses as part of the drifting plankton in the pelagic zone before settling to the bottom and developing into a benthic juvenile stage. Other species may reproduce in part within the benthos but have adults that inhabit the pelagic zone as swimming (that is, nektonic) individuals.

Many benthic organisms, especially certain algae, sponges, corals (see Cnidarians and Coral Reefs), and worms (see Annelids) that create substantial biogenic structures as they grow, are important "ecosystem engineers" within the benthos. These organisms contribute structural complexity to various marine habitats, and therefore provide new microenvironments for other benthic organisms.

—Daniel R. Brumbaugh

See also: Ecology; Ecosystems; Lakes; Oceans

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Biogeography

Biogeography is the study of how, where, and why populations and species are distributed over the face of the earth; as such it relates centrally to ecology, evolution, and biodiversity. There are two primary avenues of research in biogeography: ecological biogeography, which aims to identify those ecological and climatic factors that control the distribution of many species; and phylogenetic biogeography, which aims to identify whether several different groups distributed in the same regions have speciated in response to a common geological history. These two subdisciplines exist because the geographic distribution of organisms is determined partly by ecological factors and partly by a lineage's evolutionary history. The conservation of biodiversity involves recognizing the key ecological requirements of species and identifying the regions that have evolved unique biotas.

Many of the factors that determine where species are found relate to ecology and climate. For example, as one approaches the poles, biodiversity declines; the tropics are the source of most of the world's species. Organisms are also adapted to particular habitats and climates, and the availability of appropriate food items; different species vary in their range of habitat tolerance, such that some groups are broadly distributed while others are distributed narrowly. Some organisms will even migrate vast distances annually to track their preferred habitat as climate changes with the seasons. Understanding the ecological and environmental requirements of species can provide us with great insight into the distribution of organisms. Our understanding of ecological biogeography is based upon both static and dynamic patterns. For example, the term *tree line* describes the current elevation above which no trees can be found because of climatic extremes; below tree line, the highest elevation at which any given tree species can be found will vary. During climate changes over the last 10,000 years, North American plant species migrated at different rates and in different directions to track their preferred habitat, such that ecological communities showed no real cohesiveness through time. Other important ecological biogeographic patterns relate to the number of species that islands, or even continents, can support. For instance, there is a well-established relationship between the size of a region and the number of species it contains. This was first quantified by J. C. Willis in 1922 and later extended in important research by Robert MacArthur and E. O. Wilson in the 1950s and 1960s. Finally, research by scientists beginning with work done by Linnaeus and including experiments conducted by Charles Darwin has documented how organisms within a species can move or disperse over large distances.

Although climatic and ecological factors clearly relate in an important way to organismic distribution or biogeography, regions with very similar climates can have very different types of species, and species with similar ecologies can occur in very different regions, complicating the study of ecological biogeography. Simply understanding a region's climate and the ecology of its constituent organisms does not provide a complete understanding of the biogeography. Augustin de Candolle, a French botanist who published several important works between roughly 1815 and 1825, was one of the first scientists to recognize this fact. To understand more completely where organisms are distributed, it is also necessary to know their evolutionary relationships.

Since evolution involves species descending from ancestors, a new species arises somewhere within the range of its ancestor. The ecological requirements of the ancestral species partly determine its biogeographic distribution, but geographic barriers also determine the limits of the species' range. In terrestrial species such barriers might include mountain ranges, oceans, or regions of inhospitable climate. For marine species barriers include land masses and deep ocean basins which, at least for species that live in shallow water, are analogous to regions of inhospitable climate. Many of the barriers that affect terrestrial and marine species are formed by geological processes driven by plate tectonics. Sometimes the formation of geographic barriers, mediated by plate tectonics, can trigger evolution and speciation in several groups distributed in the same region, because the barriers that form often separate populations of several species from one another; one of the principal ways that speciation occurs is when populations become isolated. It is also conceivable that many species may expand their ranges together when geographic barriers fall, as sometimes happens with climatic changes or continental collisions mediated by plate tectonics.

Georges-Louis Leclerc de Buffon, Augustin de Candolle, and other scientists active in the late eighteenth and early nineteenth centuries recognized that different regions tend to have their own distinct complement of species, and this was a fundamental insight relating the history of species to the geological history of the regions they occurred in. Initially, this observation was explained by invoking the idea that the different species had been created for each of the different regions. Philip Lutley Sclater and Alfred Russell Wallace were scientists who came up with schemes in the middle of the nineteenth century to divide the world into a series of distinct floras and faunas. Some of the regions were equivalent to continents, but others, notably in the case of India, were within continental borders. By the time Wallace published on this topic, scientists had accepted that the differences between the floras and faunas represented differences in the regions' respective geological histories; it is now known that India was separated from Asia until about 30 million years ago, and the boundary between India and Asia, demarcated in places by the Himalayas, represents a collisional zone between what were once separate continental blocks.

Wallace's 1869 book *The Malay Archipelago* is a popular account of the differences between the animals and plants typically found on the Asian and Australian continents. The narrow transition zone between those biotas is found in the Malay Archipelago, and the geographic boundary between the biotas is referred to as "Wallace's Line"—though the precise position of the line across the archipelago has been debated.

The study of phylogenetic biogeography is complicated because different species do not always speciate at the same time when barriers are formed. Furthermore, barriers that determine the ranges of some species by preventing their movement may not affect other species. Finally, some species may be able to extend their ranges greatly through infrequent, long-range dispersal events, such that the range they occupy and their evolution are not determined simply by the history of the establishment of geographic barriers in the regions in which they occur. Thus biogeography of regional faunas is related to geological history, but it is also related to the unique ecological features of organisms.

The formation of geographic barriers, because it encourages speciation, can play an important role in regulating diversity. For example, plate tectonics can act either to separate continents and their respective faunas or to join them. During the last 500 million years of the history of life, global diversity was higher when the continents were well separated than when they were together.

The association between evolution and biogeography is also shown by the role that biogeography played in the development of ideas about evolution. Charles Darwin, in his 1839 book *The Voyage of the HMS Beagle*, described how different islands in the Galapagos had unique species that were very similar to the species distributed on other islands in the chain. One of his foremost examples involved mockingbirds—not, as commonly but mistakenly believed, finches. He later used this point in his (1859) *Origin of Species* to show how the separation of these islands and the establishment of oceanic barriers between them might have driven the evolution of the terrestrial elements of these island faunas. Alfred Russell Wallace, another important figure in the history of evolutionary biology, also discussed, in an article published in 1855, how the emergence of geographic barriers that separated formerly contiguous populations of a species could lead to evolution and speciation.

Just as biogeography relates to ecology and evolution, it figures in our understanding of the biodiversity crisis. Furthermore, biogeographic information relates in an important way to conserving diversity because it involves identifying where different species are concentrated and understanding the mechanisms that are leading to extinctions. The biodiversity crisis is largely engendered by humans' activities that relate to two biogeographic factors: habitat destruction and alien species. In addition, the current biodiversity crisis can at least be partly understood as a manifestation of those biogeographic factors that eliminate or generate biological diversity. These are established from study of both the modern and fossil biota. One of the primary factors tied up with biogeography that contributes to the current biodiversity crisis—and also led to mass extinctions in the past—is habitat destruction. Habitat destruction causes extinctions for several reasons, including the fact that there is a well-established relationship between the area that a species occupies and its likelihood of future extinction: as the area shrinks, species become more likely to go extinct.

Alien species are also contributing to the biodiversity crisis. These species come to occupy new, larger ranges because of accidental or purposeful introduction by humans. When they enter new regions they often no longer have to cope with predators, and they can expand unchecked, outcompeting or simply overgrowing native species. Such invaders can change the ecology of a region very rapidly, thus altering the selective environment in which organisms evolved, potentially making once adaptive traits of organisms no longer adaptive in the face of changing competitors. The typical biogeographic history of most groups did not involve novel combinations of species coming into contact with one another. Instead, the respective biotas of different regions came into contact only rarely, and in events such as plate tectonic collisions between formerly isolated regions. These ancient plate tectonic events often had prodigious biotic consequences. For example, the Great American Interchange is an event that occurred 3 million years ago, when North America and South America collided at the Isthmus of Panama, and the mammals of these continents, which formerly had been separated, were mixed. After the collision extinction rates climbed and speciation rates fell in both continents, but especially in South America. The modern South American mammal fauna is relatively impoverished, at least compared with its state 3 million years ago, while being relatively enriched in mammals of North American origin. Therefore the biogeographic nature of the current biodiversity crisis is an acceleration of events that formerly occurred rarely and over much longer time scales. If anything, human activities leading to the introduction of alien species equal or exceed the extent to which biotas have been mixed by plate tectonics at any time in the past.

—Bruce S. Lieberman

See also: Alien Species; Ecological Niches; Ecology; Ecosystems; Evolution

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Birds

The approximately 9,800 species of living birds belong to what zoologists call the Class Aves of the Animal Kingdom. Modern birds are easily distinguished from their fellow vertebrates such as amphibians, reptiles, and mammals by a unique feature that they all share: feathers. Even penguins, which don't fly, but swim in the sea using their flippers to propel themselves, have feathers—although their coat may look superficially like fur.

Feathers are modified scales. Unlike scales, feathers are very flexible and extremely light, because of the air inside the rachis, or stem, and the loose organization of their component parts, called barbs and barbules. With the exception of penguins, ostriches, rheas, cassowaries, emus, and some island rails, birds use their feathers to fly. Feathers are also a marvelous insulating agent that permit their owners, whether flying or not, to regulate their body temperature. Hence even small and fragile-looking birds like juncos (belonging to the bunting family) can survive without problems in cold and snow—provided they have enough food to maintain their high metabolism and internal temperature. Unlike whales and seals, birds do not have a thick layer of insulating blubber underneath their skin. However, birds can ruffle up their feathers by means of special muscles, creating an air layer between skin and feathers that isolates them from the low temperatures of the outside world. Eskimos living in the Arctic use a similar principle when they wear loose clothing of animal fur (caribou, polar bear, or seal) that leaves plenty of air circulating between their skin and their parkas and pants. Feathers also permit birds to communicate among themselves. The colors and shapes of wing, tail, or body contour feathers, when exhibited in display, convey information about sexual readiness, social status within flocks, and aggression.

Turkeys, like other birds, use feathers to communicate among themselves. The colors and shapes of wing, tail, or body contour feathers, when exhibited in display, convey information about sexual readiness, social status within flocks, and aggression. (Swift/Corbis)

The closest living relatives of modern birds are crocodiles and their kin. Modern birds are also related to several extinct groups of vertebrates, the dinosaurs, especially theropods. Recent research has suggested that although some of these dinosaurs had feathers, or featherlike structures, they did not fly. Paleontologists believe that they used their feathers for thermal insulation and regulation. As the possession of feathers is not always associated with flying, one may think that these feathered dinosaurs and modern birds are not only related but also belong in the same zoological group. Some paleontologists even argue that modern birds are descendants from dinosaurian ancestors, and that modern birds are indeed surviving dinosaurs. The hardy juncos all fluffed up against the cold at our winter feeders may be tiny flying dinosaurs.

Whether or not they are dinosaurs, and whether or not they fly, modern birds are probably the best known group of animals, vertebrates or invertebrates. For example, whereas zoologists describe dozens, sometimes hundreds, of new species of fish, beetles, or flies each year, ornithologists propose on average only about three to five new species of birds in the same period of time. Of course these "new" bird species did not just evolve. They were present all along, but it is only recently that ornithologists discovered them while exploring some of the most inaccessible areas in the world, such as remote forests in the Andes of South America or the mountains of Africa or Asia. Although remarkable, the discovery of as-yet undescribed species of birds increases their known biodiversity by no more than a fraction of 1 percent annually. Biodiversity increases only during the process known by evolutionary biologists as speciation, when one or more new species evolve from an ancestral one. The evolution of new species is a problem that intrigued Charles Darwin, but it was one that he did not solve. Ornithologists have contributed greatly to our understanding of the intricacies of the speciation process. This contribution has been made possible by our detailed knowledge of birds.

Not only are the great majority of bird species described and catalogued, they are also quite well known in term of their geographical distribution, behavior, voice, nesting habits, habitat preferences, and migration routes. Chiefly thanks to their amazing capacity to regulate their body temperature, birds are found just about everywhere over the oceans and on earth. Thus wandering albatrosses (*Diomedea exulans*) can be observed in the most isolated stretches of the turbulent Southern Ocean, bar-headed geese (*Anser indicus*) have been seen in the fall flying over some of the highest ranges of the Himalayas, above 20,000 feet, and white-winged Diuca finches (*Diuca speculifera*) have been detected roosting in glaciers at 16,000 feet in the Bolivian Andes. I have watched black-legged kittiwakes (*Rissa tridactyla*) and ivory gulls (*Pagophila eburnea*) at the North Pole; in the Antarctic, south polar skuas (*Catharacta mccormicki*) have been sighted not far from the South Pole.

Whereas the above observations have been of nonbreeding birds, of course the fact remains that birds can breed in amazing and quite unexpected places, once again showing their extraordinary ability to exploit all available niches. For example, the gray gull (*Larus modestus*) nests in the middle of one of the most arid deserts in the world, the Atacama Desert of Chile. Some snow petrels (*Pagodroma nivea*) breed on nunataks, isolated bits of bare rock sticking out of the huge South Polar icecap. A hummingbird, the Andean hillstar (*Oreotrochilus estella*), places its nest along rocky overhangs in the treeless reaches of Peru's and Bolivia's Andes, at elevations reaching 15,000 feet. At such altitudes within the tropics, nocturnal temperatures regularly dip below freezing, and in order to save energy the tiny birds lower their body temperature and go into a sleeplike state called torpor. The great dusky swift (*Cypseloides senex*) of Brazil builds its conelike nest on wet rocky ledges behind some of the waterfalls in Iguaçú National Park. And the nocturnal common potoo (*Nyctibius griseus*) of Central and South America's forests and brush lands makes no nest at all but simply lays its single egg on the top of a broken branch stub. When incubating, the adult bird looks like a branch herself. Perhaps the most amazing breeding behavior—and habitat—of all birds are those of the emperor penguin (*Aptenodytes forsteri*). In the early Antarctic winter the single egg is laid, then incubated on his feet in a pouch of skin and feathers by the male. Emperor penguin chicks hatch and grow in the middle of the long Antarctic winter night, in the coldest and harshest environment on earth, the Antarctic sea ice. No wonder that Apsley Cherry-Garrard, recounting the ordeals of the expedition that first found and collected an emperor penguin's egg, entitled his book *The Worst Journey in the World.* (The emperor penguin was then thought to be such a primitive bird that the embryology of its egg might give clues about the origin of birds. How wrong ornithologists were at that time: we now know that penguins are like all other birds, and no more primitive than crows or grackles.)

Our extensive knowledge of birds, together with their wide dispersion and the general ease with which they can be studied in the field, makes them very important biodiversity indicators. Indeed, we can now compile detailed lists of rare, at risk, or endangered species from all parts of the world. Of the nearly 9,800 species of birds, no fewer than 1,186 (or about 12 percent) are estimated to be at risk of becoming extinct in the next 100 years. Of these 1,186 species, 182 are considered to be critically endangered and 321 to be vulnerable (BirdLife International, 2000, p. 2). Hence a staggering 503 species (about 5 percent of the world total) could well disappear from the globe in the twenty-first century. If this projected extinction rate applies not only to birds but to other creatures as well, our planet is about to suffer a serious loss.

Avian biodiversity, as measured by numbers of species, is not evenly distributed among given areas, habitats, or biogeographical regions, but instead follows several broad patterns. Thus equatorial and tropical regions have more species than do temperate ones of the same surface area, and those, in turn, have more species than do boreal or arctic regions. Within the tropics, the Amazonian rain forest biome of South America has more species than the Congo forest biome in Africa. Some estimates suggest that as many as 500 bird species can be found in one square mile of Amazonian rain forest. In general, forests have more bird species than savannas or grasslands. A continental chunk of land has more species than an equivalent area on an island. And within archipelagos, remote islands have fewer species than those of similar surface area closer to a mainland. Oceanic birds too have distributional and biodiversity patterns. Many more species of petrels and petrel-like birds are found in southern seas than in the north. Thus the Arctic Ocean has but one species of petrel, the northern fulmar (*Fulmarus glacialis*), whereas the Southern Ocean has about a dozen other species in addition to the southern fulmar (*Fulmarus glacialoides*). But biodiversity of birds expressed purely in terms of species numbers masks an important part of the picture.

Just as species are not distributed evenly or randomly over the globe, the distribution of each species, and of its constituent populations, follows patterns. In general, large species, such as eagles and hawks (family Accipitridae), have extensive territories and thus lower population densities than do smaller birds such as sparrows (Emberizidae) or wood warblers (Parulidae). Tropical birds, especially species living in rain forests, often have very patchy distributions and low population densities where they are found, even though the species' total distributional range might be very large. Thus a given species found through much of Amazonia's forests may actually be unaccountably absent from many areas where these forests look (to us) suitable for its presence. In addition, the population dynamics of many species fluctuate. In other words, the numbers of birds of any given species vary over space and time. Even without clear-cut influences from human agencies, some species decrease in their range or in their relative abundance, whereas others increase.

Some bird species have benefited from our activities and clearly enjoy human environments. Well-known among these are domestic pigeons and house (or English) sparrows in cities and towns all over the world, European

Shorebirds fly over tide flats along Cumberland Sound on Cumberland Island National Seashore, Georgia. (Raymond Gehman/Corbis)

starlings in the North American countryside, and black kites and house crows in Asian cities. Unfortunately, we also know that human-induced changes in our environment as well as direct human pressures such as habitat destruction (logging, paving over agricultural land, filling marshes and swamps) and indiscriminate hunting have resulted in the extinction of several bird species. Examples include the great auk (*Alca impennis*), the emblem of the most important ornithological society in North America; the passenger pigeon (*Ectopistes migratorius*); and several species of beautiful parrots in the West Indies. Other species, said by some ornithologists to be still living, are believed by others to be already extinct. The Eskimo curlew (*Numenius borealis*), which used to be called the swiftwing (because of its flying ability) by native Americans from the Ungava Peninsula of Labrador, was once an abundant bird, whose hordes bred in northern Canada and migrated thousands of miles southward across the equator to spend the winter on the pampas of Argentina before returning to their far northern nesting grounds. Relentless hunting along its migration routes in North America and in its southern haunts in South America, combined with the complete modification of its prairie habitat in the north and of the pampas in the south, decimated the species. Although very small numbers of Eskimo curlews might still breed in the remote Canadian Arctic, none of the sightings made in the last two decades have been confirmed by reliable authorities.

There is a net (and of course irreversible) loss of biodiversity when species become extinct, whether they do so because of natural agencies (as was the case in the extinction of most dinosaurs at the Cretaceous-Tertiary boundary following the catastrophic crash of an asteroid) or man-induced changes (such as the case of the great auk). These losses, when natural, take place at slow average rates (in terms of human generation times), perhaps of the order of 1 species of bird per 100 years, according to some estimates (ibid., p. 2); more likely is 1 species every 10,000 or even 100,000 years. But more than 100 species of birds have become extinct because of man-related or man-induced causes in the last 200 hundred years, a rate of about 1 species every 2 years. If we were to continue losing bird species at the same rate, avian biodiversity would inexorably plummet toward a biodiversity desert. This loss would be evident not only in terms of how many species become extinct but also which species remain. Predictably, the survivors would be the common and ubiquitous species, as well as man's commensals, such as house sparrows, European starlings, and house crows.

Can natural evolutionary processes that result in an increase in biodiversity—namely, speciation—make up for these losses? That is unfortunately not possible. Perhaps as much as 30 percent of the enormous bird diversity of the Amazon basin, with as many as 2,000 species (about 20 percent of the world's total), has been hypothesized by some ornithologists to have originated through natural speciation events in the last million years or so. Thus about 600 new species of birds may have evolved naturally in 1,000,000 years, a rate of about 0.06 species per 100 years, or six new species per 10,000 years. Although other ornithologists have disputed these estimates, independent evidence suggests that a speciation rate of 1 new species per 10,000 years is not so far-fetched. The Antarctic island of South Georgia, in the South Atlantic Ocean, is home to only one species of land bird, the Antarctic pipit (*Anthus antarcticus*), a small and rather fragile-looking passerine (or songbird). Even though South Georgia is largely covered with snow and ice in the winter, the pipit there, which eats chiefly small invertebrates living in the intertidal zone, is resident and evidently finds enough food along the shores to sustain it during winter blizzards and cold. South Georgia's pipit is closely related to a widespread South American mainland relative, the Correndera pipit (*Anthus correndera*), which also lives on Cape Horn and the Falkland Islands. All available evidence (morphology, behavior, voice, DNA) indicates that the ancestor of the South Georgia species was carried there from South America by the strong westerly winds that prevail in the high latitudes of the Southern Ocean. Such colonization events, followed by residency in the colony and their subsequent differentiation into new species, have been documented in many other bird groups, such as the famous Darwin's finches and mockingbirds of the Galapagos Islands. Because South Georgia was entirely covered by an icecap during the latest phases of glacial advance in southern latitudes during the last 500,000 years before the present, no land bird like a pipit could have survived there. The icecap retreated from the shores and lower altitudes of South Georgia only about 10,000 years ago. Hence successful colonization of this island by a South American pipit could only have occurred 10,000 years ago or even later. The resident Antarctic pipit of South Georgia cannot therefore be more than 10,000 years old. Most ornithologists, and many other zoologists, would consider such a speciation rate very rapid. It is clear that species losses of about 1 species every 2 years

Table 1
The Major Families of Birds

Non-Passeriformes	Number of Species	Family
Ostrich	1	Struthionidae
Tinamous	46	Tinamidae
Penguins	18	Spheniscidae
Loons	5	Gaviidae
Grebes	21	Podicipedidae
Albatrosses	14	Diomedeidae
Petrels and Shearwaters	72	Procellariidae
Pelicans	8	Pelecanidae
Cormorants	33	Phalacrocoracidae
Herons, Bitterns, and Egrets	60	Ardeidae
Storks	19	Ciconiidae
Flamingos	5	Phoenicopteridae
Ducks, Geese, and Swans	149	Anatidae
American Vultures and Condors	7	Cathartidae
Hawks, Eagles, and Kites	225	Accipitridae
Falcons and Caracaras	61	Falconidae
Pheasants, Grouse, and Quail	211	Phasianidae
Cranes	15	Gruidae
Rails and Coots	124	Rallidae
Plovers	66	Charadriidae
Sandpipers and Snipe	86	Scolopacidae
Skuas	7	Stercorariidae
Gulls and Terns	91	Laridae
Auks, Puffins, and Auklets	22	Alcidae
Pigeons and Doves	309	Columbidae
Parrots and Parakeets	353	Psittacidae
Cuckoos	150	Cuculidae
Owls	204	Strigidae
Potoos	5	Nyctibiidae
Nightjars and Nighthawks	83	Caprimulgidae
Swifts	92	Apodidae
Hummingbirds	332	Trochilidae
Kingfishers	92	Alcedinidae
Toucans and Toucanets	35	Ramphastidae
Woodpeckers and Flickers	200	Picidae

Passeriformes*	Number of Species	Family
Miners and Earthcreepers	221	Furnariidae
Antbirds and Antpittas	236	Formicariidae
Tyrant Flycatchers	390	Tyrannidae
Cotingas and Fruiteaters	65	Cotingidae
Lyrebirds	2	Menuridae
Larks	85	Alaudidae
Swallows and Martins	80	Hirundinidae
Wagtails and Pipits	55	Motacillidae
Bulbuls and Greenbuls	124	Pycnonotidae
Shrikes	69	Laniidae
Wrens	69	Troglodytidae
Mockingbirds and Thrashers	30	Mimidae
Thrushes and Robins	324	Turdidae
Babblers and Wren-Tit	256	Timaliidae
Old World Warblers	376	Sylviidae
Old World Flycatchers	147	Muscicapidae
Titmice and Chickadees	50	Paridae
Nuthatches	25	Sittidae
Sunbirds	130	Nectariniidae
Honeyeaters	174	Meliphagidae
Buntings, Juncos	321	Emberizidae
Cardinals	43	Cardinalidae
Tanagers	256	Thraupidae
New World Warblers	116	Parulidae
Hawaiian Honeycreepers	23	Drepanididae
Vireos	52	Vireonidae
Grackles, Cowbirds	97	Icteridae
Finches, Serins	134	Fringillidae
Weavers, House Sparrow	114	Ploceidae
Starlings, Mynas	108	Sturnidae
Birds of Paradise	42	Paradisaeidae
Ravens, Crows, and Jays	117	Corvidae

* Perching birds or songbirds

Sources: Burnie, David, and Don E. Wilson, eds. 2001. *Animal.* New York: DK; Howard, Richard, and Alick Moore. 1998. *A Complete Checklist of the Birds of the World,* 2d ed. New York: Academic.

cannot be matched by species gains of even 1 species every 10,000 years.

—François Vuilleumier

See also: Biogeography; Evolutionary Biodiversity; Extinction, Direct Causes of; Galapagos Islands and Darwin's Finches; Speciation; Systematics

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Birds of Guam and the Brown Tree Snake

Like the serpent in the biblical Garden of Eden, the arrival of the brown tree snake (*Boiga irregularis*) brought the end of paradise for the birds of Guam. Of Guam's twelve native forest bird species, nine have been driven to extinction within the last fifty years, including five endemic species and subspecies. The primary cause of these extinctions was the unintentionally introduced brown tree snake. As the bird species disappeared before the eyes of the world's ornithologists, the culprit initially went unidentified and was extremely successful in its expansion across the island.

The island of Guam is the largest and southernmost island of the Mariana archipelago, located to the north of New Guinea. Following World War II, Guam became an important U.S. naval base and a repository for a large amount of military equipment used throughout the Pacific during the war. It is believed that the brown tree snake, a fearsome arboreal predator, first arrived in Guam as a stowaway on one of these interisland shipments. Because of similarities in markings and coloration, it is thought that the brown tree snakes of Guam probably originated in the Admiralty Islands, to the south.

The first reports of brown tree snakes on Guam were made in the 1950s, but because the snakes were initially misidentified as a predator of rodents, the threat to Guam's birds was not appreciated. The native fauna of Guam was unprepared for an invasion of predatory, arboreal snakes because they had evolved in an island sanctuary free of such dangers. The only snake native to Guam (*Ramphotyphlops braminus*) is blind and so small that it is commonly mistaken for a worm.

With an ample food supply and an absence of predators, the snake population grew exponentially, and their range expanded across the island. All species of forest birds suffered a similar pattern of decline—disappearing first in the south in the 1960s and then in a wave of decline moving north until 1986, when the last forest dwellers disappeared. Small mammals and reptiles also suffered severe population declines, and two bat species and at least three lizard species have also been lost. Bird species were particularly vulnerable because the snakes are voracious egg-eaters as well as preying on adults and nestlings. Small songbirds such as the rufous fantail (*Rhipidura rufifrons*), bridled white-eye (*Zosterops conspicillatus)*, and the Guam flycatcher (*Myiagra freycineti*) were particularly vulnerable and are among the extinct. Even the white tern (*Gygis alba*), which feeds on ocean fish, has suffered drastic declines, because its nests in trees are accessible to the snakes. The only species to escape the carnage were the marsh-living native yellow bittern (*Ixobrychus chinensis)* and introduced game birds inhabiting treeless areas. Most of the native forest species were all but extinct when they were listed as threatened or endangered by the U.S. Fish and Wildlife Service in 1984.

The species extinctions on Guam are a tragic loss of biodiversity that is compounded by secondary effects we are only beginning to understand. The decline of many insectivorous species has allowed insect populations to grow unchecked, resulting in defoliation and crop damage. Birds and bats commonly play important roles as pollinators and seed dispersers, and Guam has undoubtedly been affected by the loss of these services. Unfortunately, little was known about the ecology of many of the extinct species and their roles in Guam's ecosystem. Brown tree snakes have also caused problems for humans in more direct ways. The snakes often prey on domestic poultry and have been known to attack sleeping infants. Electrical outages are frequently caused by the snakes, which are notorious for short-circuiting power lines. Interruptions in power are costly and inconvenient.

Two of Guam's bird species have survived, thanks to heroic efforts that brought the last surviving individuals into captivity in order to establish captive breeding programs. These are the Guam rail (*Gallliraillus owstoni*), a flightless bird endemic to Guam, and the Micronesian kingfisher (*Halcyon cinnamomina)*. Several zoos have participated in the scheme of carefully planned matings intended to preserve the genetic diversity of the species and to create healthy captive populations. The breeding program for the Guam rail has been quite successful, and an attempt has been made to establish a free-living colony of rails on the nearby island of Rota. Although Rota does not have brown tree snakes, feral cats were responsible for the deaths of many of the introduced rails. Bird reintroductions in Guam are also being attempted, but only in very limited areas because of the effort required to evict the snakes.

The Micronesian kingfisher has not enjoyed the same success as the Guam rail. The current number of birds in captivity is not much larger than the founding population. The primary challenge has come from the dearth of knowledge about the species' habits and nutritional requirements. Without sound information about the ecology of the species, zoos have had to rely on techniques extrapolated from knowledge about similar species. Early reproductive failures were likely associated with lack of acceptable nesting places and dietary problems.

Control of the snakes on Guam and prevention of snake introduction to other islands is an issue of high priority. The Hawaiian islands, where bird populations have already suffered from the introduction of predators such as the cat, mongoose, and pig, as well as introduced diseases, are of particular concern. Various methods have been employed to control or eliminate the snakes on Guam. Trapping and hand catching snakes are widely practiced. Researchers are investigating possible ways of poisoning the snakes or introducing a snake-specific disease, but both of those options may pose risks to other species as well. In some areas electric barriers are placed on nesting trees, and the tree branches may be trimmed to eliminate the snakes' "highway in the sky," but both of those methods are labor intensive and costly, making them impractical over large areas. Terrestrial barriers around areas cleared of snakes have also shown promise during initial trials, but constant vigilance is required to detect breaches.

—Julie Pomerantz

See also: Birds; Endangered Species; Extinction, Direct Causes of; Reptiles

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Bivalves

See Mollusca

Black Rhinoceros

The black rhinoceros (*Diceros bicornis*) is one of five species of rhinoceros that compose family Rhinocerotidae, order Perissodactyla (horses, zebras, asses, tapirs, and rhinoceros). They are an important component of the unparalleled diversity of large mammalian herbivores inhabiting African savannas. This once abundant species is seriously endangered and at risk of extinction in the wild. Ancestral Rhinocerotidae are first recorded from Late Eocene sediments in the New and Old World; the family reached its greatest species-diversity during the Oligocene and Miocene.

Black rhinoceros (like all perissodactyls) are adapted for running (cursorial). Body weight is supported by the central digits, with the primary axis of the foot passing through the third digit (mesaxonic). The body is massive (weighing up to 1,400 kilograms) with short, stumpy limbs. Head and body length can reach up to 375 cm, and shoulder height up to 180 cm. Males are larger than females.

Despite its common name, the thick, scantily haired skin of black rhinoceros is not black but dark brown or dark gray with yellowish highlights (usually obscured by mud or dust). The two conical horns (a stubby third horn is sometimes present) are composed of compressed keratin, not bone, with the longer anterior horn averaging 50 cm (the record is 135.9 cm). Females usually have longer horns than males. The upper lip has a central, prehensile protrusion. This hooked lip and the smaller size of the black rhinoceros distinguish it from the square-lipped, larger white rhinoceros. The short tail is tipped with stiff bristles.

Black rhinoceros occur in forest, savanna woodland, and scrub, and they are not usually associated with open plains. They are browsers, gathering thin, regenerating twigs of woody plants, particularly acacias. Rhinoceros feed most intensively during early morning and evening, drink daily, frequently utilize mineral licks, and sleep at midday, often in mud or water wallows. They are not found farther than about 25 km from permanent water.

Adult males are usually solitary but sometimes feed together. A temporary group (clan) forms between an adult female and her calf; this clan persists until the next calf is born. The ranges of clans often overlap, but in dense populations, breeding males occupy mutually exclusive home ranges. Alarm, threat, and contact are communicated by snorts and olfactory cues; males mark their territories by spraying urine. Breeding occurs throughout the year. A single calf is born after a gestation of up to 478 days and weaned after two years. Captive animals have lived up to forty-five years.

The natural range of *D. bicornis* once encompassed the savannas of northern, eastern, and southern Africa. Populations have declined from hundreds of thousands to about 3,000 individuals during the last three centuries because of predation by humans, who hunted them for their hides and horns, and converted their habitats into farmland and settlements. Most populations are critically endangered, despite intensive conservation efforts that include protection of wild populations, rein-

A black rhinoceros under 24-hour guard because of the risk of poaching, Zimbabwe (Gallo Images/Corbis)

troduction of animals into areas where the species once occurred, and captive breeding programs throughout the world.

—*Mary Ellen Holden*

See also: Endangered Species; Mammalia; Perissodactyls; Preservation of Species

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Bluebuck

The nilgai (*Boselaphus tragocamelus)* is the sole species contained in the genus *Boselaphus*. Nilgai (along with bison, cattle, and chousingha) are in subfamily Bovinae, family Bovidae, and are members of order Artiodactyla (antelope, cattle, camels, deer, giraffes, goats, pigs). The nilgai, and its relative *Tetracerus* (chousingha), are the only living remnants of the bovine tribe Boselaphini, a Miocene and Pliocene radiation of species comprising twenty-one extinct and two extant genera distributed in Europe, Africa, Asia, and Java. Ancestral Bovidae date from Early Oligocene sediments of Asia.

Nilgai, like all artiodactyls, have paraxonic feet, in which the primary weight-bearing axis of each foot passes between the third and fourth digits. The first digit is absent, and the lateral digits are reduced in size. They are stocky and horse-size, with head and body up to 210 cm long, a tail up to 54 cm long, shoulder height up to 150 cm, and weight up to 300 kg. Forelegs are longer than the hindlegs. Bulls are larger than cows and have short, spiky horns; females are hornless. Fur is short and wiry. In adult bulls, the head, back, and sides are bluish gray; the neck, chest, legs, and belly are black; the rump, insides of thighs, and underside of tail are white. This pattern is broken by a white throat patch, white cheek crescents, and white spots around the muzzle, above the eyes, inside the ears, and above the hooves. Cows and younger animals exhibit similar markings but have a tawny coat. Both sexes have a short, bristly mane and a tuft of hair projecting from the throat.

The nilgai now occurs in eastern Pakistan, Nepal, and the Indian peninsula, but during the Pleistocene it ranged as far west as Jordan. In the Hindu religion the nilgai is closely related to the sacred cow, and it remained free of persecution until about 1900, when populations began to decline (to the point of extirpation in Bangladesh) in response to habitat destruction and overhunting. Captive and semiwild populations thrive in southern Texas, where up to 9,000 animals range over 2,600 square miles of mixed grassland-woodland habitat. Some ecological data are derived from wild populations, but most detailed information comes from studies of the nilgai introduced into southern Texas.

Occasionally found in open plains, nilgai prefer deciduous and thorn forests and low tropical evergreen formations. During early morning and late afternoon they graze and browse, often standing erect on their hind legs to reach high branches. Bulls are territorial, forming breeding herds during the rut that consist of one bull and between two and ten cows. Three kinds of nonbreeding herds consist of cows with young calves, adult and yearling cows, and bachelor bulls. A single young or twins (occasionally triplets) are born after a gestation period of eight to nine months. Up until they are ten months old, young males remain with cow herds, then leave to join bachelor aggregations. Males breed at around five years of age; cows reach sexual maturity after three years.

—*Mary Ellen Holden*

See also: Artiodactyls; Endangered Species; Mammalia; Preservation of Species

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Bony Fishes

The term *bony fishes* strictly refers to a large grouping of jawed vertebrates, which together compose the Osteichthyes. Among other features, osteichthyans are characterized by the presence of true endochondral bone—that is, the bones of their endoskeleton ossify internally. The members of this huge group include the lobe-finned fishes and the four-limbed vertebrates (the sarcopterygians), and the ray-finned fishes (the actinopterygians).

The remains of sarcopterygians date from the Early Devonian, but phylogenetic data indicate that the origin of the group probably long predates that and may have been as early as the Silurian. Living members of the Sarcopterygii are the lungfishes (Dipnoi), coelacanths (Actinistia), and the four-legged vertebrates (Tetrapoda). A characteristic of all sarcopterygians, fossil and living, is the possession of a so-called monobasal (single-based) articulation of the paired fins with a fin musculature extending in a fleshy lobe. The largest of the sarcopterygian subgroups, the Tetrapoda, will be dealt with elsewhere, while the "fish-like" members (lungfishes and coelacanths) will be briefly dealt with here, followed by a consideration of the bulk of the Osteichthyes, the Actinopterygii or ray-finned fishes.

The earliest known actinistians (coelacanths: *coel* = "hollow"; *acanth* = "spine") are Late Devonian in age, and the group is represented by an extensive fossil record to the end of the Cretaceous, after which no further fossils are known; the lineage was presumed to have gone extinct. The discovery of a living coelacanth in the late 1930s (Smith, 1939) was thus a great surprise and generated a strong interest in coelacanth biology and their phylogenetic relations to other sarcopterygian groups. Today, coelacanths are represented by two known living species: *Latimeria chalumnae*, from the Comores Islands in the southwestern Indian Ocean, and the recently discovered *Latimeria menadoensis*, from off Manado, Sulawesi, Indonesia (Holder et al., 1999). The coelacanth body plan is remarkably conservative, and these two species are regarded as "living fossils" strikingly similar to their long extinct relatives. They possess a typically actinistian caudal fin in which the dorsal and ventral webs are equal in size and separated by a horizontal prolongation containing the posterior extent of the notochord and ending in a small, rounded tuft. Coelacanths have a unique rostral organ in the snout that is believed to have an electrosensory function, and they share numerous additional features of the skull and paired fin skeleton that are unique to the group. The braincase of adult *Latimeria* is noteworthy in that it is made up of two parts articulated together by an intracranial joint. However, this remarkable feature is thought probably to be a primitive sarcopterygian character that has subsequently been lost in lungfishes and tetrapods.

The earliest known lungfishes (Dipnoi) are also Late Devonian in age and are today represented by three freshwater genera: the African *Protopterus* (four species); the South American *Lepidosiren* (one species); and what is thought to represent the most primitive of living forms, *Neoceratodus* (one species) from Australia. Unlike the coelacanths, living lungfishes are not very similar to their early fossil relatives. For example, the skeleton of living lungfishes is mostly cartilaginous, while that of their early relatives was fully ossified, and in living forms the dorsal fin is continuous with the caudal fin, although separate in fossil lungfishes. Despite the specializations of the living taxa, all lungfishes, living and fossil, share many characteristics. For example, all possess massive crushing tooth plates that rest on the palate and inside of the lower jaw. As their name suggests (*dipnoi* = "two lunged"), lungfishes have well-developed lungs (one in *Neoceratodus*, and two in *Lepidosiren* and *Protopterus*). The latter two breathe exclusively with their lungs, while *Neoceratodus* must respire with its gills. Pharyngeal anatomy of fossil forms suggests that obligate air-breathing probably arose rather late within the lungfish lineage, and that early lungfishes were probably exclusively gill breathers.

The discovery of living lungfishes in the early nineteenth century, and their striking resemblance in many features of their soft anatomy to tetrapods, engendered a debate as to the precise relationships of lungfishes to the land-dwelling forms. Aspects of their lungs, internal nostrils, heart structure, and paired fins were thought to indicate close affinity to (if not identity with) tetrapods. However, recent consensus suggests that the immediate relationships of the Tetrapoda lies with various Palaeozoic fossil sarcopterygians rather than with either the lungfishes or coelacanths. However, controversy still exists as to which of these two represents the closest living relatives to the tetrapods (Janvier, 1996).

The ray-finned, or actinopterygian, fishes form the largest and most diverse of all vertebrate groups. In total, the number of actinopterygian species exceeds that of all other vertebrate groups added together. The notion that life in an aquatic medium is somehow a dead end is clearly without merit, as evidenced by the enormous success of the contemporary actinopterygian radiations. Although the earliest indisputable record of actinopterygian remains dates back to the Devonian, around 400 million years ago, the origin of the group probably predates those fossil finds. The actinopterygian fossil record is rich, but unlike most other vertebrate groups, there are far more living forms than fossil. Most of the living diversity of ray-finned fishes is found in one group, the teleosts, which first appear in the fossil record around 200 million years ago. The term *teleost* ("perfect bone") refers to their position as the most advanced of all bony fishes. Compared with the teleosts, the other living actinopterygian groups are small and relictual. They include the bichirs and ropefish (about eleven species), the sturgeons and paddlefishes (about twenty-six species), the gars (eight species), and the bowfin (one species). These will be considered briefly before going on to discuss the great bulk of actinopterygian diversity, the Teleostei.

Bichirs and ropefish (Cladistia) are represented today by only two genera (*Polypterus* and *Erpetoichthyes*) with a total of about eleven species in the freshwaters of West and Central Africa. These bizarre, elongate, predatory fishes possess an intriguing combination of primitive, derived, and unique features. Since their discovery some 200 years ago, the phylogenetic position of the cladistians has proven problematic, although today most authorities agree that they represent a relict of the basal actinopterygian lineage. They possess strange, lobelike pectoral fins, a thick jacket of interconnected ganoid scales, and a distinctive series of ten to eighteen dorsal finlets. Cladistians are obligate air breathers and will drown if unable to access atmospheric oxygen. Respiration is mediated almost entirely by highly vascularized lungs, which are aspirated via elastic recoil of the encasing ganoid scale jacket.

Sturgeons and paddlefishes (Chondrostei), like the cladistians, are another relictual group possessing a mixture of primitive and derived actinopterygian features. Chondrosteans are represented today by two families, the Acipenseridae (sturgeons), with about twenty-four species restricted to fresh and coastal waters of the Northern Hemisphere, and the Polyodontidae (paddlefishes), with one species in the freshwaters of North America and another in China. Squamation is reduced to five rows of bony scutes in sturgeons and is absent in paddlefishes, except for a single row of scales along the upper margin of the caudal fin. Internally their skeletons are cartilaginous—but secondarily so, as the skeletons of fossil chondrosteans were fully endochondrally ossified. They retain strongly heterocercal tails and a spiral valve in the intestine. Perhaps as a result of their marked longevity, migratory spawning runs, and high market value (for caviar and meat), nearly all chondrosteans are today highly endangered, threatened, or already extinct. No other group of fishes has been so affected by the dam-building, habitat degradation, and overexploitation that have taken place throughout their range in the past century.

The gars (Ginglymodi) are represented by a small group of seven species arrayed in two genera, *Lepisosteus* and *Atractosteus*. They typically inhabit backwater areas of lakes and rivers in North and Central America. Like the cladistians, they retain a jacket of interlocking ganoid scales and have a fully ossified internal skeleton; internally their tail is heterocercal, but that is not always evident externally. The centra of gar vertebrae are characteristically opisthocoelous—that is, they are concave on their posterior surface and convex on the anterior, allowing for a ball-and-socket articulation, a configuration that is almost unique among actinopterygians.

Bowfins (Halecomorphi) are today represented by a single species, *Amia calva,* widely distributed in the freshwaters of eastern North America. However, the group has a rich fossil record dating back to the Early Triassic, some 240 million years ago, and during the Mesozoic it was taxonomically diversified into upward of eleven genera. Generally considered to be the closest living relative to the teleostean fishes, the living bowfin has many characteristics in common with them. Among the functionally most important of such characteristics may be the presence of a hinged maxilla, which facilitates efficient, high-velocity suction feeding. In waters of low oxygen pressure, bowfins utilize a highly vascularized air bladder to extract atmospheric oxygen.

Today, it is teleost fishes that dominate the fresh and marine waters of the planet, and they are undoubtedly the dominant actinopterygian group. Current estimates of the number of living species vary, but most authors agree that there are at least 23,500. However, for the past ten years about 200 new species have been described each year. The uniformity of this figure probably reflects a fixed number of taxonomists working on teleost species descriptions rather than any cap to the actual number of undescribed species still to be encountered; a final tally of 28,000 to 30,000 species seems reasonable.

Teleost fishes occupy almost every conceivable aquatic habitat, from high-elevation mountain springs more than 5,000 m above sea level to the ocean abyss some 8,000 m below. Perhaps not surprisingly, in view of this remarkable elevational span, the variety in manner of life, anatomy, physiology, and behavior is unsurpassed among vertebrates. A few examples serve to illustrate the extraordinary range. Some fish live for less than one year, whereas others may live for more than 150 years. Some fish live their entire lives within meters of their natal site; others migrate more than 3,000 km between spawning and feeding grounds. Some will spawn once in their lifetime, whereas others may spawn many times a year over a period of many years. Some display parental care; some are viviparous. Most are gonochoristic (that is, ovaries and testes are present in different individuals), but many are hermaphrodite (one individual has both ovarian and testicular tissue, or is sequentially male then female, or vice versa); some are even capable of self-fertilization. Some produce light, venom, and electricity, and many produce sound. Some are parasitic on other species or their own. Most are ectotherms (that is, rely on external heat sources), but some have evolved endothermy (they generate and retain their own heat). Some fishes can live in almost pure water of 0.01 parts per thousand (ppt), whereas others can live in water of up to 100 ppt (seawater usually ranges from 34 to 36 ppt). Some can withstand temperatures as high as 44 degrees centigrade; others, which inhabit frigid polar seas, produce antifreeze proteins that depress their blood's freezing point to 2 degrees below zero centigrade.

Patterns of global distribution are also of interest. Although it is noteworthy that nearly all of the living nonteleostean actinopterygians are freshwater inhabitants, among teleosts a little more than half (58 percent) of all species are found in marine habitats; about 41 percent are confined to freshwaters; and a little less than 1 percent are diadromous (that is, they migrate between fresh and salt waters). The high number of freshwater-restricted teleost species is noteworthy, as less than 0.01 percent of the earth's water is fresh (occupying only 0.8 percent of the planet's surface). However, it should also be noted that the majority of marine fish species are restricted to the relatively narrow region of the continental shelves (representing only 5.4 percent of the planet's surface), and the richness of marine species declines markedly away from those coastal areas.

The remarkable success of the teleostean fishes has resulted in a staggeringly diverse radiation, and it is difficult to summarize the extent and complexity of forms and life styles in such a short entry. In terms of their classification, there are four major teleostean lineages currently recognized: the Osteoglossomorpha (the bonytongues, mooneyes, knifefishes, and elephantfishes); the Elopomorpha (the ladyfish, tarpons, deep sea spiny eels, and true eels); the Clupeomorpha (the herrings and sardines); and the Euteleostei (a massive grouping of some 22,260 species, including such diverse members as the carps and catfishes, salmons and smelts, bristlemouths, lizardfishes, lanternfishes, cods, guppies, sticklebacks, sculpins, gobies, flatfishes, cichlids, and seabass, among many others). The interrelationships among these many fish groups are a topic of much ongoing research, and we are still far from a final consensus as to the details of the evolutionary histories of these animals.

In the face of such a diverse array of fishes, perhaps a key to understanding their radiation is the recognition that life in water is fundamentally different from life on land. Water is a dense, viscous medium that, in comparison with air, places a premium on effective generation of suction for acquiring food and efficient fluid propulsion mechanisms for locomotion. The heads of most teleosts are capable of quite remarkable kinesis and suction generation, with more than thirty movable bony parts controlled by more than fifty individual muscles. Some teleosts are capable of increasing their mouth volume by as much as fortyfold in milliseconds, and of generating negative pressures of up to –800 cm H_2O (0.7 atmosphere), a figure approaching the physical limits imposed by fluid mechanics. The dense aquatic medium, combined with an unrivaled suction generation capability, offers an unparalleled array of prey capture opportunities for teleosts that are unavailable to their terrestrial counterparts. Because density and drag are considerably higher in water than in air, locomotion is relatively more energetically expensive in the aquatic realm. In addition to hydrodynamic streamlining, perfection of caudal locomotion has been cited as the second major attribute of the teleostean radiation, and indeed much of the evolutionary transformation of the group can be seen in a series of modifications and refinements of their locomotor systems. Powered by a swimming musculature that makes up between 40 and 65 percent of their body weight, teleostean vertebral columns have a lateral flexibility and compressional rigidity capable of powering a caudal propulsion mechanism of unrivaled efficiency. Although teleostean swimming usually involves alternating contraction and relaxation of the swimming musculature, many specialized swimming modes have also evolved. For example, some species can "walk" along the bottom, climb vertical rock walls, glide on the water's surface, or even fly for extended distances. It is in the context of the two basic functions of aquatic feeding by suction generation and caudal propulsion locomotion that the tremendous success of the teleostean radiation is perhaps best understood.

Despite the remarkable potential of the aquatic medium to support life, there are also particular challenges. This is nowhere more starkly evident than in the arena of contemporary biodiversity loss. The past fifty years have seen an accelerated loss in aquatic systems whereby human activity is placing increasing pressure on fish populations, particularly in freshwaters. As in terrestrial systems, the three major sources of human-induced stress are habitat degradation (both within stream and land-based), introduction of exotic species, and overexploitation. Human dependencies upon and benefits from the world's fish species are many, and some are critical—such as for food and as indicators of water quality. For example, marine teleosts provide a primary source of protein for more than 1 billion people, and worldwide provide more people with animal protein than pork or beef. A full half of the world's growing human population is coastal, and another quarter lives within 60 km of the coast. Inland water and coastal ecosystems are among the most endangered in the world, and once perturbed deteriorate at a faster rate and with a poorer recovery prognosis than their terrestrial counterparts. The cumulative impacts in freshwaters have been profound; human appropriation of the planet's accessible runoff is now more than 50 percent, and dammed reservoirs hold five times as much water as is in rivers. Worldwide, it has been estimated that some 20 to 30 percent of freshwater teleost species are already extinct or in serious decline. Figures for marine fishes are harder to come by, but already more than 50 percent of the world's mangrove habitats have been lost; neuston (communities living on or just under the surface film of water) are impacted by the 3.25 million metric tons of petroleum products that enter the sea yearly from ships, accidents, and run-off from land; and upward of 75 percent of the world's major fisheries are considered overfished, with population declines now commonplace.

—*Melanie Stiassny*

See also: Chondrichthyes; Freshwater; Haplochromine Cichlids of Lake Victoria; Oceans

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Botany

Botany is a branch of biology that deals with the study of plants. In its broadest sense it would encompass all study concerning plant life, but it is usually limited to the study of the structure, physiology, development, genetics, ecology, and classification of plants, as well as economic botany and ethnobotany. These various specializations within botany provide the base for applied botany in other plant sciences, such as horticulture, agriculture, forestry, plant breeding, and medical botany.

Structural botany encompasses plant anatomy and plant morphology. Plant anatomy concerns itself with the actual structure of plants in terms of cells and tissues, whereas plant morphology concerns itself mainly with form and life cycles. Each of these two subdisciplines has two approaches: comparative and developmental. The comparative approach is most commonly used to generate data for systematic purposes and for the description of form and structure to understand the functional aspects of structure for ecological studies. The latter approach is often termed ecological plant anatomy. In contrast, developmental approaches to structural botany are concerned with the development of cells, tissues, and form, and they tend to interface more closely with plant physiology and plant molecular biology. Plant physiology focuses on the chemistry and physics of water uptake and movement from the soil through the plant to the atmosphere, and on the translocation of assimilates throughout the plant. It also deals with ecophysiological adaptations, mineral nutrition, and the function of plant hormones in plant development. Plant molecular biology consists primarily of the identification and study of the genes that control development, organogenesis, physiology, and the production of plant secondary compounds. The latter studies interface with phytochemistry, which is involved in the identification and biosynthetic pathways of unique plant compounds that play an ecological role and are an untapped source of potential pharmaceuticals.

Economic botany in the broadest sense is the study of plants and people. Historically, the area was mostly concerned with agricultural practices, both current and in the past, but more recently the focus has shifted toward the origin of cultivated crops—especially alternative crops found in tropical areas, in the search for new medicinals, and in ethnobotany. Of particular concern is the study of local economies and plant use in order to develop sustainable agricultural and forestry practices with minimal environmental damage and long-term economic stability. Ethnobotany interfaces substantially with anthropology, and ethnobotanists are concerned with the uses of plants by local people for medicines, food, clothing, building materials, and ceremonial purposes, in a concerted effort to preserve historical knowledge as well as to preserve and maintain local ecosystems and practices. The classifications used by indigenous people have often led to a new understanding of medical properties and to unsuspected evolutionary relationships.

Plant systematics is the study of the diversity of plant life in all environments; it involves the production of floras, monographs, and the classification of plants based upon our understanding of the evolutionary history of plant groups at all levels. Such data are gathered by plant systematists from all botanical subdisciplines (for example, anatomy phytochemistry, gene sequences, and so forth) in the reconstruction of the evolutionary history of the group(s) under study. Specialists within systematics mainly concentrate on regions such as North America, China, and the like; or on habitats such as aquatic plants, desert plants, or tundra plants; or on groups of plants. The latter is more common, and some specialties in nonseed plants include phycology or algology (red, brown, and green algae), bryology (hornworts, liverworts, and mosses), and pteridology (club mosses, spike mosses, whisk ferns, horsetails, and ferns). Within seed plants, specialties include nonflowering seed plants or gymnosperms (cycads, conifers, and gnetophytes) and flowering plants. The latter, by far the

A botanist nurtures seedlings in a greenhouse. (Library of Congress)

largest group of plants with minimally some 250,000 species, is further divided into many subgroups—for example, monocots, rosids, asterids, and so forth. The study of fungi (mycology) also is included within botany, although they are technically not plants, and these organisms are covered in botany textbooks and historically often included in floras. The understanding of the relationship of fungi to plants in terms of mycorhizal associations—that is, soil fungi with the roots of vascular plants—is fundamental in plant ecology and of value in plant systematics. Similarly, there is an association of plant pathogenic fungi, which often show coevolutionary relationships. The ultimate goal of plant systematics is to provide a classification system for all plants based upon their inferred evolutionary history.

Another important area in botany is palynology, which is the study of the pollen and spores of extant plants and in the fossil record as microfossils. Data from palynology are used in pollination biology, in systematics, to reconstruct prehistoric floras and climatic changes, and in medical studies of allergies. It is also an important source of data for the exploration for fossil fuels.

Paleobotany, the study of fossil plants, usually involves macrofossils (that is, roots, stems, leaves, cones, flowers, and so forth). The information obtained from paleobotanical studies is crucial for the development of a time line for the appearance of extant groups, the appearance of structural and reproductive innovations, and for understanding floristic changes. The distribution of fossil plants contributes significantly to understanding past climates and the geological processes leading to current and past distribution patterns so important in phytogeography (the study of plant distribution).

In summary, the discipline of botany is essential to understanding the history of life on earth and the interactions of plants and people.

—Dennis Wm. Stevenson

See also: Angiosperms; Fungi; Gymnosperms; Lichens; Protoctists; Systematics

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Brachiopods

The Brachiopoda is a phylum of marine animals whose bodies are protected by bivalved external shells. Although brachiopods are not very diverse in modern seas, with about 300 living species, they occur in a diversity of habitats, from the intertidal zone to the deep sea. They were much more diverse historically, with at least 12,000 fossil species known. Because the brachiopod fossil record is continuous from the Early Cambrian (about 570 million years ago) through the modern era, brachiopods are important in stratigraphy and in studying rates and patterns of evolution. Studies of living species have in turn been useful in understanding the lives of species known only as fossils.

The body of an adult brachiopod (which includes the gut, gonads, and shell muscles) is covered by a dorsal and a ventral valve of the shell.

Brachiopods are sometimes mistaken for bivalve mollusks (for example, clams), but those have lateral shell valves, not dorsal and ventral. The shell also encloses a large space anterior to the body, the mantle cavity. Projecting from the body into the mantle cavity are the two brachia (arms) of the lophophore, a large organ involved in feeding and respiration. The brachia, which are typically coiled in complex folds and spirals, bear fine tentacles whose cilia propel seawater through the mantle cavity and trap small particles carried in on the currents. Brachiopods feed on these particles. Most brachiopods release eggs and sperm into seawater, where they are fertilized and develop into planktonic larvae; these eventually return to the bottom and metamorphose into juveniles.

Brachiopods are divided into two groups, articulates and inarticulates. Articulates include species in which the two shell valves—composed of calcium carbonate—are connected by a hinge. Modern articulates live permanently attached to rocks (though some extinct forms lived unattached on soft substrates), attached by the pedicle, a stalk that protrudes from a hole in the posterior of the ventral valve. The guts of articulates are incomplete (the stomach opens into a blind intestine, and the remains of indigestible food must be shed from the mouth). In contrast, inarticulate brachiopods have shell valves that are not connected by a hinge and are usually made of chitin and calcium phosphate. Their guts are complete. Inarticulates have more

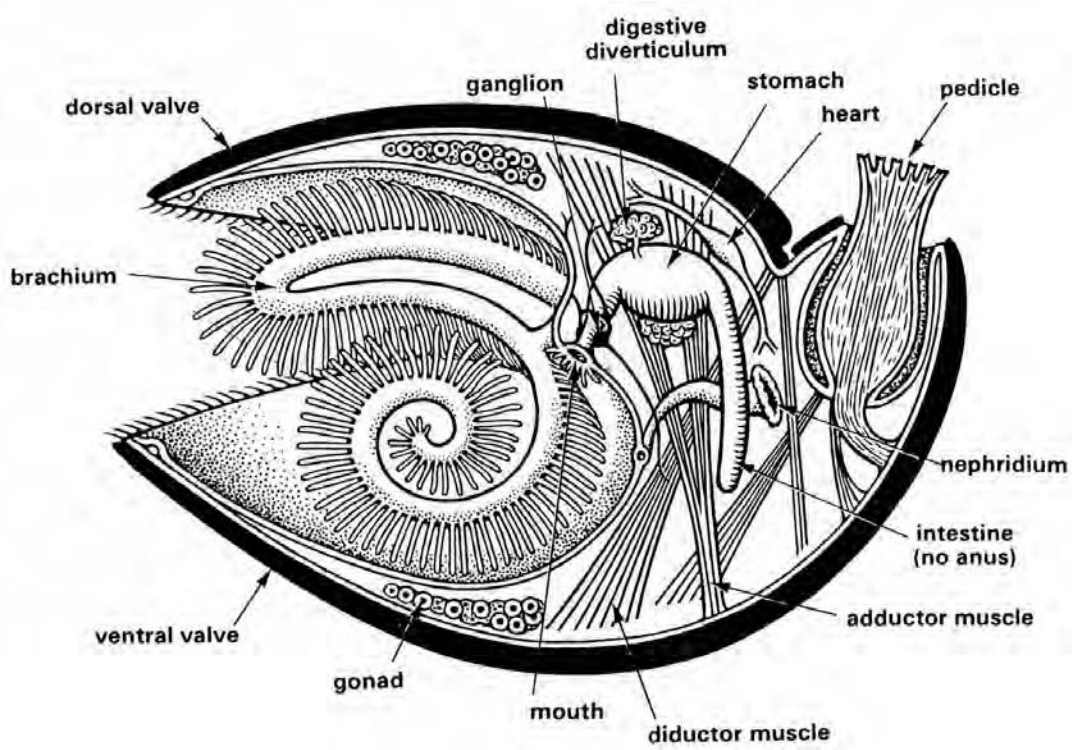

Figure 1

Diagrammatic Cross Section of an Articulate Brachiopod, Viewed from the Side

Source: Pearse, Vicki, et al. 1987. *Living Invertebrates*. Palo Alto, CA: Blackwell Scientific Publications, p. 664. (Reprinted with permission)

Note: The valves of the shell enclose the body and the mantle cavity. Only one of the two brachia of the lophophore is shown. The adductor muscles pull the two valves closed; the diductor muscles open them. The nephridium is the structure through which eggs or sperm (produced in the gonad) are released to the outside.

diverse ways of living than articulates: some live in burrows in sand or mud, and others live attached to rocks, cemented by one of their valves or a pedicle.

The evolutionary relationships between articulates and inarticulates and between brachiopods and other animal phyla are not well understood. Brachiopods appeared in the fossil record about 570 million years ago, with inarticulates appearing slightly earlier than articulates. Since then they have undergone several phases of diversification and extinction, with major crises including an end-Ordovician decline for inarticulates about 430 million years ago and an end-Permian decline for articulates about 245 million years ago. Modern species are not directly at risk of extinction as a result of human activities, because most are not edible or otherwise economically important.

—Bruno Pernet

See also: Evolutionary Biodiversity; Extinction, Direct Causes of; Paleontology

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Brown Algae

See Protoctists

Brown Tree Snake

See Birds of Guam and the Brown Tree Snake

Bryophytes

Bryophytes are the second largest group of land plants, after the flowering plants, with about 20,000 described species. Because of their small size and often delicate structure, bryophytes have a poor fossil record, dating back only about 290 million years. Because bryophyte species are often closely tied to specific environmental conditions, it is considered likely that bryophyte diversity is currently at its greatest level: the group evolved in conjunction with the evolution of flowering plant communities. Bryophytes are characterized by the dominant, leafy, or thallose (that is, a more or less flattened plant without differentiation into stem and leaves) plants being the gametophyte generation (the generation with a single set of chromosomes, which produces the male and female gametes). The reduced sporophyte generation (with two sets of chromosomes) is dependent upon the photosynthetic gametophyte for part of its existence, if not all of it. Typically, the sporophyte generation consists of a spore-producing capsule that usually is elevated on a stalk (seta). The leaves of bryophytes are mostly a single cell thick and either lack any sort of midrib or, especially in the mosses, have a single, unbranched midrib or a double midrib, forked from the base of the leaf. The midrib is never branched. Some bryophytes, such as the hornworts and some groups of liverworts, have no leaves but rather are characterized by a flat thallus, usually closely appressed to the substrate, and often several cell layers thick. The stomata found on leaves in flowering plants, ferns, and the like to allow oxygen and carbon dioxide to get into and out of the cells are found only in the capsules of mosses and hornworts, but they are lacking in liverworts. Both in flowering plants and bryophytes the stomata are found on the part of the plant with two sets of chromosomes.

Throughout the bryophytes, evolution has proceeded mostly toward the simplification of plants rather than toward more complex structures. Ecologically, although individual plants are small, bryophytes frequently play significant roles in the environment because they often occur in large populations. They are very important in maintaining humidity levels in ecosystems and in slowing soil erosion, as well as in mineral recycling. Because of their delicate structure, they are particularly sensitive to pollution and have been used to monitor air and water quality. Conservation of bryophytes depends upon conservation of their habitats. Unlike larger plants, individual bryophyte plants are often unable to survive outside of their natural habitats. Because of dissimilarities between the various groups of bryophytes, as well as recent evidence from DNA sequencing, it is now thought that bryophytes are not a natural group, and rather that the various components are not closely related. However, because of the dominant gametophyte generation, which is unique among land plants, they are often studied as a group. Following are the major groups of bryophytes.

Phylum Bryophta (mosses). These are bryophytes with leafy gametophytes and long-lived sporophytes, typically with the capsule elevated on a seta. The rootlike structures (rhizoids), which are primarily for adhering the plants to the substrate and have no transport capabilities, are multicellular, with the numerous cells in a single row. The remnants of the archegonium (which surrounds the egg cell) expand after fertilization and form a protective cap (calyptra) over the capsule. The capsules are typically dehiscent, with a lid (operculum), allowing spore release and dispersal. Most species have specialized hygroscopic structures (peristome teeth) around the mouth of the capsule to aid in spore dispersal.

Class Bryopsida (true mosses): True mosses are characterized by capsules that open because of an operculum and with peristome teeth (two-layered toothlike structures, usually sixteen in number, around the mouth of the capsule, composed of dead cell walls only at maturity, which are hygroscopic because of the different thicknesses of the two layers, thus aiding in spore dispersal). The capsule also has stomata, and internally the spores are formed around a central column (columella). This is the largest group of bryophytes, and the most conspicuous, with approximately 13,000 species. They are often the dominant component of the landscape in the Arctic and the Antarctic, as well as at very high elevations. Some forests in particularly humid areas are designated as "mossy forests" because mosses (and liverworts) form great sheaths around the tree trunks. Mosses range in size from minute plants no more than a millimeter tall, growing on soil and sometimes completing their life cycle (from spore germination to spore production) in only a matter of months, to long-lived perennial plants more than a meter in length. They occur in almost all habitats except those in direct contact with salt water. They are especially prominent in extreme habitats. For example, on the Antarctic continent, there are thirty to forty species of mosses, but only two of flowering plants. The true mosses are standardly divided into two groups based on the habit of the plants. The presumably primitive acrocarps are mostly erect, unbranched plants growing in dense tufts, with their capsules arising from the stem tip. The more specialized pleurocarps are mostly prostrate, branched plants forming mats, with their capsules arising from along the sides of the stems. In the tropics the pleurocarpous mosses often form long, pendent masses cascading from tree branches. This is also the group to which "sheet moss" in the horticultural trade belongs.

Spanish moss hanging from the branches of trees in Louisiana (Library of Congress)

Class Andreaeopsida (granite mosses): Characterized by capsules that dehisce by longitudinal slits, and with no peristome or stomata, this relatively small group of mosses (approximately 120 species) occurs worldwide, and, as the common name suggests, usually on acidic rocks. The capsules are particularly unusual within the mosses, and instead are more like those of some liverworts.

Class Sphagnopsida (peat mosses): Characterized by branches occurring in groups (fascicles) along the stems, the leaves of the peat mosses are composed of two types of cells forming a reticulum of a single cell layer: small green cells and large, hollow, dead cells. The capsules lack a peristome but have an operculum and dehisce explosively because of an increase of internal air pressure. The internal pressure can reach four to six atmospheres, a pressure similar to that in the tires of tractor-trailers, and the plants can be heard when they dehisce. Although a relatively small group (there are approximately 250 species in the single genus *Sphagnum*), the peat mosses are probably the best known bryophytes because of their use as horticultural peat and also as a source of fuel. However, as living plants they are very important in nature. In Arctic areas they are largely responsible for drainage patterns. The peat mosses are also able to absorb large quantities of water because of the dead hollow cells of the leaves, and as a result of physiological reactions they can increase the acidity of the water in which they live. Because of the absorptive properties of the peat mosses, they were traditionally used as diapers and even socks. During World War I the peat mosses were harvested and used as surgical bandages, not only because of their ability to absorb large quantities of blood but also because of natural antiseptic qualities. Even now one major manufacturer uses milled peat moss as the absorbent portion of their "all natural" menstrual pads.

Phylum Marchantiophyta (liverworts): These are bryophytes with either leaves or just a flattened thallus; when leafy, the leaves are often deeply lobed and never have a midrib. The cells of the gametophyte have a unique organelle found in no other group of organisms: the oil body. Liverworts are well known for their complex chemistry, whereas mosses usually have a very simple chemistry. Many of the complex chemical compounds are contained within the oil bodies. These structures must be viewed in living plants, or those recently collected, because they disintegrate with age. The rhizoids, which primarily hold the plant to the substrate, are composed of a single cell. The capsules are often elevated on a very short-lived seta, sometimes lasting no more than a couple of hours. The capsules typically dehisce by splitting into several valves. The spores have sterile threads (elaters) among them that are hygroscopic and aid in spore dispersal. The capsules lack both stomata and a columella. The liverworts are mostly plants of moist environments, with about 6,000 to 8,000 species worldwide. They are of little economic value but are often of significant ecological value in forest habitats.

Class Marchantiopsida (thalloid liverworts): The Marchantiopsida are characterized by thalloid plants several cell layers thick. Often there are pores in the surface of the thallus that allow gas exchange for the internal cells. The sporophytes are often elevated on a complex structure of gametophytic tissue. The capsule walls are only one cell layer thick. This group includes the relatively large, coarse thalloid liverworts often seen growing along streams and in other areas of high humidity. Because of their size and their use in biology classes as a liverwort example, this group of liverworts is the best known, although it has only about 300 species.

Class Jungermanniopsida (leafy liverworts): This class is characterized by both leafy forms and thalloid forms. The capsules are typically elevated at maturity on a short-lived seta. The capsule walls are two or more cell layers thick. When thalloid the thalli are relatively thin and structurally simple. The leafy forms are the largest group of hepatics, with almost 300 genera and at least 5,000 to 6,000 species, mostly in the tropics. There are typically two kinds of leaves, larger lateral leaves that are either entire or lobed, and smaller leaves on the underside of the stems. Sometimes the underleaves are lacking. Like other groups of liverworts, the Jungermanniopsida have little economic value. However, in areas that have high humidity and are major logging areas, such as the Pacific Northwest of North America, some liverworts, especially *Frullania,* are a significant cause of dermatitis because of the chemicals contained within the oil bodies.

Phylum Anthocerophyta (hornworts): Hornworts are bryophytes with a thin, mostly flattened thallus growing on bare mineral soil (rarely epiphytic in the tropics), and with slender, hornlike sporophytes. The cells of the thallus have only a single chloroplast, like many algae, but otherwise they are unique among land plants. Often there are colonies of *Nostoc* (cyanobacteria) embedded in the thalli. The sporophyte is unique in having a basal meristem, so that it continues to grow from the base throughout the life of the plant, with spores maturing toward the tip. The sporophyte typically splits along two longitudinal lines to release the spores. Intermixed with the spores are sterile, hygroscopic, spirally twisted structures (pseudoelaters) that aid in spore dispersal. The sporophyte has a columella (like mosses), and the wall has stomata. This small group of plants (with approximately six genera and 150 species) often grows on bare, disturbed, wet soil. Because of the thalloid gametophyte and unicellular rhizoids, the hornworts have been associated with the liverworts, but they are quite distinct. Recent research suggests that the hornworts may be the oldest living lineage of land plants.

—William R. Buck

See also: Angiosperms; Gymnosperms; Pteridophytes

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Bryozoa

Bryozoa, meaning “moss animals,” is a major phylum of common, mostly marine, filter-feeding invertebrate animals. Although there are about 4,500 described living species, recent research suggests that this number may be an underestimate by roughly a factor of five, because many groups may contain large numbers of yet-to-be detected so-called cryptic species.

All bryozoan species are colonial (see Coloniality)—that is, composed of asexually budded and physiologically connected sets of units called zooids. These zooids, typically less than 1 mm in their longest dimension, serve the basic structural, feeding, defensive, and reproductive functions of the colony. Although some colonies may contain millions of zooids and grow to be as large as 1 m high or wide, most species are relatively small. Colonies may range in shape from flat, encrusting sheets, to vinelike chains, tree- or bushlike branching forms, spiraling corkscrews, or perforated, lacelike meshes. Because small colonies are frequently inconspicuous, and other, more conspicuous colonies are commonly mistaken for small corals or seaweeds by nonzoologists, the Bryozoa remain less well known by the public than other major invertebrate phyla. They may be most noticed as “fouling organisms” when they grow on the undersides of boats, floats, docks, and water intake pipes.

Bryozoans' box- or tubelike skeletons may be completely or partially mineralized with calcium carbonate, or they may be nonmineralized. Depending upon the degree of mineralization, species may be either rigid, semirigid, or completely flexible.

Most colonies are sessile and cemented to their rock, shell, wood, or algal substrates, but a few species form free-living, cone-shaped colonies that can slowly move across sandy bottoms. A few freshwater species can also creep slowly across their substrates. Mineralized bryozoan skeletons are well preserved in the fossil record.

As filter-feeders (that is, animals that remove bacteria, nutrients, and other small particles from water), bryozoans play an ecosystem role in capturing water-borne productivity or nutrients—mostly floating phytoplankton and small detrital particles—and converting them to benthic productivity. Some colonies grow large and dense enough to be dominant structural elements in some local ecosystems as well, providing habitats for other species.

Along with Brachiopods and Phoronids, bryozoans are frequently classified into the *Lophophorata* superphylum. Bryozoa are also sometimes called *Ectoprocta,* to differentiate "true" (as currently defined) bryozoans from other groups (for example, *Entoprocta* or *Kamptozoa*) that have been mistakenly lumped with them by some specialists in the past. The phylum is divided into three classes: the *Phylactolaemata*, the *Stenolaemata,* and the *Gymnolaemata.* Phylactolaemates are found exclusively in freshwater habitats. Although they are remarkably widespread across the world, they currently number approximately only fifty species, though some researchers expect numerous cryptic species to be found in this class as well as the others. Stenolaemates, once quite speciose, widespread, and ecologically dominant in shallow seas during earlier geological periods, remain diverse and dominant only in certain ecological refuges, such as dark crevices and caves. Gymnolaemates include the vast majority of living bryozoans, having diversified and gradually replaced the stenolaemates since their apparent origin in the Ordovician.

—Daniel Brumbaugh

See also: Evolutionary Biodiversity; Freshwater; Oceans

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Bugs

See Arthropods, Terrestrial

Butterflies and Moths

See Arthropods, Terrestrial

C

Carbon Cycle

The term *carbon cycle* refers to biologists' attempts to locate and quantify the movement of the biologically crucial chemical element carbon, upon whose chemistry living organisms are largely based, as it makes its way in and out of organisms and ecosystems on the earth's surface. The study of the carbon cycle is thus part of a nascent science of what might be called biospherics, the attempts to understand how the chemistry of the biosphere operates and contributes, or hampers, the livelihood and lives of organisms. Somewhat surprisingly, such a science bears a kinship to both climatology and physiology. Over the long run, a rigid distinction between organisms, ecosystems, and the global environment is necessarily blurred, because the cyclical chemistries that maintain the identities of these systems lose their function, and the constituent atoms are returned to the biosphere. Carbon, especially important to organisms because its long, complex chains articulate organic form and function, cycles, as do other biologically important elements, in the equivalent of a global metabolism. One of the greatest indexes of the power of life is the virtual absence of carbon dioxide in the Earth's atmosphere: unlike the atmospheres of Mars and Venus, which are mostly carbon dioxide, the carbon in our atmosphere is either actively cycled by Earth's organisms or buried in its surface. The carbon in methane (CH_4), carbon dioxide, hydrocarbons, and other gases and particles—for example, pollen and smoke—make their way into organisms on the ground, such as trees. When these organisms die, the carbon atoms of their bodies are released and reused by other organisms. But the carbon also builds up, as fossil fuels (oil comes from the dead bodies of tropical seashore algae), chalk cliffs, and limestone (calcium carbonate). These are, in a way, the "bones" of the Earth, part of a wider-than-suspected sphere of biological influence. Modern people, by bringing back into circulation long sequestered parts of the bodylike biosphere, change the global metabolism. Thus understanding the carbon cycle is not just an academic exercise but also important to future attempts to describe planetary health and medicine.

—Lynn Margulis and Dorion Sagan

See also: Climatology; Evolution; Five Kingdoms of Nature; Food Webs and Food Pyramids; Lichens; Microbiology; Nitrogen Cycle; Nutrient/Energy Cycling; Protoctists; Soil; Topsoil Formation

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Carnivora

Order Carnivora is composed of predaceous mammals with large canine teeth and a carnassial mechanism (specialized shearing blades formed by the occlusion of the last upper premolar and first lower molar). Interactions between the array of carnivore species and the single living human species are mixed. Many carnivores are trapped or hunted for their coats and flesh. Pinnipeds (walruses and seals) have been an important source of fur, food, oil, and ivory. For the last 11,000 years, populations of the wolf (*Canis lupus)* have been domesticated into more than 400 breeds of dog. Since at least 3500 B.C.E., descendants of the African wild cat (*Felis sylvestris lybica*) have been cultivated into thirty to forty breeds of domestic cat. Dogs and cats have been bred primarily to serve as human companions, though they are sometimes utilized to perform work and as a source of meat. The popularity of these animals as pets has a significant economic impact: revenue is generated by the manufacturing and sale of goods, food, and medical care for the animals, but control and housing of strays in some countries is costly. Populations of large predators such as the wolf, puma, lion, leopard, and jaguar are reduced or eliminated from ecosystems where they engender fear and compete with humans for domestic animal stock (cattle and sheep). Many carnivores, especially all species of cats, are deeply appreciated for their aggressive and focused predatory instincts, graceful form, fluid movement, and aesthetic beauty.

The evolutionary adaptive radiation of most mammalian carnivores may have been a response to an expanding diversity of herbivores, their primary food source. There were only two groups of Early Cenozoic terrestrial carnivorous mammals: Order Creodonta and Order Carnivora. Creodonta (consisting of two families) first appeared in the Late Paleocene, were common throughout the Eocene in North America, Europe, Asia, and Africa, and persisted until the Late Miocene in tropical habitats in Asia and Africa. Creodonts had specialized shearing surfaces formed from either the first upper and second lower molar or second upper and third lower (unlike the pattern typical of living carnivores). They were the typical carnivores of the Early Cenozoic but were not ancestral to the modern Order Carnivora.

Members of the extinct families Viverravidae and Miacidae, Order Carnivora, lived from the Early Paleocene to the Late Eocene in North America, Europe, and Asia. They are considered by paleontologists to be ancestral to the modern carnivores. They were small-bodied (ranging from the size of a weasel to that of a house cat) and possessed the modern carnassial formed by the last upper premolar and first lower molar. The 280 species of living carnivores are arranged in 115 genera, twelve families, and two suborders, Feliformia and Caniformia. The Feliformia consists of the families Felidae (cats), Viverridae (civets and genets), Herpestidae (mongooses), and Hyaenidae (hyenas and aardwolf). Families Canidae (wolves, jackals, foxes, and dogs), Mustelidae (weasels, badgers, and otters), Mephitidae (skunks and stink badgers), Procyonidae (raccoons, ringtails, coatis, kinkajou, olingos, and lesser panda), Ursidae (bears and giant panda), Odobenidae (walrus), Phocidae (earless seals), and Otariidae (eared seals, fur seals, and sea lions) compose the Caniformia. The latter three families are sometimes placed in Order Pinnipedia, but all recent studies incorporating morphology and biochemical data indicate the pinnipeds to be a monophyletic group that is most closely related to the bears (Ursidae). Natural distribution of terrestrial species include most of the planet's land areas except Australia, New Guinea, New Zealand, Antarctica, and many oceanic islands. The dingo, a breed of dog, forms wild populations in Australia and New Guinea but was introduced there by prehistoric human settlers. Walruses, seals, and sea lions are found predominantly along ice fronts and the coastlines of polar and temperate oceans and adjoining seas; some occur in tropical regions and large inland lakes and seas.

A spectacular range in body size exists within modern carnivores. Among terrestrial species, the least weasel (*Mustela nivalis*) is the smallest, with a head and body up to 18 cm long and weighing up to 70 gm. The largest is the grizzly or brown bear (*Ursus arctos*), with a head and body up to 280 cm long and attaining a weight of up to 780 kg; *Ursus arctos* is the largest living land carnivore. The smallest pinnipeds are in the family Phocidae, such as the ringed seal (*Phoca hispida*), with a head and body averaging 141 cm and weighing up to 128 kg. Also in the same family is the southern elephant seal (*Mirounga leonina*), which is the largest living pinniped, with a head and body up to 600 cm long and weighing up to 3,700 kg. Pinnipeds are generally larger than terrestrial carnivores, an adaptation allowing energy conservation in cold habitats. Large size is an effective adaptation to cold because it favors heat conservation by decreasing surface area relative to body mass.

Most species of Felidae, Viverridae, Herpestidae, Mustelidae, Canidae, and the polar bear prey on live animals. Their entire body structure and behavior define "predator" from a human perspective. Using their acute hearing, remarkable sense of smell, and excellent vision, they capture prey by pouncing from a concealed position (most cats); stalking, followed by a swift rush (weasels and lions), a long chase (wolves); or a short burst of great speed (cheetahs). All species in these families have impressive canines and prominent carnassials, but this shearing mechanism is most highly developed in the cats, which subsist almost entirely on flesh and are the most proficient of all carnivoran predators. Many felid species kill prey as large as themselves, and some take down prey several times their own weight (puma preying on mule deer, for example). Members of Hyaenidae may prey primarily on large mammals (spotted hyena), scavenge remains at large mammal kills (brown and striped hyenas), or consume only termite larvae and other insects (aardwolf). A few species of viverrids and herpestids include fruit in their diet, and members of the Mephitidae, Procyonidae, and Ursidae are omnivorous. The carnassial configuration is least developed in procyonids and ursids.

Different techniques are used to kill prey. The long-tailed weasel (*Mustela frenata*) kills young rabbits by repeatedly biting the back of the rabbit's head and penetrating the skull again and again. Lions kill small prey with a slap of the paw; larger prey is seized by the throat and strangled or suffocated by the lion clamping its jaws over mouth and nostrils. The sea otter (*Enhydra lutris*) eats slow-moving fish, sea urchins, abalone, crabs, and mollusks. Pinnipeds forage on the most abundant sea food encountered, mostly krill (small shrimplike animals), other crustaceans, squid, mollusks, and fish. Leopard seals are the only pinnipeds that prey on other mammals and birds, capturing crabeater seals and penguins, and also eating krill, fish, and squid. The crabeater seal eats mostly krill and has specialized, notched teeth that filter the krill from the

Some terrestrial carnivores, such as leopards, are solitary, and others form small groups, such as lions, which typically live in a pride. (USDA Forest Service)

seawater. Walruses feed primarily on clams and mussels.

Terrestrial carnivores are nocturnal, diurnal, or active day and night. Most species are adapted to either living on the ground (terrestrial) or in trees (arboreal), though some utilize both substrates. Leopards capture their prey on the ground and climb trees to store or eat it. Sulawesian palm civets (*Macrogalidia musschenbroekii*), coatis (*Nasua*), and martens, fisher, and sable (*Martes*) pursue prey on the ground and in trees. The tayra (*Eira barbara*) lives in neotropical forests and is a swift and agile runner, climber, and swimmer. The amphibious otters are excellent swimmers and divers, feeding on fish, frogs, crabs, and mollusks. The sea otter spends nearly its entire life in the ocean, rarely farther than 1 km from shore. Although clumsy on land, pinnipeds are superb divers and swimmers, foraging in the water but hauling out onto land or ice isolated from humans and other predators to mate and bear young.

Terrestrial carnivores are solitary (leopards), live in pairs (many species of canids), or form small aggregations (lion prides, for example). Lions even hunt in groups, which usually consist of females. Most species produce a single litter each year; others bear young up to three times during the year, and some larger species give birth at intervals of several years. Gestation periods range from 49 to 113 days in most species; litter size ranges from one to thirteen. Bears and some mustelids exhibit delayed implantation of fertilized eggs, so the period between mating and birth is much longer than average. Newborns are blind and dependent upon adults (altricial), and they require long periods of parental care and instruction. Some temperate species hibernate, whereas others follow their ungulate prey as they migrate from mountains into valleys before winter.

Pinnipeds exhibit a range of social behavior. At one end is the Ross seal (*Ommatophoca rossi*), which lives alone during the winter; at the other is the gregarious walrus, which forms breeding colonies of several thousand individuals. Seals, fur seals, sea lions, and walruses (Otariidae and Odobenidae) are polygamous; earless seals (Phocidae) are monogamous. All species mate once each year; gestation ranges from eight to fifteen months, and one (or rarely, two) young are born on land or ice. Delayed implantation of the fertilized egg occurs in several species, possibly an adaptation allowing synchronized births in colonial species. Newborn pups can swim but do not develop sufficient blubber for insulation and buoyancy for several months. Some pinnipeds migrate to foraging and breeding areas. Northern elephant seals (*Mirounga angustirostris*) may migrate up to 21,000 km in a year, the greatest distance documented for any mammal.

In addition to the carnassial mechanism and large conical, recurved canines, carnivores are characterized by rooted teeth, a large braincase containing well-developed cerebral hemispheres, sensitive hearing, acute olfaction, and astute eyesight. Strong facial muscles are attached to a robust cranium and mandible. The mandible is articulated to the cranium in such a way that it can move only up and down (so the mouth opens and shuts), with no rotary and extremely limited transverse movements. Carnivores, unlike most artiodactyls, have a simple stomach. Species of Canidae, Felidae, and Hyaenidae walk only on their toes (digitigrade); members of Ursidae and Procyonidae walk on their soles, with the heels touching the ground (plantigrade). Cursorial (running) pursuit of prey is highly developed in some canids (wolves, for example) and cats (cheetahs), but limited in plantigrade species. The primitive number of five digits on front and hind feet is usual in Carnivora, except for the hyenas and the African hunting dog (*Lycaon pictus*), which have four digits on each front and hind foot. The digits of otters are connected by webbing, except for the clawless otters (*Aonyx*), in which the webbing is confined to the base of the digits or is absent altogether. These otters locate crabs, mollusks, and frogs in mud or under stones with their sensitive and dexterous front paws. Tails may be stubby (bears) or long (as in most terrestrial carnivores); only the arboreal Indo-Malayan binturong (*Arctictis binturong*) and neotropical kinkajou (*Potos flavus*) have prehensile tails. Ears range from small to large relative to the size of the head. The fennec fox (*Fennecus zerda*) is the smallest member of Canidae but has the largest ears relative to body size. Some species of weasels living at northern latitudes molt from a summer brown coat into winter white fur.

The body is streamlined and torpedo-shaped in pinnipeds, which creates minimal drag during swimming. Ears are small or absent; the ears and slitlike nostrils are closed while underwater but voluntarily opened out of water. Front and hind feet are modified as flippers formed by broadly webbed and oarlike digits; only those parts of the limbs beyond the elbow and knee protrude from the body surface. The tail is absent or rudimentary. These are all external adaptations to an aquatic (primarily marine) existence. Other adaptations are reflected by the shortened face, flattened head, eyes set deep within protective layers of fat, and thick but flexible neck. The interlocking processes (zygapophyses) of the vertebrae and no clavicle allow pinnipeds to bend farther backward than most mammals. These features allow great maneuverability while pursuing prey, as well as the ability to absorb the shock of ocean waves.

—*Mary Ellen Holden*

See also: Adaptive Radiation; Alien Species; Coastal Wetlands; Coloniality; Ecosystems; Endangered Species; Extinction, Direct Causes of; International Trade and Biodiversity; Intertidal Zone; Mammalia; Oceans; Plankton; Positive Interactions

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Carolina Parakeet

This extinct parrot species was the only native (endemic) parrot to occur in the United States. Its numbers declined throughout the nineteenth century, and it went extinct in the early 1920s from habitat loss and human persecution—hunting. This colorful parakeet inhabited the bottomland forests and cypress swamps of the southeastern United States and riparian woods along the rivers of the Great Plains. It ranged across the eastern half of the United States, north to Illinois, Ohio, Indiana, and New York, south through the Gulf Coast states to Texas, and as far west as Kansas, Nebraska, and even eastern Colorado. Like most other parrot species, this bird was highly social, feeding in large flocks and nesting and roosting in large old-growth trees. As vast expanses of the United States were cleared for agriculture and settlements, the Carolina parakeet populations declined till the cypress swamps of Florida became their last stronghold. In 1918, "Incas," the last Carolina parakeet in captivity, died at the Cincinnati Zoo, and Charles Doe, then curator of birds at the University of Florida, saw the last birds in the wild at Lake Okeechobee's cypress swamps in 1926 (Forshaw, 1989). Unconfirmed sightings of parakeets persisted until the late 1930s, but more likely, these birds were escaped cage parrots.

Taxonomy

This parakeet is one of the 332 species in the Psittacidae family of parrots. Although most parrot species live in tropical habitats, the Carolina parakeet was one of the few temperate parrot species. The closest relatives of this monotypic (single) parakeet genus, *Conuropsis*, are the *Aratinga* parakeet species of Mexico and Central and South America. Two subspecies of *C. carolinensis* were recognized: *carolinensis*, which was confined to the southeastern United States from Florida north to southern Virginia; and *ludovicianus*, which was formally distributed throughout the Mississippi and Missouri drainage system in the eastern United States.

Description

The Carolina parakeet was a bird of medium size, measuring 13 inches (30 cm) in length. It had the characteristically strong, convex beak and "yoked-toed" or zygodactylous foot (two toes pointing forward and two toes pointing backward) adaptations of parrots. These characteristics allow parrots to use their beaks as nutcrackers and eat the hardest of nuts and seeds while also using their feet as "hands" to grasp and hold food. The adult Carolina parakeet was largely green in color with a yellow head and scarlet to orange patches on the cheek and forehead. The sexes were similar, while young birds were duller in color and lacked the prominent yellow head color and associated patches of orange. Adult plumage appeared in the second year of a juvenile's life. They had long, gradated tails and long, pointed wings. When they flew, patches of yellow from the tips of their wing feathers were visible. The Carolina parakeet was quite striking, as can be seen in John James Audubon's famous painting of a family of parakeets in Louisiana.

Distribution

In the eighteenth and early nineteenth centuries, this species was widespread and common throughout much of the eastern United States. It favored heavily forested river valleys; old bottomland forests of beech, oak, and sycamore; and cypress swamps. Greenway (1967) noted that its range contracted to the west and southeast as forests were felled for agriculture and human settlements. In the twentieth century, it was restricted to large uninhabited cypress swamps of Florida.

Habits

Much of what is known of the habits of the Carolina parakeet comes from anecdotal information contained in accounts of early setters on the Great Plains and from ornithologist John James Audubon (Audubon, 1840–1844), who was among the first of the early naturalists to describe this parakeet and its habits. He wrote: "[O]ur parakeets are very rapidly diminishing in number, and in some districts, where twenty-five years ago they were plentiful, scarcely any are now to be seen. . . . I should think that along the Mississippi there is now half the number that existed fifteen years ago."

John James Audubon's painting of the Carolina parakeet, c. 1827–1830. (Academy of Natural Sciences of Philadelphia/Corbis)

The Carolina parakeet was a powerful flyer and foraged widely for food. When it was abundant, feeding flocks of 200 to 300 birds were a common sight on the Great Plains. It was most active in the early morning and early evening hours. During the middle of the day, flocks rested in large, shady trees. Such behavioral activity is typical of parrots worldwide. It was able to tolerate the cold winters in parts of its range. Like most parakeet species, this bird was highly vocal, and its characteristic flight call was described as a "loud, screeching "*qui . . . qui . . . qui . . . qui . . . qui—ii*" (Forshaw, 1989). Parrot vocalizations help maintain flock cohesion while flocks feed over large areas, and they aid in the recognition of family members in large flocks.

The bird's diet consisted of blossoms, seeds, and fruits of grasses and trees. A favorite food was the seed of the cocklebur (*Xanthium strumarium*), a hardy weed species that was abundant in the plains habitat and marginal forest areas. It also fed on the fruits of hackberry, mulberry, beech, oak, sycamore, and cypress trees; the seeds of pine and maple trees; and the seeds of burgrass and thistle. This parakeet species traveled great distances foraging for food, and its movements may have been nomadic. Budgerigar parakeets in Australia exhibit similar behavior today, traveling large distances in search of food and water. As its natural food sources became scarce when land was cleared for agriculture, this parakeet switched its diet to cultivated crops. It raided grain stores and decimated fruit orchards of apples, pears, cherries, and grapes. By becoming an agricultural crop pest, the parakeet exacerbated its decline, and large numbers were shot by farmers.

The Carolina parakeet was also known to visit saline soil deposits, often along river banks. There they extracted salts and minerals from the soil deposits. Such behavior is still seen today in the large macaw and Amazon parrot populations of South America. Scientists theorized that such mineral feeding helps the birds to remove plant toxins from their bodies and provides birds with the minerals needed in their diet. The seeds of cocklebur, a favorite Carolina parakeet food, are known to concentrate plant toxins.

The nesting habits of the Carolina parakeet were poorly understood. It remains unclear whether the species nested in spring or summer, but one can speculate that the timing of the nesting cycle was tied to food availability; hence, when widespread, populations may have bred at different times of the year. The parakeet nested in the hollow cavities of large trees, some of which were probably excavated by larger species of woodpeckers, and possibly in riverbank holes excavated by kingfishers. The breeding of most parrot populations today is limited by the availability of suitable nest cavities, and the Carolina parakeet most probably suffered the same fate. If old and dead trees were the more likely trees to be logged, parakeet populations faced increasing pressure to find suitable nest sites. Parrot species are categorized by ecologists as "k-selected species." The characteristics of such species are to be long-lived, to produce few offspring with high parental care, and to have delayed sexual maturity. Therefore, these populations may not show signs of an immediate decline caused by poor breeding and juvenile recruitment, since the adults have high survival rates and live so long.

Like most parrots, the Carolina parakeet laid round, white eggs at the bottom of its nest, and the chicks hatched in an altricial state (helpless, blind, with wisps of downy feathers covering their bodies). Very unusual among parrots, however, was the reported communal nesting behavior of the Carolina parakeet (Audubon, 1840–1844), whereby several females laid their eggs into the same nest. The monk parakeet (*Myiopsitta monachus*) of South America is also a communal breeder and occurs in grassland and forest habitats. Each female Carolina parakeet is thought to have laid a clutch of two eggs. The species did breed in captivity in zoos, but in insufficient numbers to produce a sustainable captive population. In captivity, the species had the distinction of being inattentive parents, and chicks often died from neglect—an all too common problem stemming from captivity and poor husbandry knowledge. In the wild, young Carolina parakeets were still fed and cared for by the adults after they had left the nest ("fledged").

Relationship with Humans

Although the ultimate cause(s) for the Carolina parakeet's decline will remain unknown, we do know that the parakeet's population numbers declined with the colonization of the eastern United States and the spread of human settlements and agriculture. We also understand some of the proximate causes (habitat loss, hunting, and capture for pet trade) that played a key role in the parakeet's extinction.

Habitat loss and degradation probably was the most significant factor affecting the overall conservation status of this species. The loss of natural feeding areas and roost and nest cavities in large trees would decrease adult survivorship and the recruitment of juveniles into the population. The loss of new individuals entering populations also causes a loss of genetic diversity, and, subsequently, as populations became smaller, inbreeding and the fixation of deleterious genes may have had serious effects. Daniel McKinley (1980) recognized competition from the pioneers' introduction of honeybees as an additional proximate cause for the parakeet's decline. He postulated that the spread of European honeybees in the parakeet's range had driven it away from the tree hollows that it had used for roosting and nesting. Parakeets had to compete with honeybees for this limited resource, which became even scarcer because of clearing and logging. This hypothesis has some scientific merit, inasmuch as another endangered parrot, the Puerto Rican parrot (*Amazona vittata*), is encountering a similar threat in its remaining tropical forest habitat today. This parrot's nest sites are actively managed to protect honeybees from taking over the parrot's remaining, traditional nest cavities in old trees. Such interspecies competition can only further stress populations experiencing habitat loss.

The hunting of Carolina parakeets for food, as agricultural pests, for capture to supply the live pet market and for the millinery trade, and by collectors when the bird became rare all contributed greatly to the species' extinction. Such a proximate cause can be the force that drives an already declining population over the edge to extinction. This gregarious and social bird was an easy target for hunters, who could remove large numbers of birds at a single time. One particular behavioral habit made the species increasingly vulnerable to hunters. Like other parrot species, the parakeet showed a defensive behavior, mobbing or flocking to the area where several of its cohorts lay injured and calling with distress calls. Although advantageous if the predator is a hawk, drawing attention to the hawk and removing the predator's element of surprise, it is clearly disadvantageous if the predator is a man with a gun. This defensive behavior caused birds to remain in the area after the first shot was fired, and hunters could continue to shoot at roosting and flocking birds. Such slaughters of Carolina parakeets were routine and resulted in great losses of birds with little effort. Audubon (1840–1844) describes this situation vividly: "[T]he husbandman approaches them with perfect ease, and commits great slaughter among them. All the survivors rise, shriek, fly round about for a few minutes, and again alight on the very place of most imminent danger. The gun is kept at work; eight or ten, or even twenty are killed at every discharge. The living birds, as if conscious of the death of their companions, sweep over their bodies, screaming as loud as ever, but still return to the stack to be shot at, until so few remain alive, that the farmer does not consider it worth his while to spend more of his ammunition. I have seen several hundreds destroyed in this manner in the course of a few hours, and have procured a basketful of these birds at a few shots, in order to make choice of good specimens for drawing."

The conservation threats that Carolina parakeets experienced are the same severe threats facing the world's parrot species today. Parrot species are still faced with the loss and degradation of their habitat, as well as overexploitation to supply the live bird market. Birdlife International estimates that 86 (26 percent) of the 332 extant parrot species are at "risk of extinction," and 36 species are "near-threatened" (del Hoyo et al., 1997). These figures do not include cockatoo species, which are placed in a separate family, and of which seven species are at risk of extinction and four considered near-threatened. It would be fitting if the Carolina parakeet's extinction could act as a warning to offset the global threat of parrot extinction.

—Rosemarie Gnam

See also: Birds; Extinction, Direct Causes of, Preservation of Species

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Cephalopods (Squid and Nautilus)

See Mollusca

Cetacea (Whales, Dolphins, Porpoises)

Cetaceans are the only completely aquatic mammals and are among the most spectacular of all vertebrates. Seafarers have appreciated the beauty and grace of cetaceans for centuries. Whale hunting (whaling) began as early as 1000 C.E. Although some cultures consumed whale meat and utilized the meat and by-products as dog and cattle feed, whales historically have been hunted for their baleen ("whale bone") and oil derived from their blubber. Small cetaceans, particularly dolphins, have also been hunted, but their biggest threat comes from being incidentally caught in tuna fishing seines. Although the pressures of exploitation are ever present, international agreements protect some cetaceans, and some populations that were overhunted are increasing. Modifications of seines and equipment have greatly reduced the number of dolphins accidentally killed by fishermen.

Cetaceans are remarkable swimmers and divers. Their bodily form, skeleton, physiology, and behavior are modified for feeding, communicating, locomoting, and reproducing within salt and fresh waters. All are intelligent and exhibit complex social behavior; many can echolocate. Some species of whales are the largest animals that have ever existed, exceeding the biggest dinosaurs in body size and weight.

As unlikely as it seems, modern cetaceans are more closely related to living cattle, antelopes, and bison than to any other group of modern mammals. Cetaceans evolved from primitive terrestrial artiodactyls and represent a secondary adaptation to a completely aquatic existence. Fossil evidence of the most primitive whales come from Eocene rocks in India and Pakistan, sediments deposited in the eastern Tethys Sea nearly 50 million years ago. These

Humpback whale breaching. Cetaceans are the fastest of all marine animals, with body forms suited to remarkable feats of swimming and diving. (Brandon D. Cole/Corbis)

early cetaceans were amphibious, toothed predators, spending time on both land and in the water. Recent paleontological discoveries indicate that some supported their bodies on land with hoofed digits on the hands and on the soles of the feet; they probably moved like a modern sea lion. In the water, the animals propelled themselves by paddling webbed hands and feet and by body undulations.

Living cetaceans (Order Cetacea) are grouped into the suborder Odontoceti (67 species, thirty-five genera, and nine families of toothed whales, porpoises, and dolphins) and suborder Mysticeti (eleven species, six genera, and four families of huge whales with plates of baleen instead of teeth). All cetaceans have a nearly hairless, fusiform (torpedo-shaped) body that lacks sweat and sebaceous glands. Just beneath the skin is a thick, insulating, fibrous layer composed of fat and oil (blubber). Hind limbs, external ears, and ear muscles are absent. Nostrils (blowhole) open at the highest point of the head: odontocetes have a single blowhole, mysticetes a double blowhole. The blowhole connects directly with the lungs (which prevents milk from entering lungs of suckling calves), and it is closed during submergence. The water spout from a blowhole is condensation of water vapor entering the cooler air from the warmer lungs, not water ejected from the lungs. The bones are spongy and saturated with oil.

Cetaceans are the fastest of all marine animals. Powerful vertical movements of the tail raise and lower the body and propel the cetacean forward. The dorsal fin and flippers are used to steer. Most dolphins are shallow divers (to 30 m), but the sperm whale descends to more than 1,000 m.

Cetaceans must breathe atmospheric air, but they are adapted to alternate between normal breathing (eupnea)and long periods of not breathing (apnea). Most of the smaller dolphins and porpoises can hold their breath for up to five minutes; some whales (the sperm whale, for example) can remain submerged for an hour or longer. Various physiological adaptations are associated with cessation of breathing during prolonged diving and submergence. Before diving, the animal expels most of the air from its lungs. Cetaceans have twice as many erythrocytes (red blood cells that transport oxygen to tissues) per volume of blood as do terrestrial mammals, and up to nine times as much myoglobin (a molecule in muscle that stores oxygen and releases it to the tissues). The oxygen from these sources accounts for up to 90 percent of the supply utilized during diving. Heart rate decreases to half of that at the surface, thus decreasing oxygen use. Vascular networks shunt the peripheral blood supply to the brain and decrease the supply to the muscles; the oxygen debt sustained in muscular tissue is repaid when the animal surfaces to breathe again.

Most cetacean species are gregarious and have long parental care and maturation. A single calf is born after a gestation ranging from ten to seventeen months. Born underwater, the calf is pushed to the surface by its mother for the first breath.

Odontocetes (dolphins, porpoises, belugas, narwhals, sperm whales, and beaked whales) occur in all oceans, seas connected to oceans, and some rivers and lakes in North and South America, Asia, and Africa. All have conical teeth, and most species eat fish and squid; sperm whales take giant squid, large sharks, and fish; killer whales prey on fish, seals, porpoises, and small baleen whales. All have acute echolocation ability, used for communication, orientation, and detecting and stunning prey.

Mysticetes (right whales, rorquals, gray whales, and pygmy right whales) inhabit all oceans and are filter feeders, engulfing huge concentrations of zooplankton (minute crustaceans and other tiny animals). Instead of teeth, these cetaceans have long, thin plates of baleen (modified mucous membrane) that act as sieves; the plates are suspended from the palate at right angles to the long axis of the head. The animals swim with their mouths open through swarms of zooplankton. When the mouth is closed, the baleen acts as a strainer, trapping the zooplankton inside but allowing the water to pass through. The largest baleen whale and largest known animal (living or extinct) is the blue whale (*Balaenoptera musculus*). The longest blue whale ever measured was 34 m, and the heaviest was 190,000 kg. Many species of baleen whales migrate long distances. Gray whales (*Eschrichtius robustus*), for example, feed in the North Pacific during the summer and migrate 10,000 to 22,000 km to winter along the Korean coast in the western Pacific, and the coast of Baja California and Sonora in the eastern Pacific.

—*Mary Ellen Holden*

See also: Artiodactyls; Mammalia; Oceans; Plankton; Rivers and Streams

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Chiroptera (Bats)

Order Chiroptera (Greek for "hand wing") contains the only mammals that have evolved true flight (colugos and flying squirrels are gliders, not flyers). Living bats compose the second largest mammalian order (constituting about a fourth of all living mammals), and they play important ecological roles in insect control, pollination, seed dispersal, and fertilizer production.

Bats literally fly with their hands. Except for the thumb, the bones of the upper arm, forearm, and the four fingers are slender, elongate, and covered by thin flight membranes extending from the sides of the body and legs; another membrane connects the legs with the tail. The earliest well-preserved bat is *Icaronycteris index* from the Late Paleocene–Early Eocene, though the evolutionary origin of bats may date back to the Late Cretaceous.

The more than 1,000 bat species are arranged into suborder Megachiroptera, containing one family (Pteropidae, Old World fruit bats or flying foxes), and suborder Microchiroptera, with seventeen families. Bats are cosmopolitan in both hemispheres, except for polar regions and remote oceanic islands. The highest diversity of bat species occurs in the neotropics, where some localities have more species of bats than all other mammal species combined. Flying foxes are the largest bats, with wingspans of up to 2 m and body

Leaf-nosed bat flying at night. Bats are nocturnal mammals that use echolocation to navigate and to track prey. (Joe McDonald/Corbis)

lengths up to 430 mm (*Pteropus vampyrus*). Hog-nosed bats of Thailand (*Craseonycteris thonglongyai*), weighing about 2 gm, with a body length of up to 30 mm (about the size of a bumblebee), are the smallest bats and possibly the smallest living mammal.

Bats are nocturnal. Most megachiropteran species use vision for orientation and seeking food. Microchiropterans echolocate for orientation and capturing prey. They produce sound from the larynx, emitting pulses (usually ultrasonic) through an open mouth, or through the nostrils in species having elaborate nose-leaves. Echolocation, which allows bats to perceive and navigate their nocturnal environment, is essential in capturing prey and avoiding obstacles. The abilities of bats to fly and echolocate are prominent factors in the successful evolutionary radiation of bats into most of the ecological niches that are occupied by diurnal birds. This diversity of species and ecologies is reflected in their food habits. Most species are insectivorous, preying upon a wide variety of insects they catch in the air, on the ground, or on the tops of leaves. Some are carnivorous, eating other bats, small rodents, frogs, and lizards. A very few species catch and eat small fish. Three neotropical species feed on the blood of other mammals and birds. Many tropical species feed exclusively on fruits and flowers or nectar and pollen.

Historically, humans have looked upon bats with fear and revulsion. Laboratory and field studies have revealed much about the fascinating biology and behavior of bats. Many people now recognize that bats are not a menace to humans, and that they play integral roles in various ecosystems. Despite the shift in many peoples' attitudes toward bats, they are still persecuted in some regions: roosts are destroyed, forest habitats are logged, and the larger-bodied flying foxes are overhunted for food.

—Mary Ellen Holden

See also: Adaptation; Adaptive Radiation; Arthropods, Terrestrial; Biogeography; Convergence and Parallelism; Evolutionary Biodiversity; Extinction, Direct Causes of; Food Webs and Food Pyramids; Mammalia; Speciation; Tropical Rain Forests

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Chondrichthyes (Sharks, Rays, Chimaeras)

The class Chondrichthyes, or cartilaginous fishes, comprises the sharks, rays (including skates), and chimaeras, and it is one of the major groups of aquatic, gill-breathing jawed vertebrates. Approximately 1,050 species of chondrichthyans are living today, but their extensive fossil record dates back to the Late Ordovician (some 450 million years ago); the number of extinct species is not precisely known. Most chondrichthyans inhabit marine continental shelf areas, but some are deepwater and about 4 percent are freshwater.

Chondrichthyan fishes share several unique evolutionary specializations indicative of their common ancestry, such as a cartilaginous skeleton reinforced by superficial deposits of prismatic calcification, internal fertilization through claspers (male intromittent organs), and a special mode of tooth attachment and replacement (teeth occur in numerous rows and are constantly shed and replaced or fused into tooth-plates). Sharks and rays are fur-

Mouth of a Caribbean reef shark (Jeffrey L. Rotman/CORBIS)

ther united in the subclass Elasmobranchii ("plate-gill," referring to the individual gill clefts of their branchial arches), while the forty or so species of chimaeras form the subclass Holocephali (with the upper jaws fused to the braincase). A few Paleozoic taxa may fall outside of these subclasses (for example, the Devonian *Pucapampella* and *Cladoselache*), but their classification is uncertain.

Living chondrichthyans share specialized sensory and reproductive systems. Their fine-tuned sensory receptors, perhaps partly responsible for their evolutionary longevity, include the inner ear for sound, lateral line for perturbations in the water, and ampullae of Lorenzini for electrical field detection, along with advanced olfactory and visual units. Their reproductive strategies parallel those of mammals; some ground sharks nourish developing fetuses in the oviduct through maternal-fetal connections, and stingrays produce "uterine milk." Even intrauterine cannibalism has been documented (mackerel sharks). Gestation strategies vary within certain orders, but about 40 percent of all species (including catsharks, skates, chimaeras) lay egg cases, while the rest give birth to live young directly. More than one egg is fertilized at a time, and there is no rearing of the pups after birth. Chondrichthyans sexually mature at advanced ages in comparison to bony fishes (more than thirty years for some species), produce relatively few young per gestation, and may have prolonged gestation periods (more than two years for the spiny dogfish).

Fossil History

Fossil chondrichthyans are known primarily from isolated teeth, denticles, and fragmentary skeletal remains; complete fossilized skeletons are rare. The earliest chondrichthyan fossils, from the Late Ordovician of Colorado, are small external teethlike structures called placoid scales, similar to those coating modern sharks. The earliest fossil teeth are from Early Devonian deposits of Spain (*Leonodus*, 400 million years ago), but teeth become more common in the fossil record only during the Carboniferous. The earliest skeletal fragments are neurocrania (cartilaginous skull encompassing the brain and cephalic sensory organs) from the Middle Devonian (380 million years ago) of Bolivia and South Africa (*Pucapampella*) and Antarctica (*Antarctilamna*).

Relatively little is known from the earliest phases of chondrichthyan evolution, but many different lineages became established by the Late Devonian and Early Carboniferous, even though some of these were short-lived. Early elasmobranchs were morphologically very diverse, including the eel-like and mostly freshwater xenacanths (with conspicuous bifurcated teeth—for example, *Triodus* and *Orthacanthus*), stethacanthids (with "spine-brush" complexes), cladoselachians (perhaps the best known early sharks), and ctenacanthids (with more modern pectoral fin endoskeletons). Some two dozen new families flourished in the Carboniferous, including the distinctive edestids and eugeneodontids (for example, *Edestus* and *Helicoprion,* with vertical tooth-whorls), and morphologically bizarre relatives of modern holocephalans (for example, *Harpagofututor* and *Belantsea,* from the Bear Gulch limestones of Montana, 325 million years ago). Some chondrichthyan groups persisted into the Triassic (xenacanths, edestids), but many families vanished in the Permian.

Elasmobranchs with the features of modern sharks, such as calcified vertebrae, appeared during the Jurassic (for example, *Palaeospinax* and *Hopleacanthus*), along with the first rays (for example, *Spathobatis* and *Asterodermus*, similar to modern guitarfishes). One prominent group of Mesozoic sharks was the hybodonts, which originated in the Paleozoic (Pennsylvanian), diversified in the Mesozoic, but did not survive beyond the Cretaceous, going extinct when many living shark families became established. Some modern lineages can be found in the Late Jurassic Solnhofen limestones of Bavaria (150 million years ago—for example, angelsharks, hornsharks, and chimaeras), but the earliest record of a fossil shark belonging to a living family (Hexanchidae) is from the Early Jurassic, some 200 million years ago. Most modern families, many known only from isolated teeth, became established during the Cretaceous and Paleocene. Significant Cretaceous fossil sites include Cenomanian (97 million years ago) and Santonian stages (87 million years ago) from Lebanon, with sawfishes, guitarfishes, and skates, along with sharks, all modern in appearance. More complete fossil remains are also known from Eocene deposits (52 million years ago) of Monte Bolca, Italy, (marine rays, sharks) and Green River, Wyoming, (freshwater stingrays).

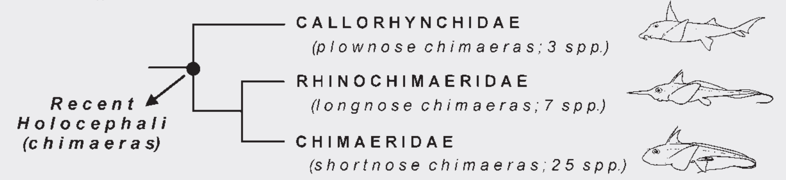
Phylogenetic Relationships and Modern Diversity

Recent phylogenetic studies unite certain Mesozoic elasmobranchs along with living sharks and rays in the group Neoselachii ("new sharks"), while Paleozoic elasmobranchs are more distantly related to neoselachians. Studies of evolutionary relationships among modern elasmobranchs indicate that rays are monophyletic (with a single origin and containing all lineages descended from the original ancestor) and are descended from sharklike ancestors sometime during the Early Mesozoic. In this scenario, "sharks" are not a natural group, as some squalomorphs (including cow, bramble, squaloid, angel, and sawsharks) are more closely

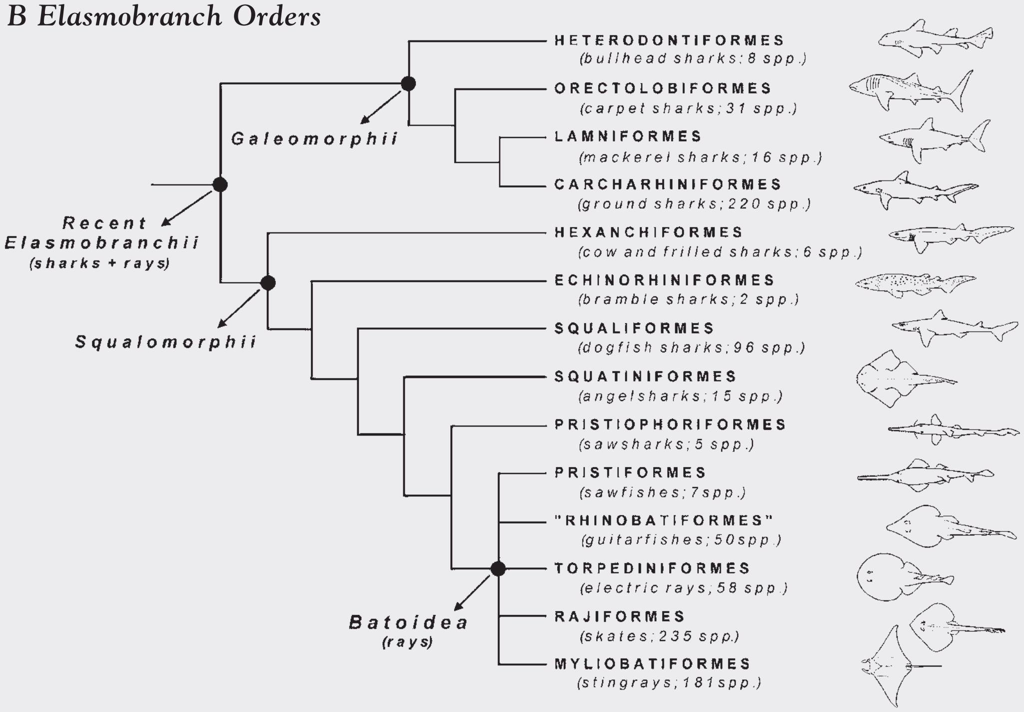
Figure 1A, B

Evolutionary Relationships among Living Holocephalan Families and Living Elasmobranch Orders

A Holocephalan Families



B Elasmobranch Orders



Sources: Modified from Nelson, J. S. 1994. *Fishes of the World,* 3d ed. New York: John Wiley; and Carvalho, Marcelo R. de. 1996. "Higher-level Elasmobranch Phylogeny: Basal Squaleans and Paraphyly." In *Interrelationships of Fishes,* edited by M. L. J. Stiassny, G. D. Johnson, and L. R. Parenti; Numbers of species are compiled from various sources.

Note: Living families and orders are in upper case, with common names and current number of species in parentheses. The relationships among rays are still uncertain (unresolved in the cladogram); Rhinobatiformes are in quotation marks because their monophyly is highly doubtful at present.

related to rays than to galeomorphs (including bullhead, carpet, requiem, tiger, mako, and white sharks). The morphological transition between shark and ray is evident in one fossil elasmobranch (the Jurassic Protospinax from Solnhofen). This evolutionary scheme is at odds with the fossil record, as large gaps remain for some shark groups (for example, squaloids, bramble sharks), even though it is the most corroborated theory to date.

Elasmobranchs constitute about 95 percent of living chondrichthyan diversity; only three out of the approximately sixty families are of chimaeras. Living families of sharks are grouped into eight or nine orders (containing some 400 species), and they usually have elongate bodies, one or two dorsal fins (some with fin spines), a forked or lunate caudal fin for propulsion, paired pectoral and pelvic fins, and five to seven lateral gill slits. Sharks vary in size from whale sharks of 15 m to lantern sharks of 15 cm, and they range from bluish-gray pelagic forms to colorful benthic species. The 580 or so species of rays are usually divided into five orders, most with enlarged pectoral fins continuous with the head forming the disc (except in sawfishes and guitarfishes), and ventral gill slits (water intake is usually done through enlarged, muscular spiracular openings). Rays vary in size from 7 m across the disc (manta rays) to 15 cm in length (some electric rays). They inhabit from the shoreline to abyssal depths and are morphologically diverse (including sawfishes, electric rays, skates, guitarfishes, and venomous stingrays). South American potamotrygonid stingrays are exclusively freshwater, and some marine stingrays are pelagic. Both sharks and rays are carnivorous, but some of the largest species filter plankton for food.

Conservation

Consumer demand for shark-related products has increased over the past decades, and consequently many populations have declined by an estimated 70 to 90 percent because of overfishing (for example, dusty and sandbar sharks off the northeastern United States). Most countries do not manage their shark fisheries, and predatory fishing practices that kill indiscriminately are commonly employed (for example, long-lining and finning). Some species are already depleted (for example, sawfishes in the Gulf of Mexico), and others face extinction in the near future. Elasmobranchs are increasingly important in the growing ecotourism industry, contrary to their maligned, popular *Jaws* image. Chondrichthyans are ecologically important apex-predators, and their reproductive peculiarities (internal fertilization, slow sexual maturation, long gestation, and production of few young) render them especially vulnerable to population decline.

—Marcelo Carvalho

See also: Bony Fishes; Evolutionary Biodiversity; Geological Time Scale; Phylogeny; Systematics

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Chordates (Nonvertebrate)

The phylum Chordata is traditionally considered to consist of all of the classes of the subphylum Vertebrata (that is, fishes, amphibians, reptiles, and birds), plus several other groups that lack a brain case but share with vertebrates three fundamental anatomical features: (1) a so-called notochord (precursor to the vertebral column, or "backbone," of vertebrates), associated with (2) a dorsal hollow nerve cord (the "spinal cord" in vertebrates), and (3) gill slits in the pharynx ("throat" region) at some point in the life cycle. (Recall that human embryos have gill slits during development).

Of the two or three major groups considered to be nonvertebrate chordates, only one (the Cephalochordata) resembles vertebrates at all; the rest look like either worms or invertebrates with simple, sacklike bodies. Some modern classifications, while recognizing the close evolutionary affinities of these very different-looking groups, prefer to split them into separate phyla: the Hemichordata, the Urochordata, the Cephalochordata, and the Vertebrata (sometimes called the Craniata). All of these groups, along with echinoderms and some other phyla, are deuterostomes (see Evolutionary Biodiversity), considered to be close evolutionary relatives because of features they share in their embryological development.

Hemichordata. The "acorn worms"—enteropneusts and pterobranchs—share with the urochordates and cephalochordates gill slits in the pharynx, but they are not considered to have true hollow nerve cords or notochords. Living either as burrowers or secretively in tubes, all species are marine. Hemichordates feed either by removing bacteria and organic particles (detritus) from the surface of sand grains, or in some cases by straining suspended plankton directly from seawater ("filter feeding"). Poorly known, the hemichordates nonetheless have a long fossil record, dating from the famed Burgess shale some 500 million years old. Paleontologists also consider the graptolites, a diverse group with a rich fossil record in the Lower and Middle Paleozoic, to have been hemichordates.

Urochordata. Urochordates, also known as tunicates, salps, sea squirts, and ascidians, all have the dorsal hollow nerve cord and the notochord and gill slits in their larval stages, but all of them lose the nerve cord and notochord in the adult stage (except for the aptly named "larvaceans," which gain sexual maturity while retaining many of the features of the larval stage, a process known as neoteny).

Most urochordates live as adults attached to the seafloor, rocks, wharves, and the like. They develop a saclike structure that completely envelopes the body—which, internally, consists mostly of the pharynx lined with gills slits, with which they strain food particles. Equipped with a heart, a digestive system (including a liver), gonads for reproduction, and other organs, the deceptively simple-looking urochordates have all the complexities of the advanced animals they are, despite resembling from the outside much more simple invertebrates.

The urochordates are by far the most common of the nonvertebrate chordates. They are exclusively marine and often are found in a variety of bright colors: yellow, green, purple, and red.

Cephalochordates. Sometimes called the "acrania" because they resemble true vertebrates but without a skull, the cephalochordates are the "lancelets" of biology dissection labs—picked for study because they are the closest living relatives of true vertebrates. The notochord, dorsal hollow nerve cord, and pharynx with gill slits all remain with the animal throughout its life. Looking like a miniature fish, *Branchiostoma* (or "amphioxus") uses a circle of small tentacles around the mouth to intercept particles too large for digestion; the water then continues into the pharynx, where food particles are removed as it passes out through the gill slits. Lancelets feed by poking their heads out of the sandy bottom (all are marine, living in sandy, shallow-water environments). But lancelets are not rooted to the seafloor as are their close relatives, the urochordates. Rather, each individual is capable of swimming—mostly to avoid predators if disturbed, or to take up residence in another portion of the seafloor.

—*Niles Eldredge*

See also: Evolutionary Biodiversity

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Ciliates

See Protoctists

Circumboreal

See Biogeography

Classification, Biological

Our present system of biological classification grew out of the need to find a way of organizing the growing lists of new plants and animals carried back to Europe during the Age of Discovery. Prior to Linnaeus, organisms were named in a variable manner, usually with a descriptive phrase. The Linnaean system supplanted earlier forms of classification, primarily because it replaced more ponderous ways of naming species with the simple and flexible binomial system. (For example, genus and species: our species is *Homo sapiens*, with the name of our genus [*Homo*] always written before our species epitaph [*sapiens*].) This, coupled with the Linnaean system of ordering hierarchically and showing relative hierarchy through the use of additional categorical ranks, provided subsequent biologists with a flexible and readily modifiable system that was capable of absorbing our ever-expanding knowledge of biological diversity.

Darwin changed forever how we interpret biological classifications. Before the general acceptance of evolution as a process and phylogenetic descent as a pattern, there was considerable diversity of opinion as to how the form and meaning of biological classifications should be understood. In general, organisms were placed together into larger taxonomic groups using some criterion of similarity. Actual classifications took various forms. For example, the quintarians were firmly convinced that groups occurred in fives and classified accordingly. Religiously minded scientists, such as Louis Agassiz, interpreted truly natural classifications as a plan of how God created. (Thus, taxonomy could almost be thought of as the discovery of how God thinks about things.) One of Darwin's political successes, no doubt, was the fact that one could simply change the way one thought about existing classifications without having to abandon them. One simply switched from interpreting an existing classification as a scheme of similarity to interpreting the classification as a reflection of descent with modification.

Today there are two aspects of biological classification that must be understood; one is conceptual, the other is purely technical. The conceptual issue can be stated directly: what is a classification meant to represent? The technical aspect can also be stated directly: what rules should be adopted so that all can understand biological classifications?

Changing Concepts

Darwin suggested that classifications should portray the genealogical history of organisms. Of course, he also recognized that our knowledge of genealogy was woefully deficient, a situation that still exists. Much research was invested in trying to understand the major line of evolution in plants and animals during the latter part of the nineteenth century and the first half of the twentieth. However, the use of rigorous and programmatic methods to reconstruct phylogenetic history was not widely adopted until the German entomologist Willi Hennig introduced phylogenetic systematics around 1950. Hennig suggested two major reforms. First, he suggested that "relationship" in a rigorous evolutionary sense meant one and only one thing: genealogical relationship. This is the relationship between parent and child or ancestral species and its descendent (daughter) species. Before this refinement, there was a dual concept of the meaning of relationship: relationship of similarity and relationship of genealogical descent. They had coexisted as equal partners in biological classification since the general adoption of the evolutionary paradigm. Prior to Hennig, one could justify a particular classification either by claiming that species should be placed in a genus (or a genus in a family, and so forth) because they were similar to each other, or because they shared a common ancestor. It is important for us to understand that the criterion of grouping because organisms are similar (or the more "modern" refinement of phenetic similarity) is a pre-evolutionary idea that carried over through the Darwinian revolution. Although it may be true that we can expect genealogical relatives to be similar, it is not always the case. For example, crocodiles "look" more like lizards, but they are the closest living genealogical relatives of birds (both are archosaurs, as are dinosaurs). Hennig insisted that genealogy was primary, while similarity was secondary.

The second refinement grew out of the first. Before Hennig's work, systematists recognized two kinds of groups. Monophyletic groups were supposed to correspond to the descendants of a common ancestor, while polyphyletic groups were composed of organisms that did not share a common ancestor included in the group. For example, Mammalia is a monophyletic group, but a group composed of birds and mammals (Homeothermia) is a polyphyletic group, since the last common ancestor of both would be classified as a reptile. Hennig recognized that many "monophyletic" groups were not monophyletic at all. He called these groups "paraphyletic." Paraphyletic groups contain some descendants of a common ancestor but leave some other descendants out, usually because they are not very similar to members of the paraphyletic group. For example, Reptilia are a paraphyletic group because it leaves out mammals (Mammalia) and birds (Aves). Hennig asserted that paraphyletic groups were as unnatural as polyphyletic groups. This was a major threat to existing classifications, because as the phylogenies of major groups were refined, systematists found that many familiar and widely used groups were paraphyletic. Reptilia is one example (crocodiles and dinosaurs being classified with lizards rather than with birds). An example closer to home is the Pongidae, a group that consists of the great apes but that excludes humans (which are placed in their own family, Hominidae but are actually closely related to gorillas and chimpanzees). Such luminaries as G. G. Simpson, Ernst Mayr, and Steven J. Gould attacked Hennig's assertion that paraphyletic groups should be abandoned in true evolutionary classifications. However, it turns out that Hennig was right. The philosopher David Hull, even before reading Hennig, pointed out that paraphyletic groups were logically inconsistent with the phylogenies they sought to summarize. This places those who wish to continue to use paraphyletic groups in the awkward position of advocating a system of classification that is illogical relative to the phylogenies they accept as good hypotheses.

Adoption of these two refinements allowed Hennig to formulate a consistent method for recovering phylogenetic relationships by using only those homologies that are directly relevant to corroborating or refuting genealogical relationships at a particular level of analysis. His method, and later refinements, form the techniques universally applied by modern systematists to reconstruct the evolution histories of organisms.

To summarize: Hennig wished to reform systematic biology and make it truly Darwinian. Building on the work of earlier German taxonomists, he formulated a consistent and rigorous method of reconstructing evolutionary history. He asserted that genealogical relationships were the primary criterion of relationships. And he uncovered a kind of unnatural group that had previously been recognized as a kind of monophyletic group, the paraphyletic group. With the recognition that paraphyletic groups are illogical relative to evolutionary descent, Hennig's assertion that paraphyletic groups should be abandoned in favor of classifications containing only monophyletic groups is growing in acceptance.

What Biological Classification Can and Cannot Do

Scientists as well as teachers and students frequently expect that classifications embody certain kinds of information that they are not capable of containing. This leads to dashed expectations and even problematic science. As a form of hierarchical language, biological classifications are capable of informing a reader about the groupings of organisms. If the reader understands the intention of the person who does the classifying, then the reader understands the criterion of grouping. For example, if you know that I intend to classify using the criterion of grouping by common ancestry, you can interpret the grouping I form as my hypothesis of the genealogical/evolutionary relationships of the organisms I classify. You might then be able to compare my classification with my phylogenetic tree hypothesis and evaluate how well I actually reflected the common ancestry relationships. If, on the other hand, I am working with a poorly known group of obscure marine worms, I may not have a hypothesis of the common ancestry relationships of the worms. I may simply be attempting to organize the diversity as well as I can, using similarity or even intuition until such time as I, or others, might be able to study the phylogeny of the group. The vast majority of all classifications actually fall under the category of this second group: classifications that reflect best guesses of relationships rather than actual phylogenetic hypotheses. As I understand more about the evolution of my group of marine worms, my classifications will change to reflect this increase in knowledge. A classification made on the basis of a first guess looks as well organized and solid as a classification made on the basis of a detailed knowledge of evolutionary relationships. There are no warning flags saying: "This classification is a solid reflection of evolutionary relationships, while that other one is an arbitrary arrangement." Both equally reflect one and only one thing: the group relationships hypothesized by the taxonomist to exist between the organisms classified.

In an earlier and simpler time, biological classifications were thought capable of conveying much more than grouping relationships. It is common to find the following myths, and it is easy to find defenders of these myths even today among practicing taxonomists:

Myth 1. Classifications can convey some sense of the distinctiveness of a taxon by adjusting the rank of that taxon. It is true that one can raise the rank of a taxon to reflect your idea of its novel and distinctive nature (not that everyone will agree with you!). However, you cannot retrieve that information from the classification. For example, asserting that birds are a class of vertebrates does not automatically give a clue as to how distinctive birds are from their closest relatives, crocodiles and dinosaurs. Further, the matter of how distinctive a particular group might be is a matter of opinion and thus a subjective criterion rather than an objective one. Why, for example, are birds a class of vertebrates while bats are simply an order of mammals?

Myth 2. Distantly related taxa ranked at the same categorical level are comparable. Modern phylogenetic classifications use ranking purely to denote subordination (that is, the position of a taxon within a hierarchy). An order or family of insects is not comparable to an order or family of fishes. Indeed, one family of fishes may not be comparable to another family of fishes. Only when these two taxa of fishes are closest relatives ("sister groups") are they directly comparable. The idea that distantly related groups ranked at the same level are biologically comparable is a vestige of the old idea of the *scala naturae*, the idea that organisms could be arranged in order of increasing perfection.

Myth 3. Classification should remain stable and unchanged. Taxonomic classifications are really hypotheses. In science, hypotheses are tested. If a classification is found deficient, it is replaced by a better hypothesis. To ask a taxonomist not to change a classification when she understands more about the relationships of her organisms is like asking any other scientists not to change their hypotheses with increased knowledge. The effect would be to remove taxonomy from science. Rather than lamenting the fact that we have to learn a new classification, we should be celebrating the progress of scientific understanding. Believe it or not, students actually understand this point.

Myth 4. Textbooks present classifications that are logical relative to known phylogenies. I know of no secondary-level textbook and few college-level textbooks that present summary classifications of organisms that contain only monophyletic groups. The continued presentation of paraphyletic groups to students perpetuates the myth that classification is not very relevant to evolution. Alternatively, such classifications actually mislead students who may think that classifications should reflect phylogenies. A classification that groups humans in one family and chimpanzees in a different family creates the impression that humans are no more closely related to chimps than to gibbons. A classification that groups birds as a class and crocodiles and dinosaurs in another class creates the impression that birds are not related to dinosaurs or crocodiles any more than birds are related to lizards and snakes.

—*E. O. Wiley*

See also: Linnaean Hierarchy; Phylogeny; Systematics

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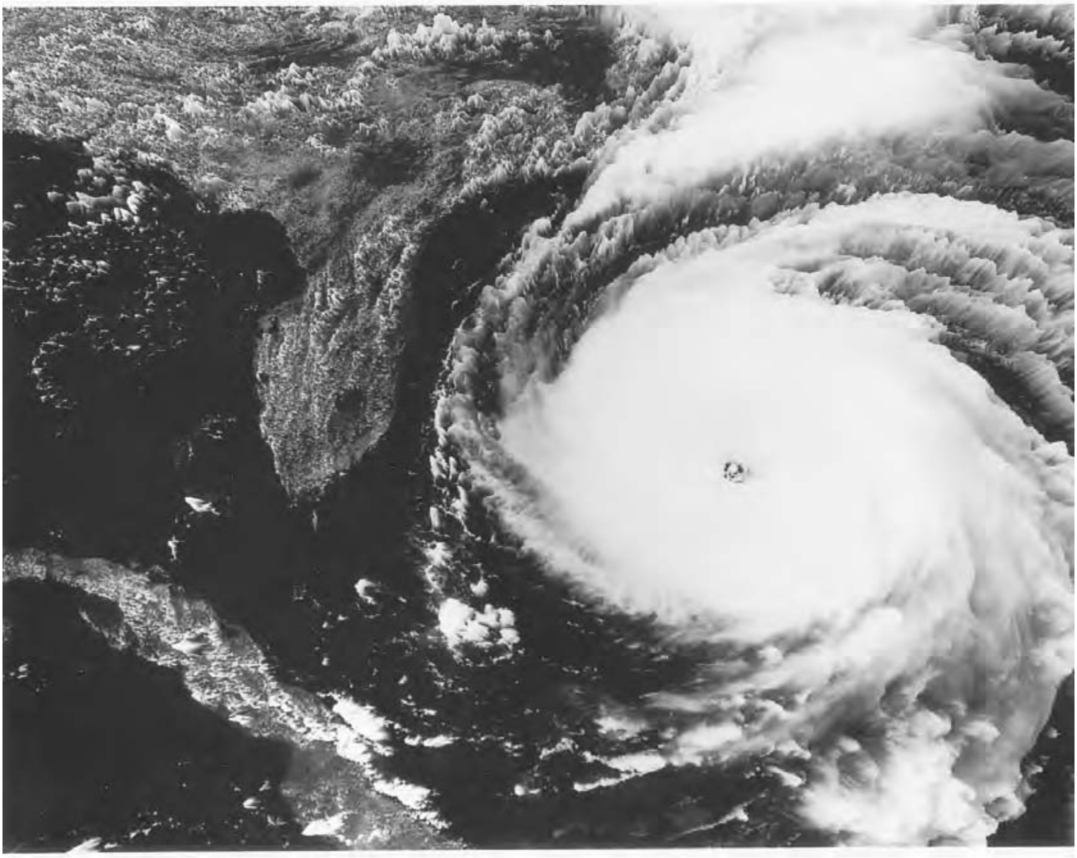
Climatology

Climate is defined as average long-term weather patterns, and it describes the state of the atmosphere's behavior and its variation from place to place over time. Climatology is concerned with both the description of climate and the analysis of the causes of climate differences, climate changes, and their conse-



Photograph of Hurricane Fran taken from a NOAA/National Weather Service satellite, September 4, 1996 (NASA)

quences. These factors are controlled by latitude, irregular distribution of land and water, prevailing winds, jet stream position, belts of high and low pressure, ocean currents, terrestrial altitude and relief, and the difference between highest and lowest elevations.

Climatology is often considered a branch of meteorology, the study of the atmosphere and all its phenomena, ranging from global patterns to the long-term heat and wind effects of a house or building in an urban setting, a pond in a farmer's field, or the consequences of microclimate on an ant colony.

On a global scale, climate is dependent upon the amount of solar energy intercepted by the atmosphere, which in turn depends on the earth-sun distance and the angle of the earth's inclination at any given place, which changes daily with the earth's rotation. Thus climate study includes the physical laws that determine how solar energy is converted to heat, and other factors such as air pressure, wind, and the distribution of land and sea.

In the equatorial regions the earth heats up more than it cools, while in polar regions it loses more heat than it receives. If it were not for the transfer of heat from equatorial zones to polar zones by wind and ocean currents, the polar regions would get colder and colder and the equatorial regions hotter and hotter.

Climatology is concerned not only with fluctuations in climate caused by variations in solar radiation and changes in the earth's orbital parameters, but also with movement of continents, distribution of land and sea, and volcanic activity. Over time the rise or erosion of mountains causes changes in wind direction and precipitation that affect plant and animal distribution and alter climatic zones. Oceans, because they are warmer in winter and cooler in summer than the adjacent continents, help to moderate climate. This explains why large landmasses such as North America are hotter during the summer and colder in the winter in their interiors, which are far from the sea.

Climate is also a very important factor in terrestrial ecology. Maps presenting vegetation patterns and climatic zones show a close correlation, and plants affect the distribution and abundance of the animals that depend on them. Plants are not only the source of food but also provide habitats for many animals.

Mountaintops at the equator are very cold, and the temperature range between a mountain's base and summit is much like the changes between the warm latitudes and the polar regions. For example, it is not uncommon for tall peaks to have a deciduous forest at their base, evergreen forest on their upper slopes, and tundra above treeline. Snow and even glaciers may be found at a mountain's crest. Mountains may also alter rainfall patterns. As air rises along the mountain front, it cools and therefore cannot hold has much moisture as it did when it was warmer. The moisture is precipitated out, and as dry air flows down the leeward side of the mountain it causes moisture in the soil to evaporate. This resulting climatic feature, the rain shadow, may cause a desert to form at the base of a mountain.

Compared with the past, continents today stand high above sea level, and there is probably more land today than during most of Phanerozoic time. As a result there is a steep temperature gradient between the poles and the equator: the equator is tropical, while the average temperature at the poles is below freezing. In the past, as shown by fossils and sediments, polar regions were warmer than they are today, and there weren't as many climatic belts.

Waldimir Köppen, a botanist, recognized climate as a major factor in the distribution of vegetation, and he used the relationship as an indicator for major climatic gradations. Köppen produced his first map in 1918 and named his climates, in part, according to vegetation formations—tropical rain forest climate, tropical savanna climate, and so forth. There have been several attempts to improve on his early classification of climate by using such criteria as global radiation, precipitation, and temperature.

Human activity such as forest clearing and other large-scale land use changes, as well as the production of carbon dioxide and other greenhouse gases, affect and alter weather and climate. Climate also affects human activity, such as agriculture, which is influenced by the length of the growing season, amount and distribution of rainfall, and temperature. Climate affects transportation, restricting it with storms, fog, ice in rivers, and heavy snowfalls. It also determines the amount of fuel needed to heat and cool buildings.

—*Sidney Horenstein*

See also: Atmosphere; Atmospheric Cycles; Carbon Cycle; Global Climate Change; Hole in the Ozone; Layer; Hydrologic Cycle; Meteorology; Oxygen, History of Presence in the Atmosphere

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Cnidarians (Sea Anemones, Corals, and Jellyfish)

Cnidarians are a major phylum of aquatic (and mostly marine) invertebrates that include many of the most recognizable shoreline creatures, including sea anemones, jellyfish, and corals. The name of the phylum derives from *cnidos*, meaning "stinging nettle" in Greek, and refers to the stinging nematocyst class of cnidae—the microscopic structures that define the phylum. (In addition to nematocysts, the other two classes of cnidae are spirocysts and ptychocysts.) The phylum first appears in the late Precambrian or Vendian period, and the group is generally considered the sister group of all metazoans besides sponges (Porifera). Cnidarians are divided into four extant classes—Anthozoa (containing sea anemones, stony corals, soft corals, gorgonians), Scyphozoa (true jellyfish), Cubozoa (box jellies or sea wasps), and Hydrozoa (hydroids, fire corals, jellyfish, siphonophores, Portuguese-man-o'-war). The phylum contains approximately 10,000 species.

Some jellyfish are active predators that use their tentacles to capture and subdue prey; others are filter feeders that catch small prey and food particles that drift by in the water column. (Henry Horenstein/Corbis)

The basic body organization of cnidarians is simple: a radially (or biradially) symmetrical animal composed of two cell layers (the ectoderm/epidermis and the endoderm/gastrodermis), with a single body opening—the mouth. The mouth is surrounded by tentacles covered with the cnidae, and the body is either shaped into a tubelike polyp stage usually attached to the benthos or a mushroomlike medusa stage ("jellyfish") generally found swimming in the water column. A jelly layer with relatively few cells, called the mesoglea, is found between the ectoderm and endoderm. In some groups, this layer is quite thin, while in others (for example, jellyfish), the mesoglea makes up most of the mass and the structural support of the animal. The saclike body cavity is called the coelenteron (hence the alternative name of the phylum, Coelenterata). It functions in digestion, circulation, gas exchange, and as a hydrostatic skeleton for support and extension of polyps and tentacles, and in medusae for swimming. Many cnidarian polyps also secrete mineral or organic endoskeletons or exoskeletons. In the case of coral reef–building scleractinian (stony) corals, these skeletons can be quite massive.

The life cycle of an idealized cnidarian species alternates between the medusa and polyp phases, though the medusa stage is completely absent in anthozoans and missing from many hydrozoan life cycles. Other hydrozoans lack the polyp stage. Regarding the idealized life cycle, however, male and female medusae spawn sperm and eggs in the plankton. These gametes unite and develop into small, ciliated, pear-shaped larvae called planulae. A planula settles to the bottom and metamorphoses into an upright, feeding polyp. In many cnidarians, this polyp develops into a colony or clone as the polyp buds new polyps that either remain connected or divide, respectively. After this period of asexual growth, the polyp asexually buds new medusae into the water column, which upon sexual maturation repeat the cycle.

Although the evolutionary relationships among these classes are still controversial, most scientists consider Anthozoa to be the basal group, with the other groups diverging later. If correct, this suggests that cnidarians originally evolved with a single phase of sexual polyps (as in current anthozoans). Only later, with the evolutionary appearance of the other classes, did the sexual portion of the life cycle physically partition off into a planktonic medusa phase. Alternatively, the earliest cnidarians had both medusa and polyp phases, and the former were lost during the divergence of the Anthozoa. Such evolutionary modifications and losses of medusa are seen within Hydrozoa. Within certain hydrozoan groups, the sexual medusa phase has gradually declined in importance, as medusae have become smaller, shorter lived, and weaker swimmers. In other groups, the medusa no longer detach from the polyp, while in others (for example, *Hydra*), they are so completely reduced that they are expressed as simple gonadal tissue in the polyps. In contrast, in other hydrozoans, scyphozoans, and cubozoans, the polyp stage has been reduced or lost, and most time and growth is devoted to the jellyfish stage, which can become quite large in the true scyphozoan jellyfish. The great variety of ways in which the polyp and medusa phases have evolved within Cnidaria clearly demonstrate the evolutionary versatility of this seemingly simple phylum.

Ecologically, all cnidarians are predators, using their tentacles and cnidae to capture and subdue prey, which then gets transferred into the mouth of the polyp or medusa. Individual polyps and colonies are either passive filter-feeders (also called suspension-feeders), in which colonies capture small prey and food particles that drift by in the water column, or sit-and-wait predators that catch prey that walks or falls into their tentacles. Some jellyfish are somewhat more active, catching prey that gets sucked into reach of their tentacles as they pulse and swim. Others float motionless and act as completely passive sit-and-wait (or ambush) predators. Some cubozoans are known to have particularly potent toxins in their nematocysts, causing the deaths of a small number of swimmers every year. Because of their stinging abilities, cnidarians have relatively few predators, though exceptions include animals that have evolved specialized abilities to deal with these defenses. Many cnidarians also contain diverse secondary metabolites that serve as additional chemical defenses against would-be predators, and many of these compounds are being investigated as potential sources of new drugs.

In addition to being predators, many anthozoans and fewer hydrozoans and scyphozoans have evolved internal symbiotic relationships with microscopic algae (including dinoflagellates, called zooxanthellae, and green algae, called zoochlorellae), allowing the cnidarian-algal associations to photosynthesize and function as primary producers. Arguably, this primary producer ability reaches its height in tropical reef-building corals, and the productivity of coral reef ecosystems is largely driven by these symbiotic associations. In addition, the ability of many benthic cnidarians—such as hydroids, hydrocorals, black corals, gorgonians, and scleractinian (stony) corals—to contribute to and even define the three-dimensional structural complexity of their habitats makes these groups important ecosystem engineers within their communities.

Within the water column, some species of jellyfish have reportedly become more common in recent decades, with populations periodically experiencing explosions. These blooms have been interpreted as a sign of competitive release, with the overexploitation of many predatory fish species leaving an expanded role for jellyfish as higher-level pelagic predators.

—Daniel R. Brumbaugh

See also: Adaptive Radiation; Benthos; Coloniality; Communities; Coral Reefs; Plankton; Protoctists

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Coastal Wetlands

Coastal wetlands are plant-dominated communities that occur along the shoreline of bays and where rivers meet the sea. Coastal wetlands, because they occur at the interface between terrestrial and marine environments, provide important and unique ecological services. They are highly productive, and supply food and habitat for fish, shellfish, and birds. In addition, they play a major role in decreasing coastal erosion and buffering marine environments from nutrient loading and pollution.

There are two types of coastal wetland communities: salt marshes and mangrove swamps. Salt marshes occur in temperate climates, whereas mangroves are found in tropical regions, between 30 degrees north and south latitude, where surface water temperatures are greater than 16 degrees centigrade. Mangrove swamps do not occur at higher latitudes, on account of frost sensitivity.

Salt marsh in the Pacific Northwest. Note different bands or zones of vegetation with elevation. (Sally Hacker)

Salt marshes are low-species-diversity communities characterized by halophytic (salt-loving) grasses, herbs, and small shrubs.

Commonly associated animals include shellfish, insects, and birds. Salt marshes are some of the most productive communities on earth. Productivity can be as high as 3,000 grams dry plant weight per square meter per year, higher than that of most agricultural crops. Nearly 50 percent of the productivity can be exported into adjacent marine habitats and used in aquatic food webs.

Mangrove swamp communities are dominated by halophytic trees that have large, branching prop roots, creating an ideal underwater habitat for fish, shrimp, and root-encrusting animals, including sponges and oysters.

The above-ground portion of mangroves provides extensive habitat for birds, alligators, and crocodiles, and for mammals such as bears, pumas, and wildcats. Mangrove communities have similar productivity but higher species diversity than salt marshes.

Coastal wetlands are influenced by tides, which move water up and down across their surface at least once a day. Daily tidal inundation combined with a natural elevational

Mangrove trees in the Caribbean. Note the large roots produced by the tree trunk and branches. (Sally Hacker)

gradient, from low elevation near the water's edge to high elevation near the terrestrial border, creates bands or zones of varying species associations and physical conditions. Low zones are frequently flooded, producing salty, low-oxygen conditions with high sedimentation. High zones are less frequently flooded and have low salinity and sedimentation but higher oxygen levels. Wetland plants play a major functional role in mediating physical conditions. Plants efficiently shade the soil, causing decreased evaporation and salt accumulation, and extensive and specialized roots increase sedimentation and oxygen concentration.

Coastal wetlands have experienced widescale human disturbance for many centuries. Close to 90 percent of North American coastal wetlands have been lost, and salt marshes are used for grazing livestock, agriculture, and development. Some major cities, including Boston, San Francisco, and London, are built on filled or drained wetlands. In addition, salt marshes and mangrove swamps reside at the discharge end of rivers, where they receive high levels of nutrients, heavy metals, and other pollutants. Conservation has increased in recent times, and many remaining wetlands are protected under law.

—Sally Hacker

See also: Communities; Draining of Wetlands; Ecosystems; Erosion; Estuaries; Extinction, Direct Causes of; Interior Wetlands; Intertidal Zone; Lagoons; Nurseries; Preservation of Habitats; Reptiles; Sponges; Tides; Topsoil Formation; Topsoil, Loss of

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Coevolution

The concept of coevolution has been defined in various ways, but it generally refers to an evolutionary change in one species that is a result of evolutionary change in another species. Evolutionary change can be physiological or involve a fixed behavioral pattern, and commonly it involves a morphological structure—but it always implies a genetically based change. Evidence of coevolution derives from the study of fossils, the phylogeny of modern species, and their ecology. There is a spectrum of types of coevolution: escape and radiate, guild coevolution, arms race or escalation, and cospeciation or parallel cladogenesis.

Escape and radiate coevolution involves the radiation of one species into many as a result of an adaptive breakthrough that frees it from the selection pressures of predation or parasitism. An example is the radiation of many kinds of mollusks as a result of the thickening of their shells over time. By evolving thicker shells in response to various predatory fish and gastropods, certain mollusks were able to become ecologically dominant and diverse. In response to thickening shells, some predatory gastropods evolved a radula (a filelike structure with teeth) that is drill-like, capable of penetrating a very thick shell and thereby allowing its inhabitant to be consumed.

Guild coevolution involves evolutionary change in a species or group of species in response to a suite of predators, competitors, parasites, or other interacting species. Excellent examples of guild coevolution are plants and the insects that feed on their leaves or pollinate their flowers. Many plants defend themselves against herbivory with noxious or toxic chemicals that repel most insects. Some insects, though, have evolved defenses against the poisons, which are physiological and even behavioral. Milkweeds (Family Asclepiadaceae) derive their name from the sticky latex that oozes from wounds to the stems or leaves. The latex gums up the mandibles of chewing insects, and it contains poisonous cardiac glycosides. As a result, there are suites of insect species—such as certain chrysomelid beetles, plant bugs, and monarch butterfly caterpillars—that feed on particular species of milkweeds. These specialized insects can detoxify the poisons and even sequester them in their bodies for use in defending themselves against predators. Some milkweed-feeding insects even chew a cut into the base of the main vein of the leaf to prevent the latex from reaching the more distal parts of the leaf, where they will then feed. Guild coevolution is predominant among angiosperms and their insect pollinators. Flowers have evolved "syndromes" of color, structure, and fragrance to lure particular types of pollinators. Pollinators, in turn, have evolved various behaviors and structures that make them particularly efficient at harvesting pollen and nectar from certain kinds of flowers—and therefore at transferring the pollen. Flowers with long spurs containing nectar, for example, are usually pollinated only by certain moths, flies, and bees with extremely long tongues.

Arms race, or *escalation*, coevolution refers to multiple adaptations in interacting species, each one a response to adaptations in the other species. Cheetahs, for example, are uniquely adapted among all cats for running down their prey during the daytime in high-speed chases. All other cats are usually nocturnal, ambushing predators. Cheetahs are inefficient at overwhelming larger animals but highly specialized for preying on Thompson's gazelles ("tommies"), particularly by tripping them up during the chase. Tommies, in turn, flee extremely fast. Their small size makes them proficient in darting, which makes it particularly difficult for lions and leopards to catch them. The cheetah's specialization is evolutionarily precarious, should tommy populations crash, say, from a virus, but it does allow a coexistence with predators that kill zebra, wildebeest, and the other large ungulates of East African plains.

In tropical regions of South America lives a diverse genus of understory nymphalid butterflies, *Heliconius*. The caterpillars feed on plants in the Passifloraceae, or family of passion fruit vines. Species of *Heliconius* usually live very specifically on particular species of *Passiflora*, having become physiologically adapted to detoxifying certain glycosides that make the foliage of *Passiflora* inedible to most herbivores. Female butterflies will not lay eggs on *Passiflora* vines that have caterpillars or even eggs on them. The *Passiflora* plants have evolved, in response, specialized glands and stipules that mimic *Heliconius* eggs and often deter ovipositing butterflies.

Cospeciation, also called *parallel cladogenesis*, occurs when speciation in one organism results in the speciation of another. Cospeciation can lead to situations in which the phylogeny of, say, a group of host species matches the phylogeny of the parasites that live on them. Indeed, cospeciation is found in situations where species are intimately associated, usually obligate (where the existence of at least one is dependent upon the other). These especially include organisms that are parasites, or symbiotic mutualists. One of the best examples of cospeciation involves a basidiomycete fungus that lives exclusively in the nests of leaf-cutting ants of the New World tropics, the Attinae. The ants provision their underground nests with chewed vegetation, but they actually feed on the fungus that grows on the rotting plant material. The ants and fungi are codependent, and the phylogeny of the ants matches the phylogeny of the fungus: as the ants speciate, the fungus genetically diverges accordingly. Certain groups of lice on their mammal and bird hosts show similar patterns, as do some tapeworms and other parasites.

—David Grimaldi

See also: Adaptation; Ecological Niches; Evolution; Herbivory; Natural Selection; Phylogeny; Pollination; Positive Interactions; Speciation

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Coloniality

Coloniality, in the context of invertebrate zoology, refers primarily to the general morphological plan in which the genetic individual (or genotype) is composed of physiologically connected units or modules (called polyps, thecas, zoids, or zooids, depending on the taxonomic group). Coloniality usually develops through some process of repeated budding in which the daughter modules remain attached to the parent modules. If individual modules separate, these are collectively and individually considered to be a clone and clones, respectively. Because connected sets of modules can also separate from other sets to become clones of subcolonies, however, the terminological distinction between colonial and clonal is rather flexible, and all colonies are potential clones (though all clonal taxa are not colonial). Found in protozoans, sponges, cnidarians, bryozoans, entoprocts, urochordates, and hemichordates, coloniality is widespread within Metazoa (that is, multicellular animals) and important ecologically in many communities. The concept of coloniality is also closely analogous to that of plants as "populations" of node and internode units. Nonclonal organisms, such as most vertebrates, are known as unitary organisms.

Phenotypic plasticity and modular polymorphism are two morphological characteristics that are closely associated with coloniality. Phenotypic plasticity, in this context, refers to the ability of a single genotype to alter the expression of its phenotype across a range of environments (the phenotype is the appearance of a genotype in a particular environment). Although all organisms modify their phenotypic expressions of traits to various extents, the overall morphology of colonial individuals is often especially "plastic" in this way. For example, a branching coral colony growing in an extremely wave-exposed site will tend to grow with its polyps close together in wider branches, thereby forming denser, stouter branches. If one cloned this colony by carefully collecting a branch from this colony and transplanting it to a site with much calmer water, the regenerating coral would likely grow with less dense polyps arranged along thinner, more stretched out branches. Hence, the arrangements of the modules (that is, polyps) that collectively make up the shape of the colony is phenotypically plastic across these two environmental conditions.

Modular polymorphism refers to the ability of colonial organisms to produce modules of different types during their growth. For example, some colonial species produce one type of module to function primarily in the capturing of food, whereas other types are produced for other functions, such as defense against predators or reproduction. Such polymorphisms are actually a specific type of phenotypic plasticity, since within a colony the phenotype of the modules changes while the genotype remains the same. Scientists believe that both general phenotypic plasticity and modular polymorphism provide mechanisms for colonial organisms, many of which remain attached to the benthos throughout their lives, to adapt to their local environmental conditions as much as possible.

Note that an alternative usage of coloniality from the behavioral sciences refers to the close and cooperative living association of unitary (that is, nonclonal) individuals. Such associations are found in kin groups in many species of vertebrates, as well as in social insects and other arthropods.

—*Daniel R. Brumbaugh*

See also: Bryozoa; Cnidarians (Sea Anemones, Corals, and Jellyfish); Sponges

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Communities

An ecologic community is a group of organisms living together in a specific location at a particular time. This is the definition that many ecologists would accept; but the term *community* has been used in many other ways, and no real consensus has ever emerged. Some ecologists would use the definition with which I began, but would add that different species occur together because they share the same environmental requirements or limitations; and some would go further to say that some organisms occur together in such groups because of environmental constraints and because of interactions among the components. Others would stress the vagaries of recruitment and colonization. In the ecologic literature of the last twenty years or so, a community is most often considered to be either the organisms living in a defined space (the "geographic definition"—the ecologist specifies the space) or the local representatives of a higher taxonomic group (bird, lizard, or mammal communities—the "taxonomic definition").

Ecologists have spent a lot of time arguing about what communities are supposed to be and how they should be recognized: whether they are arbitrary units or natural associations, the nature of their boundaries, and the issues of stability and membership rules versus continuous variation and open membership. Some have even suggested dropping the term altogether, and using *patch*, *association*, or *assemblage* to refer to local co-occurrences of species. Others see communities as reflections of local ecosystems, consisting of population systems and at the same time forming the working parts of regional ecosystems. It is at least safe to generalize that when ecologists talk about communities, they are stressing composition; when they talk about ecosystems, the emphasis is on processes. In this sense, description of community patterns provides a picture of the organization of organisms within local ecosystems—in other words, communities are the tangible frameworks of dynamic ecologic systems.

Community Composition

One can think about compositional properties either as parts of an idealistic community concept (the things that make communities what they are) or as attributes that can be measured quantitatively and used in statistical comparisons. One can arbitrarily define the extent of an association of interest, or analytic techniques can be employed to delineate the community. Listed and defined below are some of the most common attributes or properties used in community ecology.

- *Species composition*—A list of the different organisms co-occurring at a particular place or in a sample is the most fundamental characterization of a community. In most studies, a favorite taxonomic group is emphasized, or a functional group of unrelated organisms is the focus of attention. Few community inventories are exhaustive, because of limited taxonomic expertise, desire to study what are thought to be the most revealing parts of an assemblage, or time limitations on the study. The first thing a community ecologist does in a field survey or when processing a sample is to compile an accurate list of the species.
- *Species richness*—Species richness is simply the number of species in an area of interest or a sample unit. The basic measurement of species richness is the most straightforward description of biodiversity. For example, a tree canopy in a Louisiana swamp might contain a hundred species of invertebrates of various kinds, but one in a mature tropical forest in Ecuador might contain more than a thousand. Ecologists want to know what produces such striking differences in richness.
- *Abundance*—The number of individuals belonging to different species is another basic community attribute. When one gives the results of a census in terms of raw numbers of individual organisms, the pattern is one of *absolute abundances;* giving the results in the form of percentages is an expression of *relative abundances;* and ordering species from most to least abundant is the pattern of *rank abundances*. It is also possible to report abundance in terms of biomass, coverage of surfaces, productivity, or other means that relate more to function than simply to numbers of organisms.
- *Species-abundance distributions*—Relationships between species richness and abundance can be portrayed in several ways, and doing so is one of the most important representations of community composition. The basic method involves plotting the log of relative abundances against the rank order of species in a community. The resulting patterns are called dominance-diversity curves.
- *Diversity and dominance*—In ecology, diversity is a measure of the evenness in distribution of the individual organisms among the species present. Communities with few species—and most individuals concentrated in just one of them—are low-diversity assemblages; communities containing many species—with the individuals more evenly spread among the component species—are high-diversity assemblages. The diversity index used by most ecologists is some version of the following formula: *Diversity* $= -\sum p_i \ln p_i$. (In equations such as this, p_i is the proportion [n/N] of each species in a sample; *ln* is the base of natural logarithms.) Dominance can be thought of as the inverse of diversity: communities with low diversity usually have low evenness and are often high-dominance assem-

Table 1
Diversity and Dominance Indices for Four Hypothetical Communities

Species	*Communities*			
	I	II	III	IV
A	75	25	251	50
B	8	23	39	48
C	2	23	38	47
D	1	15	29	45
E			21	45
F			18	42
G			15	40
H			10	39
I			4	36
J			1	34
Number of individuals in each community:	86	86	426	426
Species richness (number of species present, S):	4	4	10	10
Diversity ($-\Sigma\, p_i\ In\ p_i$):	0.48	1.37	1.47	2.30
Dominance ($\Sigma(p_i)^2$):	0.77	0.26	0.37	0.10

Source: Based on Table 19-1 in MacNaughton, S. J. and Wolf, L. L. 1979. *General Ecology,* 2d ed. New York: Holt, Rinehart and Winston.

Note: In both indices, p_i is the proportional abundance of each individual species represented by a population in a community. The values computed obviously are sensitive to both p_i and the species richness, S, and could be compared using simple statistical methods.

blages. One way to estimate this is as follows: *Dominance* = $\sum (p_i)^2$. Table 1 illustrates the application of these formulas in the analysis of different kinds of communities.

- *Functional categories*—Another way to express community composition is to list the species in functional categories (guilds). Imagine an intertidal sandbar containing several species of invertebrate animals positioned mostly at the surface (epibenthic); other species living 5 to 10 cm below the surface (shallow endobenthic); and a few others tunneling 30 to 40 cm below the surface of the loose sand (deep endobenthic). These animals belong to different species that divide the vertical space of the sandbar and collect food at different levels and in different ways. Mobility is greatest among the surface dwellers that produce no tunnels, moderate among shallow burrowers that build temporary domiciles, and essentially absent among the deep burrowers confined to thick-walled tubes. These categories are separate guilds or lifestyle divisions within the sandbar community. One could also simply divide the same community into feeding groups, including photosynthetic *primary producers* (algae, cyanobacteria), *primary consumers* (animals that directly exploit the primary production), *predators* and *parasites*, and *scavengers*. A simple class-frequency (histogram) or “pie” diagram could be used to illustrate the proportions of organisms in the various categories. Obviously, knowledge of the ways of living of the different kinds of organisms would be a prerequisite for recognizing these functional groups.

Organization of Communities

The attributes alone say little about the organization and development of communities and the ecosystems they represent. What are the factors responsible for structure and complexity of food webs in different kinds of communities, or in the same community at different stages of development? Are communities assembled so that they are capable of resisting disturbances, or is community organization entirely a reflection of constantly changing environmental factors or continuous variation along environmental gradients?

What controls the diversity of communities? Are such assemblages subject to intrinsic membership rules, such that only a select subset of the regional biota is ever represented? Or is membership essentially open, with internal organizing processes exerting minimal influence on organization? Are communities a reflection of a discrete functional entity (local ecosystems) consisting of many species interacting to produce the structure we see? Or do variations in colonization (recruitment) and coincidental adaptations of the component organisms account for the composition and structure? Determining the relationships between the parts of communities, how the components work, and how they originated sheds light on these basic questions in ecology.

- *Food webs*—The exact relationships between the members of the various feeding groups are used to map out food webs, which reflect the *trophic structure* (the composition and organization of the energy-materials transfer system). The energy-importing organisms underwrite the requirements of the rest of the components of a community: they provide the fuel that sustains all the organisms connected in the food web. Most food webs are based on photoautotrophic organisms (such as blue-green bacteria, algal protists, and plants), which convert sunlight into biomass. In some communities, chemoautotrophic organisms provide the same service. In terms of absolute abundance and biomass, these primary producers dominate most communities. Many kinds of animals have evolved to take advantage of this resource. These primary consumers may be generalists associated with many kinds of primary producers, or specialization may develop, involving one consumer organism intimately associated with only one producer organism. Secondary and tertiary consumers are the low- and high-level predators, respectively, that exploit the primary consumers. The farther removed from the primary source of energy, in terms of levels in the food pyramid, the fewer are the consumers, although some may be very large. Scavengers and decomposers of various kinds form a recycling loop that returns nutrients and energy to lower levels in the pyramid. A diagram of these relationships, showing exactly which species occupy the different functional positions, is not only a picture of the flow of energy through an ecosystem but also a way to assess complexity in such a system.
- *Other interactions*—Other kinds of connections between component species giving structure to a community include antagonistic interactions (for example, competition for limited resources) and beneficial relationships (for example, commensalism, direct mutualism, facilitation, and certain forms of indirect interaction—as when a predator disrupts a competitive relationship between two consumers). Together with food web relationships involving predation and parasitism, these interactions make up both the internal framework of communities and the functional “wiring” of the local ecosystems they represent.
- *Disturbance and stability*—Environments rarely stay the same for very long. Some are characterized by high-amplitude, aperiodic changes in environmental factors, while others have a periodic or seasonal swing in the defining factors over time. Some environments experience rare disruption or have disturbances (which include the action of organisms) that are small-scale, localized events. Ecologists know that communities in stressful environments often have low species richness, low diversity, and simple organization; communities in more benign environments are richer in species, more diverse, and can be exceedingly complicated in terms of their internal organization. Communities that rarely experience any kind of disturbance, however,

may come to be dominated by one or a few supercompetitors. Thus it appears that an intermediate level of disturbance is required to maintain the most diverse communities, such as those of coral reefs and tropical rain forests. The ability of communities or ecosystems to bounce back to a previous organizational state following a disturbance (resilience) or resist a change in structure in some other way (resistance, persistence) is a reflection of the stability of those assemblages or systems. Communities may recover along more or less repeatable pathways collectively known as secondary succession, in which internal interactions dominate the recovery process. In situations in which the waxing and waning of a community are paced overwhelmingly by outside processes, such as change in climate or nutrient availability, the resulting fluctuations in composition and structure are called *community response*. When assemblages are significantly changed owing to changes in the array of habitats, exceeding any ability to rebound to a previous organizational state, *community replacement* has taken place.

- *Are communities natural associations or convenient fictions?*—One of the longest running debates in community ecology is over the question of the natural reality of communities. Some ecologists have claimed that communities are real biologic entities (or reflect real entities), having a definable life history including a "birth" (establishment, termed *primary succession*), a history of disturbances and recoveries, and an eventual end (replacement); limited membership drawn from a regional pool of potential member species; and internal organization largely resulting from connection between component species (the Clementsian-Eltonian model). Others hold that communities are happenstance assemblages of organisms that are recruited to a site and coincidentally tolerate the conditions prevailing there (the Gleasonian model). All communities owe their composition and organization to the interplay of environmental factors defining the possible habitats (including spatial and temporal variation, or *heterogeneity*); the *disturbance regime* (local departures from the ordinary environmental characteristics—as during storms); recruitment from outside sources; resources, including nutrients/food and space; and interactions with other organisms, including *incumbency* (interference by established occupants) and *facilitation* (early components paving the way for later colonists). Most ecologists would be willing to recognize a spectrum of different assemblages, with some having the attributes of the tightly organized, durable, distinct units of organization dominated by internal connections among species; some appearing to be chance associations of species that share the same environmental requirements or were simply thrown together owing to probabilistic aspects of colonization and having few obligate connections; and some characterized by a mix of both kinds of properties.

—*William Miller III*

See also: Carbon Cycle; Coevolution; Conservation Biology; Coral Reefs; Ecological Niches; Ecosystems; Evolution; Extinction, Direct Causes of; Food Webs and Food Pyramids; Global Climate Change; Habitat Tracking; Hydrologic Cycle; Oceans; Paleontology; Succession and Successionlike Processes

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Compositae

See Angiosperms

Conservation Biology

It makes sense to commence a discussion of conservation biology with a concise definition of the discipline. There are, however, a variety of definitions for this emerging field, ranging from those that focus on the biological elements of biodiversity to those that emphasize integration of the biological and social sciences. Proponents of the former believe that the field should focus mainly on developing biological principles for conservation, often on the assumption that training someone in all the relevant fields will result in practitioners who know a little about many things but do not have the depth of knowledge in biology needed to make effective decisions. Others believe that the social sciences are equally important elements, as it is clear that knowledge of biological principles alone is insufficient for successful management of biodiversity. Political, cultural, and economic factors heavily influence the success of any particular conservation strategy. A number of excellent undergraduate texts on Conservation Biology are currently in use (for example, Hunter, 2001; Meffe and Carrol, 1997; Primack, 1995, 1998; see also http://conbio.net).

For the purposes of this essay, we will define conservation biology as an applied discipline that integrates the natural and social sciences for the purpose of maintaining the earth's biological diversity.

Setting boundaries for the field of conservation biology has been and continues to be a major undertaking. In principle, conservation biology emerges as a distinct field in at least three major ways (Meffe and Carroll, 1997a). First, it is an interdisciplinary field, embracing input from both the social and biological sciences. Biological information is most effective when placed into a political, economic, or social context. Therefore social sciences—philosophy, economics, political science, urban planning, anthropology, and so forth—are often critical to successful conservation measures.

Second, previous conservation efforts were overwhelmingly undertaken at the species level and focused on utilitarian objectives (for instance, high yield of game species). Conservation biology, on the other hand, encompasses all levels of biodiversity (from genes through populations, species, communities, and ecosystems to landscapes), and emphasizes the importance of diverse and functioning ecosystems as well as so-called noncharismatic organisms, such as invertebrates, fungi, and bacteria. Knowledge of the patterns of biodiversity distribution and the processes of evolutionary change are critical to effective management of resources.

Third, as originally conceived, conservation biology is designed to meld theoretical and applied approaches, and though the feasibility of this is still in question, conservation biologists still aspire to this fusion.

Several other general principles underlie (and further complicate) conservation biology. The natural world is dynamic—maintenance of ecological structure and function often depends upon natural disturbances such as fire, flooding, drought, hurricanes, and storms. Conservation biologists try to consider these (often decade-scale) disturbances when making decisions. Lack of data on these issues often compels them to turn to modeling and a focus on large-scale patterns. Conservation biologists use similar approaches as they seek to sustain the evolutionary processes that lead to the generation and maintenance of biodiversity. The unpredictability of the natural world forces them to incorporate uncertainty into their models and decisions. Another important element of the field is that humans must be included in every aspect of conservation planning.

The field of conservation biology is a relatively young one. Impetus for its development arose from heightened awareness of the impact of human actions on the natural world. Conservation biology arguably emerged as a full-scale discipline in the late 1970s, with the First International Conference on Conservation Biology held in San Diego, California, in 1978, and the resulting book, *Conservation Biology* (Soulé and Wilcox, 1980). The attending scientists highlighted the sense of urgency in responding to the increasing scale and scope of species and habitat loss, calling conservation biology a "crisis discipline." They advocated looking at biodiversity broadly, emphasizing diverse and functioning ecosystems in place of a focus on economically valuable or threatened species. Early efforts that set the stage for this movement by fusing evolutionary ecology with resource conservation include Dasmann's *Environmental Conservation* (1959) and Ehrenfeld's *Biological Conservation* (1970).

Scientists from a medley of disciplines (including wildlife ecology, natural resource management, agronomy, forestry, fisheries biology, and basic biological sciences such as ecology, genetics, zoology, and botany) who were writing and researching in the decades preceding the 1980s contributed to the genesis of the field. For instance, the first issue of the *Journal of Wildlife Management* (1937) is replete with references to the "new and growing field of conservation biology" (Errington and Hamerstrom, 1937) and called for study and conservation more than just economically important species (Bennitt et al., 1937). Yet in subsequent years, the focus of wildlife management was predominately on managing game species (mammals, birds, and fish) for sport. Conservation biology arose because none of these individual disciplines was broad enough to address the complex issue of biodiversity conservation.

Studies at the genetic level have been prominent since the emergence of the discipline, because of the fear that increasing fragmentation and decreasing population size would lead to a loss of genetic variation and the concomitant decrease in fitness of wild populations. Conservation biologists use both theoretical and empirical methods to assess the impacts of fragmentation on wild populations. These studies have allowed decision-makers, scientists, and managers to estimate the viability of populations and to guide protected area design. Employing paradigms from evolutionary biology and systematics, conservation biologists have worked to better identify natural units—definitions critical for managing translocation and reintroduction efforts, prioritizing taxa for conservation, tracking trade in endangered species, and designing captive breeding programs for targeted species.

Early species-level conservation efforts in conservation biology concentrated on rarity and loss, exploring how to maintain genetic diversity in small populations. In the mid-1990s, Caughley (1994) suggested that intervening when a population is already in crisis might not be the most effective strategy, and instead recommended that efforts be made to identify and mitigate the factors that lead to declining populations. Both of these perspectives are important for effective management in the field, but individual practitioners may have more use for one or the other, depending upon the problem they are trying to solve. Increasingly, conservation biologists are focusing on monitoring and management of populations.

This increasing emphasis on understanding the causes underlying the declines of species or communities led conservation biologists to consider even larger, ecosystem-level approaches to managing processes that influence many species' status. To develop principles for the design of protected areas, early conservation turned to ecological and biogeographical theories such as MacArthur and Wilson's 1967 theory of island biogeography and the species-area relationship, which describes the interplay between island size, isolation, immigration, extinction, and the number of species that can ultimately inhabit a given island. This concept was adapted for use in fragmented terrestrial landscapes, where reserves become "islands" of natural areas in a "sea" of human-dominated landscapes. Using this paradigm, Jared Diamond (1975) and others developed a set of recommendations for spatial location and shape of terrestrial protected areas.

Although conservation biologists aspire to take an ecosystem approach to studying, managing, and conserving biodiversity, logistics and resources often limit the feasibility of its implementation. One avenue they have taken for large-scale conservation is to design effective systems of protected areas given the distribution of available wildlands and the ranges of species of concern. Rarely do biologists or decision-makers start from scratch in designing systems of reserves, so the first step in a regional system of reserves is to determine what is already protected. A "gap analysis" is often used to compare what is currently protected with what "should" be protected (essentially looking for "gaps" in the protected-area system). This analysis uses satellite remote sensing, geographic information systems, and other techniques to help assess the current status and distribution of biodiversity, to locate areas managed primarily for biodiversity, to identify biodiversity that is not present or is underrepresented in managed areas, and to set priorities for conservation action.

Conservation biologists have recently embraced broader scales (including landscape-level conservation efforts that promote conservation on private lands), as well as newer tools such as adaptive management—essentially learning by doing—developed to help deal with uncertainty at all levels of biodiversity. Each management decision becomes an experiment, testing outcomes against proposed goals. If the goals are not met, an alternative management strategy is proposed, forming another experiment, and so on.

As the field of conservation has evolved, several challenges have emerged. First, there is an inherent tension in the field between academics struggling to capture the complexity and unpredictability of natural systems in bodies of theory and practitioners who need to make finite decisions quickly, often based on little available empirical data. Important basic research on community dynamics, population and community modeling, and levels of genetic diversity contributes to effective management of populations and communities. Baseline data on distribution of species across space are critical to setting priorities effectively and to monitoring populations over time to assess conservation strategies.

However, academics generally do not get credit within their institutions for undertaking applied conservation, and they are often actively discouraged from participating in practical conservation work. Conversely, practitioners ordinarily do not have the time to read the kinds of papers and books for which academics do get credit. The fact is that both perspectives are important to managing biodiversity. As the field continues to develop, this gap clearly needs mending.

A second tension lies with the question of advocacy. Conservation biologists are by definition interested in the preservation of biodiversity. Some fear that using their data to argue for one conclusion or another in the political arena taints their objectivity as a scientist. Others feel that conservation biologists are best placed to offer opinions that influence policy, as they are most familiar with the indications of problems such as population decline.

The complexity of biodiversity, spanning levels from genes to landscapes, and encompassing interactions and processes between and among the levels, sets a cumbersome task for conservation biologists. We know effectively little about how natural systems work and much less about how they respond to perturbations, both large and small. We are just beginning to think about how altered systems can be restored to a "natural state." As humans transform both terrestrial and aquatic environments—for instance, by appropriating extraordinary amounts of primary productivity, by moving species from one ecosystem to another (willfully or no), and by releasing beings created in the laboratory into the environment—the term *natural* takes on new meaning. These are some of the challenges that confront future conservation biologists concerned with maintaining the earth's biodiversity in an increasingly human-dominated world.

—Eleanor Sterling

See also: Conservation, Definition and History; Ethics of Conservation; Organizations in Biodiversity, The Role of; Stemming the Tide of the Sixth Global Extinction Event: What We Can Do; What Is Biodiversity?

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Conservation, Definition and History

Conservation is a term used to describe the prudent use of natural resources: "consumptive and nonconsumptive use without complete destruction/conversion" (Redford and Richter, 1999, p. 1247). It is closely allied, and often confused, with several terms including *preservation*. Preservation is often defined as the maintenance of natural resources free from human intervention. Conservation of an area, for instance, may include selective harvesting of a resource, such as game birds, at a level that ensures the continued existence of that resource over time. Preservation of an area would not allow harvesting of any sort.

The origins of conservation are older than written records, and it is next to impossible to determine what were the first conservation efforts. Myriad examples of conservation activities pepper historical accounts across cultures, regions, and over time. Some of the first recorded laws protecting the remaining forests were decreed in Ur in 2700 B.C.E. Alison (1981) notes that the earliest recorded efforts to conserve natural resources were simple statements of penalties for destroying a designated marshland or cutting down trees unauthorized.

Middle Eastern pharaohs regulated water fowl hunting through licenses, and civilizations from as far back as 3,000 years ago and as distant as China and South America have recorded decrees setting aside land for the protection of plants and animals.

Around 400 B.C., the Greek general Thucydides, one of the first known historians, tried to protect forest lands in northern Greece. When these efforts failed, he turned to writing the history of the Peleponesian War.

The Peloponesian war itself (431–421 B.C.) transformed vast areas to wasteland, resulting in soil erosion and flooding. Theophrastus of Erasia, Aristotle's biographer, developed a theory that linked deforestation to decline in rainfall in Greece and Crete. His writings influenced Rennaissance scholars when his Historia Pantarum was republished in 1483.

Pliny and Vitruvius both wrote about the potentially serious consequences of deforestation, yet no serious efforts to control deforestation emerged in the Roman Republic or the Empire.

Many of the early conservation efforts were undertaken by royalty to exclude the commoners. In medieval Europe, kings and princes set aside royal forest—11,000 hectares in the eleventh century alone—to support game species for royal hunts. Early governmental efforts at conservation, such as the Forest Code introduced in France in the 1300s, focused on reserving resources for government use (in this case, reserving wood products for the French Navy).

A reforestation project near Lima, Peru, to prevent the spreading of the desert. (UN photo/Shawn McCutcheon)

The common people often resented and either ignored or fought edicts put forth by royalty or governments. For instance, in India in 1720, hundreds of Bishnois Hindus of Khejadali died trying to protect trees from the Maharaja of Jodhpur, who wanted wood to fuel the cement kilns to build his palace.

In the late 1700s, Western writers and scientists began to focus attention on the natural world. William Wordsworth (1770–1850), one of the first of the English romantic poets, deemed the Industrial Revolution an "outrage done to nature." In 1835, Ralph Waldo Emerson published his essay "Nature," initiating the American-based Transcendental movement, continued by Thoreau, Fuller, Walt Whitman, and others (see Ethics of Conservation).

The roots of modern Western conservation efforts were born in the European colonial period. The unprecedented scale of ecological change in response to European expansion prompted conservation measures.

These measures themselves were an amalgam of philosophies drawn from colonizers and colonized. Indian and Chinese forestry and horticulture methods, and local classification and interpretation of nature throughout the tropics, heavily influenced European colonists.

In the late 1700s and early 1800s, Alexander von Humboldt, a German explorer and geographer, devoted his life to the natural environment. Von Humboldt championed an ecological concept of relations between humans and the natural world drawn from Hindu philosophers. His work in South America highlighted the consequences for natural areas of cutting down trees in upland areas, as well as for croplands downstream, thus influencing governments to conserve upland forest reserves.

Pierre Poivre, Philibert Commerson, and Bernardin Saint-Pierre, some of the pioneers of modern environmentalism, were concerned about deforestation and its impact on climate and species extinction, as well as the potentially global consequences of European economic activity on people and environments of colonized lands. Their conservation efforts drew on local as well as Indian and Chinese conservation practices. Conservation efforts in Europe itself were developed as foresters returned from their service in the "Empire" with new ideas about the relation between humans and their environment.

The conservation movement in the United States drew its roots from European ideals. The first inklings of citizen-driven action as well as public policy emerged in the mid- to late-1800s. One seminal event in the birth of the conservation movement was the public outcry in 1852 when the "Mother of the Forest," a giant sequoia tree 300 feet high, 92 feet in circumference, and about 2,500 years old, was cut down for display in exhibitions and carnival sideshows. The tree grew in Calaveras Grove, part of what would eventually become Yosemite National Park.

In 1864, George Perkins Marsh wrote *Man and Nature: The Earth as Modified by Human Action,* heralding forest preservation and soil and water conservation. Marsh, von Humboldt, and Ernst Haeckel (1834–1919) were pioneers of environmental science and the scientifically based conservation movement.

Conservation efforts between 1870 and 1910 led to two major developments. The first involved setting aside large tracts of forest that came under federal ownership and were managed for "wise use"—an early term for "sustainable use." Yellowstone National Park, the first national park in the United States and probably the world, was set aside in 1872. The second major development was the use of fire suppression for managing forests, a legacy that haunts U.S. forests to this day.

Two opposing viewpoints dominated conservation pioneers in the United States. The so-called aesthetic viewpoint—termed the romantic transcendental conservation ethic—championed by the likes of John Muir, Ralph Waldo Emerson, and Henry David Thoreau, emphasized the importance of rare species, old growth wilderness areas, and the rights of wildlife. Opposing that philosophy were the pragmatic Gifford Pinchot and Theodore Roosevelt, who led what was called the resource conservation ethic movement. These men forwarded a "multiple-use" concept for the nation's land and water, encouraging logging, grazing, wildlife and watershed protection, and recreation simultaneously. Their emphasis was on rapid productivity, abundance of game animals, and rights of access to resources.

These two philosophies were melded in part by Aldo Leopold in the middle of the twentieth century in a movement now called the evolutionary-ecological land ethic. Leopold provided the philosophical foundation for the development of conservation biology (see Conservation Biology). In his writings, Leopold drew on the analogy of a watchmaker, noting that a watch is not a collection of independent parts but a complex and integrated system of interdependent processes and components. The proper functioning of each part depends on the other components; together they make the watch function. Leopold stressed that a wise tinkerer saves all the parts, explaining that ecological processes are greater than the sum of individual species.

Modern U.S.-based conservation efforts are based on a mixture of the three philosophies. Single individuals had a tremendous impact on the development of these conservation efforts. Theodore Roosevelt, as governor of New York state, fought to develop conservation strategies for the state's forests and rivers; as president of the United States, and working with his chief forester, Gifford Pinchot, he brought conservation to the fore as a national priority for the first time. Rachel Louise Carson, a scientist and an eloquent writer, wrote *Silent Spring* in 1962, calling for an end to indiscriminate pesticide use and, more broadly, a change in the way we view nature. Her literary and scientific focus helped catalyze the formation of a new body of environmental law that fostered the development of conservation biology.

—Eleanor J. Sterling

See also: Conservation Biology; Ethics of Conservation; Preservation of Habitats; Preservation of Species; Stemming the Tide of the Sixth Global Extinction Event: What We Can Do; Why Is Biodiversity Important?

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Continental Shelf

The continental shelf is the part of the continent that extends below the sea to where there is a marked increase in angle—the beginning of the continental slope. This generally occurs at about 130 m, but it can be as little as 50 m or as much as 550 m. Passive continental margins are broad—some as much as 500 km (such as the shelf off Newfoundland) or even up to 1,500 m (for example, the Siberian shelf in the Arctic Ocean). Active continental margins, for example, like parts of the Pacific coast of the United States, may be as narrow as a few tens of meters. Continental shelves on passive sides are flat and have a gentle seaward tilt, about 0.1 degree—a drop of about 2 m for every kilometer.

Many broad shelves contain incised valleys that were cut when sea level was lower, several times during the last glacial period. These valleys are usually extensions of rivers on land and continue across the shelves and become deep canyons where they intersect the continental slope. The Hudson, Ganges, and Congo rivers are examples. Narrow shelves found along the active margins of continents have rocky shorelines and plunge downward after a short distance into trenches.

Wide or narrow, most shelves are covered with relatively young sediments that contribute to their flatness and hide the complex geological structure beneath them—which, for the most part, is the same as that of the adjacent land. The sediments, derived from the continents, are sandy near the shore and muddy in deeper water, but the outer part of the shelf may be covered with coarser sediment deposited when it was near the shore, when sea level was lower. Currents move the sediments around, and underwater exploration has revealed large sand waves on the surface of the sand. When sea level is high, estuaries and barrier beaches develop and trap sediment, reducing the amount that reaches the open sea. More sediment is deposited within the Hudson estuary than is deposited in the adjacent sea.

Shelves in tropical regions may be covered with carbonate biogenic deposits (the skeletons of plants and animals) as well as carbonates that are direct precipitates from seawater. Some shelves are swept clean by fast currents, their sediments carried off and deposited in deeper water.

Even though shelves represent only 8 percent of the entire ocean area, they are most important to people as the main source of fish and other sea life. But, incredibly, they are also the dumping site for all kinds of waste: sewage, garbage, construction debris, chemical by-products, and the like. In addition, the continental shelves are the major sites for oil and gas extraction. They are also the source of sand, the dredging of which disturbs the bottom habitats of plants and animals. Each year in the United States, millions of tons of sand are dredged for beach replenishment.

—Sidney Horenstein

See also: Abyssal Floor; Beaches; Continental Slope and Rise; Oceans

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Continental Slope and Rise

The continental slope and rise marks the edge of the continent. The slope begins at the edge of the shelf, where there is an increase in the downward dip of the surface. Slopes typically have an angle of 4 or 5 degrees, but on charts and cross-sections of the seafloor they are exaggerated to make them clearer to the viewer. Farther down the slope the surface inclination becomes gentler, a decrease that marks the beginning of the continental rise, which typically slopes at an angle of 1/2 degree. The slope and rise are among the least known parts of the ocean basin, but beneath their surface lies the transition between continents and oceans.

Some 8.5 percent of the ocean floor is covered by the continental slopes and rises. Usually a thick wedge of sediments covers them, but occasionally rock outcrops appear on the surface of the slope. Slumping (that is, a downslope composed of sediment and organic debris) and turbidity currents carry sediments beyond the shelf and dump them on the slope, where they stay temporarily until gravity and occasionally earthquakes move the material to the rise and farther, to the deeper seafloor. Additional material, composed both of clastic and biogenic particles, settles down through the water column.

Many of the great rivers of the world, including the Hudson, Amazon, Ganges, and Congo, have submarine extensions on the continental shelf that extend to the slope, where deep canyons are incised into the surface. These submarine canyons are among the most spectacular features on earth. Although they are seen in a variety of sizes and shapes, they usually have steep walls, curving courses, and a tributary system something like the Grand Canyon of Arizona. At the base of the canyon great aprons of fan-shaped deposits are found on the rise, built of sediments that traveled down the canyons. The origins of submarine canyons are not entirely clear, but lowered sea level, faulting, and turbidity currents play a role in their cutting and shape.

—*Sidney Horenstein*

See also: Abyssal Floor; Beaches; Continental Shelf; Oceans

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Convergence and Parallelism

Convergence and parallelism are two very similar evolutionary phenomena. Convergence occurs when species from two unrelated lineages develop very similar adaptations—sometimes to the point at which their identities can be confused. Parallelism is the evolution of similar species from closely related lineages—with the sense that it is more likely that similar organisms will evolve in lineages that are quite closely related. In practice, however, it is often difficult to distinguish cases of convergence from cases of parallelism—and the term *convergence* will be used as a (near) synonym throughout the rest of this entry.

Convergence is one of the most persuasive lines of evidence for the importance of adaptation in the evolutionary process. Because there are often optimal solutions to particular mechanical or design problems faced by animals and plants in their daily lives, natural selection has fashioned similar solutions to such problems time after time in evolutionary history.

Consider the classic example of evolutionary convergence: the body shapes of sharks, dolphins (porpoises), and the extinct ichthyosaurs. The body is fusiform in many species within each of these groups—that is, streamlined for the rapid swimming needed for a predatory mode of existence. Although early observers were confused by the superficial similarity between sharks and dolphins, biological research soon showed that sharks are a type of primitive cartilaginous fish (see Chondrichthyes), while dolphins, with their mammary glands, three middle ear bones, and placental development of the young are just as obviously true mammals. When ichthyosaurs were discovered in the nineteenth century as fossils of the Mesozoic Era, it was soon realized from the details of the bones in their heads that, whatever their dolphinlike shape might suggest, they were actually a unique group of reptiles.

Similarly, the wings of birds, bats, and the extinct flying reptiles known as pterosaurs were also developed in separate evolutionary histories. That bats are mammals is obvious from the presence of hair plus the other mammalian features mentioned above for dolphins.

That birds are actually a kind of surviving feathered dinosaur—which were reptiles—is perhaps not so obvious, but it is nonetheless the conclusion of paleontologists and anatomists. Birds share many features with dinosaurs like *Tyrannosaurus rex*. On the other hand, the pterosaurs, though Mesozoic reptiles like dinosaurs, were nonetheless not as closely related to the dinosaurs as are modern birds. Moreover, the internal bony structure of the wings of birds, bats, and pterosaurs is different—each group having a different configuration of the webbing or feathers attachment to one or more of the fingers of the "hand" of the forelimb. This in itself is clear evidence that the similar-looking wing of each of these groups has been evolved independently from separate four-legged ancestors.

But convergence can take on a larger dimension—as when even larger scale groups appear very similar and often occupy the same general niche. As an example of what perhaps might be best considered as "parallelism," the Rugosa, one of the major groups of corals that lived almost the entirety of Paleozoic time, became extinct in the great mass extinction in the Late Permian Period (the so-called Permo-Triassic mass extinction of 245 million years ago, the greatest of all mass extinctions to have struck life so far). For several millions of years thereafter, there were no longer any corals left on earth. But then modern corals (Scleractinia) suddenly appeared. Anatomical and molecular biological (genetic) evidence indicates that the closest relatives, living or extinct, of modern corals are sea anemones, which live just like corals but lack the calcified external shell of true corals. Paleontologists now believe that modern corals evolved from the naked sea anemones after the Rugose corals of the Paleozoic had become extinct—an example of parallel evolution from another branch of close relatives.

—*Niles Eldredge*

See also: Adaptation; Chondrichthyes (Sharks, Rays, Chimaeras); Cnidarians (Sea Anemones, Corals, and Jellyfish); Evolution; Mammalia; Mass Extinction; Natural Selection

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Coral Reefs

Coral reefs are among the most diverse and productive biological communities in the world, though their future status appears increasingly threatened from widespread changes in tropical marine systems. Dating back approximately 30 million years, "modern" coral reefs may contain as much species diversity as tropical rain forests—or even more—though reefs are much richer in terms of higher-level diversity (for example, orders, classes, and phyla). Estimates of coral reef species richness range from 0.618 to 9.47 million species, with intermediate estimates of around 1 to 2 million species. Phyletic richness includes thirty-two of thirty-four phyla (compared with nine in rain forests and sixteen in tropical freshwaters). Such biological diversity is especially notable given that coral reefs, covering an estimated 284,300 square kilometers, take up just 0.089 percent of the world's ocean surface, less than 1.2 percent of its continental shelf area, and 2.9 percent of its tropical coastal areas. Moreover, coral reefs thrive in some of the least fertile (that is, oligotrophic) waters, where low levels of dissolved nutrients prevent substantial planktonic productivity. Rather than being plankton dependent, reef production relies on the existence of particular benthic animal-plant symbioses, especially those between many corals and single-celled, dinoflagellate algae known as zooxanthellae. Photosynthesis by zooxanthellae living inside coral tissue allows these coral colonies to act, at least in part, like plants: algal photosynthetic metabolites supplement and often surpass the nutrients that corals capture directly from prey. Because of this extra, plantlike growth ability, zooxanthellate corals are typically the most productive and important reef-building (also called hermatypic) coral species, with the trophic efficiency of the symbioses contributing to the high productivity of these ecosystems. In turn, this productivity, coupled with the rich, three-dimensional habitat complexity produced by corals and other sessile organisms and the accelerated rates of evolution that seem to be typical of tropical environments, has led to the massive proliferation and radiation of life in coral reef ecosystems.

Unfortunately, the health of coral reefs appears to have declined substantially over the last several decades. Coral reefs are now threatened globally from a variety of factors, and as these ecosystems continue to degrade, so too will the various benefits provided by reefs, upon which many people depend. These benefits include food from artisanal and commercial fisheries (for which, on many small islands, there are no alternative sources); recreational opportunities; employment in fisheries and tourism; coastline protection against waves; calcium carbonate (limestone) for natural beach replenishment and for building materials (as sand and rock); genetic resources for traditional and new medicines; collectibles such as pearls, shells, and corals used for jewelry and curios; as well as live animals for the aquarium trade. Since the maintenance of these potentially renewable resources depends on retaining healthy, intact coral reef ecosystems, these resource uses must be balanced and sustainable, a goal that is still far from being realized.

Despite the consensus on their importance to biodiversity and to humans, there are a wide range of definitions regarding what constitutes a coral reef. This situation arises from the various ways in which coral reefs have been valued and studied over the last few centuries. European explorers of tropical seas initially defined coral reefs simply as those navigation hazards (that is, reefs) associated with corals. Most current scientific definitions, however, center on certain geological and ecological features. Geologists have focused their interest and definitions on the biological processes and patterns of carbonate production, regardless of whether the resulting carbonate is shallow enough to obstruct boating. Coral reefs are therefore those biogenic (that is, biologically created) carbonate frameworks that have built up and continue to grow through the actions of scleractinian corals and other sessile organisms over decadal and longer time periods. Reefs that have previously developed, but no longer do, are considered to be fossil reefs. In contrast, some ecologists extend the concept of coral reefs beyond such structural definitions to nonstructural coral communities, where coral species play important ecological roles as primary producers, filter-feeding consumers, and contributors to habitat complexity even though the communities have no net carbonate production. In these systems, despite the possible presence of reef-building corals, ecological and physical processes such as bioerosion, dissolution, disturbance, and export of rubble prevent the gradual geomorphological buildup of limestone beyond a thin veneer of living and dead corals.

Where carbonate frameworks do develop, scientists generally recognize several broad categories based on their proximity to land. Reefs running close to (that is, less than 1 km) and parallel to the shoreline are called fringing reefs; those developing farther offshore (more than 5 km) and parallel to the coast are barrier reefs; and circular reefs forming around subsided oceanic volcanoes are atolls. In some places, there are also reefs that appear to fit intermediate categories, such as the so-called bank-barrier reefs, which lack the deep lagoons of true barrier reefs, and bank or platform reefs, which may be similar to atolls but which develop on submerged hills or pinnacles rather than around subsided volcanoes.

A number of different reef zones or geomorphological features are also frequently recognized within a given reef system. Depending on the underlying topography, the age of the reef, or the exposure to waves, however, individual reefs may lack one or several of these zones or features. The reef crest is classically the shallowest part of the reef, where incoming swells may break into waves. A reef flat may occur immediately behind the reef crest, followed by so-called back reef areas bordering or extending into a lagoon if there is one. Fore reefs and reef slopes occur in front (relative to the dominant direction of wave exposure). Patch reefs are generally considered to be smaller structures that lie within lagoons behind other reefs (for example, barrier or atoll reefs).

Coral reefs, as structurally defined above, are largely restricted to shallow tropical seas, where a combination of warm water temperatures, high light levels, high water clarity, and low nutrient concentrations provide the conditions under which reef-building corals thrive. Found primarily between 30 degrees north and south latitudes, and along the western sides of ocean basins (for example, the Indo-Pacific and the Caribbean), these conditions have lasted continuously over a much longer evolutionary period and across a wider area in the Indo-Pacific. The result has been the evolution of dramatic species richness there.

As one moves to higher latitudes, coral reefs generally become rarer as water temperatures drop. Most reef corals cannot survive temperatures of 16 to 18 degrees centigrade for prolonged periods, either because of direct mortality or because their growth rates decline to the extent that they are susceptible to being overgrown by macroalgae. Although coral reefs, as conventionally defined, may disappear in these cooler waters, it is important to note that there are temperate and even subtemperate species of non–reef building corals that contribute to nontropical coral communities. In some cases, such corals (for example, *Lophelia*) even form extensive, deep sea carbonate frameworks that qualify in many ways as reefs, though these structures remain less cemented and looser than in shallow tropical reefs.

At the regional and local scales, coral reefs also tend to develop more extensively around islands or off the shore of continents. This is due to the fact that substantial freshwater, sediment, and nutrient runoff from large rivers either kills or impedes the growth of corals.

A number of general threats to coral reefs are known, including overexploitation of marine populations, pollution, habitat destruction and degradation, climate change, and invasive species. In practice, since reefs are found predominantly in developing countries, these ecosystems tend to face both the common environmental impacts relating to poverty (rapid population growth, poor nutrition, low literacy rates, lack of infrastructures for environmental mitigation and enforcement, and so forth), as well as the larger-scale, global impacts that are being driven by developed nations.

Given the paucity of alternative sources of protein and income on small islands, many poor human communities within reef ecosystems are currently forced to contribute to the overexploitation of reef biota. Unfortunately,

Underwater coral formations of the Great Barrier Reef (E.O. Hoppé/Corbis)

many reef species are especially susceptible to this overfishing. For example, large, territorial, slow-growing, and late-maturing predatory species with high economic value as table fish are easy to overfish because of the slow recovery times of such populations. Similarly, slow-growing red and black corals can be easily overexploited by those selling to the jewelry trade. Although the aquarium trade tends to favor smaller, faster growing species, the large international demand for certain species can also easily lead to the strip mining of these resources from local reefs. Beyond simply removing individual species from reefs, overexploitation tends to remove whole ecological groups of species, such as large fish predators and herbivores, thereby causing fundamental (and difficult to reverse) changes in the way these reef communities function.

The major form of pollution on reefs is nutrient enrichment, the result mostly of the runoff of sewage and agricultural wastes. Enrichment can alter reef community dynamics is various ways, with the major direct effect being to enhance the growth of benthic and planktonic algae. Since benthic macroalgae often compete with corals for space and light on reefs, increased algal growth can lead to the overgrowth and death of corals. Planktonic blooms (that is, rapid increases in populations) of algae may also favor other coral competitors, such as filter-feeding sponges and zoanthid cnidarians, which collect small, drifting organisms or bits of food from the plankton. Sedimentation from coastal and inland development, deforestation, and agricultural activities is also problematic for reef-building corals, smothering them if intense enough, and otherwise diminishing their competitive abilities.

The destruction and degradation of coral reef habitats is sometimes intentional, though more often it occurs as a by-product of other activities. For example, when ports decide to dredge and destroy relatively small areas of reef during the construction of channels, the consequences of the altered circulation and wave exposure patterns often lead to unintended but more widespread habitat degradation from sedimentation and storm disturbances. Similarly, the deforestation and conversion of mangrove habitats for shrimp aquaculture frequently have many indirect effects on nearby coral reefs, including increased sedimentation and the loss of nursery grounds for reef species. Even fishers who depend on reefs for their livelihoods, and who do not intend to harm reef habitats, use certain techniques that contribute to extensive reef damage and degradation: anchoring on fragile corals; using nets that become lost and entangled on reefs; using toxicants such as sodium cyanide and chemical bleach to stun animals; and especially "blast fishing" with explosives to nonselectively kill whole assemblages of fish (as well as their living habitats).

Although environmental tolerances of reef-building coral species can be relatively broad across their whole range, coral populations in particular places seem to have evolved relatively narrow tolerances (for example, 4 degrees centigrade is the normal range of annual temperatures experienced by corals on a reef slope). These environmental requirements make corals and other reef species especially vulnerable to climate change, particularly the periodic warmings of surface waters in the ocean that cause mass "coral bleaching" events. Coral bleaching (not to be confused with the use of chemical bleach mentioned above) refers to the dramatic whitening in a coral's appearance that results from the loss of its symbiotic zooxanthellae, or the zooxanthellae's loss of its photosynthetic pigments. Bleaching can be caused by various stresses, such as exposure to pollution, air, high levels of UV radiation, and extreme temperatures. Of these, thermal factors seem to have the widest impact, and increases in water temperature of 1 to 2 degrees centigrade above the normal maximum for a period of several weeks are sufficient to cause mass bleaching events, affecting a significant fraction of coral colonies and other zooxanthellate taxa. Corals can often recover from mild or even moderate bleaching, but severe bleaching leads to death. Some coral populations seem to have evolved greater resistance to bleaching, but it is uncertain whether other populations can similarly adapt to changing sea temperatures.

In addition to predictions of increased bleaching with climate change, there are other predictions that subtle changes in the chemistry of sea surface water, resulting from the absorption of higher levels of atmospheric carbon dioxide, will reduce the ability of corals and other calcareous species to grow their skeletons. As this occurs, it will likely shift the balance between carbonate production and erosion toward the latter, causing some reefs to gradually lose rather than gain material. Given that this shift away from reef buildup will occur during the same time that sea levels are expected to rise (via thermal expansion of water and melting of the polar ice), the consequences for reef ecosystems, including those human communities relying on reefs, is expected to be substantial.

Although these threats to reefs are widespread, they differ in importance and differentially interact, depending both on the region of the world and on the local socioeconomic conditions. For example, blast fishing is much more common in the Indo-Pacific than elsewhere, and diseases of sea urchins, corals, and sea fans, presumably caused by invasive pathogens, are especially widespread and damaging in the Caribbean. Since the incidence of these diseases has increased in the last few decades, it is likely that stresses from other factors (for example, nutrient and sediment pollution, competition with algae, and thermal stress) are causing marine organisms in certain regions to become increasingly susceptible to disease. At local scales, overexploitation of reef species and pollution both have dramatic effects on reefs, though the latter impacts (including both sedimentation and sewage releases) may be especially exacerbated near human settlements; the effects from overfishing may be more widespread, given a well-developed commercial fleet and expanding economic demand. Certain industries, such as tourism, may also affect reefs in multiple ways—for example, by causing more pollution from coastal development, by driving up the seafood demand in restaurants, and through physical impact on reefs by poorly trained snorkelers and boaters.

Given this onslaught of diverse threats, what conservation efforts can help to protect these valuable but fragile ecosystems? Apart from critical, long-term efforts to stabilize human populations and achieve reductions and greater equity in our consumption of resources, coral reef conservation efforts have focused on several core areas, including better education of the public and decision makers about the importance of coral reef ecosystems, and ways to increase ownership of reef resources and responsibility for their management.

Although many traditional societies formerly had extensive rules governing the sustainable use of coral reef resources, modern societies have generally treated their marine resources as relatively open and readily exploitable (or degradable) by anyone. Since such open access frequently leads to a race to exploit and take advantage of resources before others can, the establishment (or reestablishment) of various legal controls for ownership, stewardship, or other modes of responsibility are essential for coral reef conservation. Such responsibilities need to be allocated not just among coastal communities but also between coastal and inland jurisdictions, in order to prevent upstream activities (for example, careless deforestation practices) from having severe downstream effects on coral reefs.

With ownership and a shared value of stewardship for future generations in place, the tendency for short-term benefits to outweigh long-term benefits is reduced, allowing groups to balance opportunities for present and future resource use. Indeed, abundant evidence shows that, in cases where communities are relatively cohesive and heavily dependent on their natural resources, these groups can effectively and sustainably manage their resources if allowed to do so. Other communities may require alternative methods of cooperative resource management, comanagement between communities and national authorities, or even exclusive management by the latter.

Because of the ease of overexploiting many marine species, better stewardship requires some limitation of fishing practices. Such restrictions may affect the number and identity of people allowed to enter the fishery, the types of fishing gear or technologies that can be used, the species that can be caught, the numbers that can be caught, the time periods when they can be caught, or the places that they can be caught. In many locations, these options are tailored in species-specific ways that require substantial knowledge about the natural history and local ecology of each exploited species, as well as intensive monitoring and enforcement. Alternatively, some of these rules can be implemented in broader forms that simultaneously address the needs of multiple interacting species and their habitats.

The use of marine protected areas (MPAs), especially marine reserves that restrict the exploitation of all species, provides one example of an "ecosystem management" approach. MPAs have proliferated in recent decades, and many have suggested that marine reserves are particularly appropriate for coral reef ecosystems. By protecting habitats and providing refuges to populations that are particularly vulnerable to overexploitation, marine reserves can rebuild overexploited populations and enhance surrounding fisheries in relatively short periods of time (for example, two to five years). Coral reef MPAs also provide sites for economic development of nonconsumptive uses of protected marine resources, such as dive tourism. Revenues from tourism in areas with large fish populations and healthy reefs frequently surpass those from nearby fisheries. Of course, for tourism to be part of an effective conservation strategy, part of the revenues from tourism must be directed to the management of the resources, and potential negative impacts of the tourism need to be monitored and strategically managed.

The suite of conservation approaches for coral reefs also includes mariculture—the farming of marine life for food, the aquarium trade, and for reef restocking—as well as other forms of reef restoration. These areas, despite various scientific controversies and uncertainties, warrant further research. Because of ongoing losses to coral reef ecosystems, successful conservation will eventually require not only approaches for preventing further degradation (for example, marine reserves) but also techniques for active and widespread recovery of degraded ecosystems.

Finally, more effective communication is needed between reef scientists, conservationists, the public, and decision-makers. Public awareness of the ongoing crisis in coral reef ecosystems remains low, hampering the ability of well-intentioned decision-makers to make positive changes to conservation policies. More effective cross-sectoral attention to reef conservation will likely only occur after enough people become aware of the ecological, cultural, and economic importance of coral reefs, their current downward trajectories, and the cost-effectiveness of active management of these resources. As awareness of coral reef issues increases, other methods of conservation, such as consumer choice in seafood, aquarium fish, and ecotourist destinations, will likely become more viable and effective. Although environmental interests are too often latent within the larger public, market-based conservation tools—assisted by "ecolabeling" certification programs—offer immense potential in harnessing and directing these interests once they manage to cross the critical threshold of public attention. Such private sector approaches to conservation will become increasingly important complements to local and national regulation as economic globalization continues to expand this century.

—Daniel R. Brumbaugh

See also: Adaptation; Benthos; Carbon Cycle; Cnidarians (Sea Anemones, Corals, and Jellyfish); Coloniality; Communities; Ecosystems; Extinctions, Direct Causes of; Food Webs and Food Pyramids; Lagoons; Protoctists

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Creationism

See Evolution

Cretaceous-Tertiary Extinction

The Cretaceous-Tertiary (K-T) mass extinction defines the K-T boundary and represents one of the five largest biotic crises that punctuate the Phanerozoic record. The broad consequences of this event on the earth's biota can be seen in that it demarcates the transition from the Mesozoic ("middle life") into the Cenozoic ("modern life"). During this interval numerous groups that had dominated both marine and terrestrial Mesozoic ecosystems disappeared or suffered substantial reductions, whereas the aftermath—especially within the terrestrial realm—is characterized by the rise to dominance of new animal and plant groups. Furthermore, interest in the K-T boundary has been focused on the question of causation. This mass extinction event has the clearest record of extraterrestrial impact, as well as additional evidence for flood-basalt volcanism. This evidence has given rise to a lively and often contentious debate on the nature of geologic data and how these data relate to the fossil record across the boundary.

Environmental Setting

The K-T boundary occurred during a period of gradually declining global warmth and retreating sea levels, although the overall conditions are still considered "greenhouse"—that is, the dominant climatic mode of the Cretaceous. Superimposed upon the general thermal and sea level trends are two important shorter-term events that influenced the paleoenvironment: (1) the extrusion of the Deccan Traps, a voluminous flood basalt that erupted in and covered much of west-central India; and (2) a bolide impact. The Deccan Traps represent a series of eruptions that produced an estimated 512,000 cubic kilometers of basalt. Based on the most recent radiometric dates measured from the various flows, the eruptions commenced approximately 67 million years ago (that is, roughly 2 million years prior to the K-T event) and ceased at 65 million years ago (soon after the K-T boundary).

The evidence for an impact directly at the K-T boundary was initially proposed based on the large increase in iridium found within sediments from this interval. Iridium is generally found in extremely small quantities at the earth's surface, but in a study of the element through the Maastrichtian (the last stage of the Late Cretaceous) strata of Gubbio, Italy, extremely high concentrations were found. Because there are no known terrestrial sources capable of producing such an increase in iridium, an extraterrestrial source—namely, an iridium-rich meteorite—was suggested as a source. After this initial discovery, not only were iridium anomalies found in sections globally, but other indicators of impact—such as shocked quartz, potential soot layers, and evidence for acid rain—were also found. The primary missing component of impact was a crater—the so-called smoking gun. Finally, in 1991, scientists rediscovered a subsurface feature in the Yucatan, the Chicxulub structure, and after extensive investigation concluded that this crater was of the proper age and proper size, as hypothesized by the available data for the impact event.

A more detailed examination of the record suggests that the interval surrounding the K-T boundary was one characterized by substantial fluctuations in the atmosphere-ocean system, as reflected in various geochemical proxies, especially $d_{18}O$ and $d_{13}C$, that are used to monitor paleoconditions. Approximately 1.5 million years ago, prior to the boundary, there was a pronounced oceanographic event that is believed to indicate an important decrease in deep-oceanic temperatures. Furthermore, the K-T boundary itself records a dramatic geochemical event termed the Strangelove Ocean, and this has been interpreted as a major disruption of carbon cycling in the oceans, tied to a pronounced reduction in primary productivity.

The Biotic Impact

Given the various changes across the K-T mass extinction that may have affected the fauna and flora through the interval, it is critical to examine the biotic record in detail to determine the nature of the biotic response. From a broader overview, however, estimates of the level of extinction of higher taxa across the K-T boundary suggest that approximately 15 percent and 37 percent of marine families and genera, respectively, went extinct, with potentially higher rates for the terrestrial biota. Furthermore, there is abundant evidence that both marine and terrestrial organisms were affected by the events, suggesting that the causal mechanism(s) had to have global impact. The boundary is marked by the complete disappearance of a number of important terrestrial and marine groups, including non-avian dinosaurs, ammonites (shelled cephalopods), rudistid bivalves (the primary reef builders of the Late Cretaceous), and inoceramid bivalves. Furthermore, many marine and terrestrial ecosystems and the species composing them—such as mammals, plants, bivalves, gastropods, brachiopods, bryozoans, and numerous members of the plankton family—suffered significant reductions, which in some cases led to the disappearance of various communities, such as reefs, for extended periods following the extinction.

Examining the available data in more detail reveals important extinction patterns, as well as geographic differences that offer insight into the event. First of all, there are important extinction events that precede the K-T boundary. The reef-building rudistids as well as the inoceramids, both mollusks, go largely extinct approximately 1.5 million years prior to the boundary. The virtual extinction of these groups—which dominated reefal as well as most epifaunal marine communities during the Late Cretaceous—suggests that there were important environmental changes occurring prior to the boundary that were beginning to stress a biota that had evolved under greenhouse conditions. Furthermore, a number of groups show accelerated levels of extinction prior to the boundary, and it is possible that this was coupled with a reduction in species origination that resulted in decreased biodiversity. Against this backdrop, there is also abundant evidence, especially from marine planktic groups, such as foraminifers and coccolithophores, that there was a dramatic extinction event directly at the K-T boundary. This event has also been documented in certain floral studies, suggesting that the perturbation affected both marine and terrestrial habitats. Therefore, the overall pattern is one of an initial interval of declining diversity punctuated by a dramatic biotic event directly at the boundary.

From a geographic perspective there are also several important trends that have been documented. First of all, within the marine realm, whereas planktic groups and other shallow-water marine organisms suffered significant reductions, deep-marine taxa, such as benthic foraminifers, were unaffected by the event. Additionally, within the affected environments, the data suggest that tropical regions suffered a greater degree of extinction than did higher latitudes. For example, whereas rudist-dominated, platform reef communities were completely destroyed, the mass extinction primarily reorganized the taxonomic composition of higher-latitude communities. Secondly, within the terrestrial realm, higher-latitude faunas, especially those in North America, suffered significant changes in diversity and abundance, although a similar pattern has been documented in other areas. In many cases, the so-called fern-spore spike directly overlies the iridium layer, suggesting that the flora underwent a drastic, albeit fairly short-lived, compositional change. However, the tropical flora, which are generally less resilient to changes in the earth's climate, apparently suffered little to no change through the interval.

Analyzing the Evidence

One of the advantages to studying the K-T mass extinction is that, at least from the perspective of geologic time, it is relatively recent. This results in a much more completely preserved geologic record than for any of the other so-called Big Five mass extinctions. To evaluate the effects of these biotic crises, it is critical to have continuous sections that represent a wide spectrum not only of different geographic settings but also of various paleoenvironments. This increases the likelihood that global effects can be distinguished from local changes. For the K-T boundary there are a wide variety of different sections that have been studied on all continents. Furthermore, because there are a large number of cores that have been recovered through deep-ocean sediments across the boundary in numerous places, the geographic distribution of fossiliferous sediments is excellent. Furthermore, these sections represent a variety of depositional environments that compose marine as well as terrestrial sections, making possible a comprehensive analysis of the extinction dynamics.

An important component to consider when attempting to unravel the dynamics of a mass extinction is how the pattern of biotic response (for example, biodiversity changes and variation in community structure) compares with what would be expected from the presumed effects of the hypothesized extinction mechanism. Different mechanisms should produce distinct patterns, with unpredictable, short-lived events like bolide impacts resulting in the catastrophic extinction of numerous taxa and the instantaneous disruption of widely variable ecosystems; more predictable, longer-term events, such as climate or sea-level change, would be expected to produce more gradual, ecologically graded mass extinctions. Discerning biotic patterns from the geologic record is, however, confounded by a number of thorny questions.

Firstly, the fossil record is notoriously incomplete, and this hinders attempts to accurately determine the stratigraphic ranges of the various taxa. Secondly, there are various measures that can be used to analyze the biota, ranging from compilations at familial and generic levels, to the stratigraphic ranges of individual species, to the abundance of individuals within individual taxa. The questions being asked play a large role in determining which approach offers the best data to answer the question. For addressing the issues related to the short-term biotic response to mass extinction events, stratigraphic ranges (used to investigate changes in local to global biodiversity) as well as abundance (used to determine changes in ecologic structure) offer the best measures. However, it is also critical to have sufficient knowledge of these variables during "background" intervals, so that changes forced by the mass extinction can be differentiated from variability inherent within any ecosystem and its constituents. Finally, to evaluate the long-term evolutionary impact of a mass extinction event, it is important to be able to track individual ecosystems over time.

Biotic Recovery

One of the commonly overlooked elements of mass extinctions is the postextinction biotic rebound. It is obvious that the biota recovered from this mass extinction, and this implies that there must be a number of surviving stocks from which this new biodiversity is derived. Following the K-T event, most ecosystems, with the notable exception of shallow-water reefs, recovered geologically rapidly, especially in light of the intensity of the extinction. The biotic response appears to be largely controlled by the duration of the environmental perturbations, and to be based on various geochemical proxies; the environmental disruption at the K-T boundary, although severe, extended only into approximately the initial 500,000 years of the Paleocene. During that interval, taxa with broad ecologic tolerances thrived under highly variable environmental conditions. This is exemplified by the dominance of ferns, a group with a relatively long geologic history that today is often one of the first colonizers following environmental devastation. There are, however, important differences, especially in terrestrial ecosystems, between Late Cretaceous and Cenozoic ecosystems. The best-documented change is the transition from nonavian dinosaurs to mammals within terrestrial vertebrates. In addition, more subtle changes—but of potentially critical ecologic significance—occurred in many other marine and terrestrial ecosystems, in which taxa that dominated Cretaceous ecosystems either went extinct or lost their dominance across the boundary.

Lessons for the Present Biodiversity Crisis

Given the current rate of biotic extinction, it is critical to look for an analog from the geologic past to use as a potential model for the future of the earth's biota. The biotic response to the K-T boundary shows that the extinctions occurred over an interval of approximately 1.5 million years, and that the bulk of them occurred in close association with the Chicxulub impact. This suggests that environmental conditions were deteriorating at the close of the Cretaceous, initiating the extinction of various biotic elements, such as the inoceramids and rudistids, and also stressing other biotic elements. Because conditions were already in flux, the addition of the short-term, intense disruptions caused by the impact had a pronounced effect upon the biota. Clearly, humans are causing various environmental and ecologic disruptions, and those disruptions, be they through overhunting or chemical emissions, are creating a biota at risk. However, because of the differences in causation, these analogies can be carried only so far. The K-T boundary and the other documented mass extinction events were all forced by changes in environmental factors. In the current case, the extinctions are being forced by a biotic element: humans. Therefore, the lessons learned from an analysis of the fossil record may best serve to show how life will rebound, although they will be unable to predict the path of the current crisis.

—Peter J. Harries and Neil H. Landman

See also: Adaptive Radiation; Mass Extinction; Mollusca; Valuing Biodiversity

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Crinoids

See Echinoderms

Crocodilians

See Reptiles

Crustaceans

See Arthropods, Marine

Cultural Survival, Revival, and Preservation

The potential loss of traditional lifeways and distinctive cultural groupings poses a special threat in an age of rapidly accelerating modernization and globalization. Culture, as a system of learned norms and behaviors, is not a tangible thing but a process composed by living individuals. The struggle by small, often dispossessed native groups to sustain their traditional modes of livelihood, religions, languages, customs, and rights is an attempt to maintain distinct identity in the face of homogenizing pressures from the larger and more powerful societies in which they must live.

Throughout history, cultures have adapted, assimilated, and changed. Except for cases of sudden mass extinction of entire peoples, they rarely disappear without a trace; rather, certain traits are passed along and become part of new cultural formations. Even cultures and peoples considered extinct—societies that have disappeared because of invasion, war, famine, disease, or intermarriage—leave living legacies in their influence on other groups and their own mixed-blood descendants. The possibility for renewal depends on prevailing definitions of race, ethnicity, and culture. Definitions of aboriginality are increasingly tied to land claims and official status. Historically, blood quanta and racial theories have been used to discriminate against people. At the turn of the twenty-first century, however, in many places there are some advantages to claiming official minority ethnicities, often in states where native status had previously been more of a hindrance than a help.

Many groups known in prehistory and history have died out, from protocultural formations encountered in archaeological excavations like the Diukhtai of northern Asia to the mighty Aztec empire following the European invasion. The Taino, Arawak, and Carib peoples of the Caribbean rapidly died off shortly after the arrival of Columbus in 1492. Disease, caused by imported germs to which native Americans lacked immunity, was the main cause of ethnocide in a holocaust of cataclysmic proportions. An estimated 1 million people lived on the island of Hispaniola in 1492. A mere twenty-six years later, the island's indigenous population had declined by some 98.5 percent to around 15,000. The Caribs, with a population estimated at 3.79 million in 1492, were declared extinct in less than a single generation. In the nineteenth century, the death toll of smallpox and other diseases in the Americas was devastating. On the northwest coast of North America, a disastrous decline in the Indian population was the tragic result

Plowing the ground in a traditional manner, Egypt (UN Photo)

of a smallpox epidemic, spread through blankets distributed to the Indians by the English.

As with habitat range and endangered animal species, land is vitally connected to the viability of distinct small native populations. The dependence of Saami and Evenki peoples in Lapland and northern Russia, respectively, on reindeer breeding and herding means that their continued existence as distinct peoples is threatened by the loss of this way of life. Sea-mammal hunters in the circumpolar Arctic have adapted their traditional means of subsistence to new ways of life and economic modes.

At the 1992 Earth Summit in Brazil, the World Conference of Indigenous Peoples on Territory, Environment and Development issued a statement asserting inherent rights to self-determination and inalienable rights to land, territories, resources, and environments. The urgent concern of sustaining and empowering endangered cultures through land reform and other measures has emerged in the decade since as a global human rights issue.

Tasmanians reemerged at the end of the twentieth century as a surviving people, with an altered but continuous heritage. The aboriginal Tasmanians were thought until recently to have died out entirely, victims of the European invasion. Prior to the arrival of Europeans, the aboriginal population of Tasmania was comparable to that of mainland Australia. The 1642 population was estimated at some five thousand; two centuries later it had fallen to a recorded low of just six individuals. During the 1820s, pastoralist settlers expanded their land holdings in a series of conflicts known as the Black War, forcibly driving the starving Tasmanians off their island. Before her death in 1876, a woman named Truganini became famous in Europe as the last surviving Tasmanian. During the twentieth century, Australians with aboriginal Tasmanian ancestors blended invisibly into the population. With no incentive for self-identification, descendants of the Tasmanians did not declare themselves as such until changes in state policy and benefits were enacted in the early 1970s. The official census figure showed a more than fourfold increase in aboriginal Tasmanian self-identification between 1971 and 1976. The figure more than doubled again over the next decade, growing at a rate some three times that of the aboriginal population in Australia at large, to 6,716 in 1986. The many descendants of the Tasmanians went unrecognized by majority white Australians because they are of mixed heritage, and their physical appearance no longer resembles the once typical dark-skinned aboriginal profile. In the face of land claims and a growing movement for social justice, Tasmanian people are reasserting their identity and claiming a status tying them to the land and its resources.

Cultural survival, revival, and preservation initiatives are tied to the establishment and maintenance of protected zones such as biosphere preserves, game parks, and forests. Land and habitat are keys to sovereignty and ethnic survival for the Yanomami of the Amazon as for the Ainu of northern Japan. The rhetoric of ecological and ethnic extinction reflects the threat to both cultural diversity and biological diversity. The impact of the environmental and economic changes brought about by modernity and development has ruptured long-established patterns of human-nature interaction. The loss of environmental knowledge encoded in traditional cultures proceeds in parallel with the loss of endemic species. The emerging paradigm of biocultural diversity looks at ecosystems as a whole, including the dynamics of human-nature interactions and seasonal variants.

The remarkable comeback of the Mashantucket Pequot nation in southern New England provides a dramatic illustration of how the continued existence of a tribe was made possible by maintaining a small parcel of land. Once the dominant power in southern New England and Long Island Sound in the pre-Colonial seventeenth century, the Pequot nation was challenged when neighboring tribes allied themselves with British settlers. The Mashantucket Pequots were officially exterminated in 1638, in a devastating massacre by British troops pursuing a formal policy of genocide, and they were legally declared extinct. Yet survivors and their descendants, enabled by politically savvy leaders, managed to maintain a relationship with the colony and later the state of Connecticut, and to hold on to a small parcel of apportioned land. Despite out-migration, religious conversions, and a diminishing reservation area, the Mashantucket Pequots continued to survive. By the 1980s, the local tribal contingent on reservation land had been reduced to two old women, who kept the tradition alive through basket-making and picking berries. A sudden, dramatic reversal of fortune occurred when the tribe won federal recognition and the right to establish commercial gambling on the reservation. By the early 1990s, they had built the enormous Foxwoods resort, which quickly became the Western Hemisphere's most profitable casino complex. After three and a half centuries of official extinction, the Mashantucket Pequot tribe is a major employer and once again a dominant economic power in the region. A tribal registration drive, construction of housing and schools, and a selective repopulation of the reservation has solidified their tenure. The task of cultural revitalization, however, was more problematic. The Pequots had lost their language and artifacts, been widely dispersed, and lacked a continuous, integrated culture. How does a small people, cut off from its own history and vanished traditions, reconstruct and represent its own image? Through large-scale public endeavors such as a massive museum and research complex and one of North America's largest annual Pow-Wow gatherings, the Mashantucket Pequots are facing the challenge by creatively engaging the preserved folklore of the New England tribes, the association of indigenous ecology with natural history and prehistory, settlement archaeology to recover the past, the adoption of stylized pan-Indian symbols, and identification with a growing pan-Indian movement to forge a modern identity.

The situation of this small Northeastern tribe, long on financial resources but short on available cultural traditions, is the opposite of that faced by many Indian peoples of the western United States. The Euroamerican vanquishing of these tribes was more recent and less complete. Although the traditions and identity of their past are closer to living memory, tribes were relegated to the poorest lands, worst education, and bleakest economic opportunity. Alcoholism and abuse, a grim legacy of colonialism, are persistent problems in contemporary Indian communities. Revivals of Indian religion and modern spiritual rekindlings provide one avenue of recovery. Repatriation of human remains and sacred arti-

A farmer winnowing rice in Uttar Pradesh, India. (UN Photo/C. Srinivasan)

facts from museums is another. The Native American Graves Protection and Repatriation Act (NAGPRA), passed by the U.S. Congress, permits federally recognized Indian tribes, Alaska native corporations, and indigenous Hawaiians to file claims for the return of human bones, relics, associated funerary goods, and other heritage objects from museum collections to authorized representatives of affiliated tribal groups. The somewhat controversial law was passed to provide a means for the reestablishment of broken threads from the past, the fostering of a sense of pride and the value of distinct identity in new generations of Indian people, and a more equitable relationship and dialogue with the institutions and hierarchy of the dominant society.

—Thomas R. Miller

See also: Ethnoscience; Linguistic Diversity; Subsistence

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D

Dams

Dams are built across streams and rivers to create reservoirs. The purpose of the reservoirs is capturing floodwaters to provide a consistent water supply for domestic use, irrigation, and power generation, and also to create lakes for recreation.

Very often a single reservoir is used for multiple purposes, and when water levels are low there is a conflict for the division of the water. There are many examples. Shall water be released for irrigation or to save downstream fish and habitats? For drinking purposes or to enable locks to operate to aid navigation? To keep water levels high for recreation use (swimming, boating, fishing) or to prevent salt water from entering valleys adjacent to coasts? People living around reservoirs want water levels to remain high, because exposed mud flats are esthetically unpleasant.

Dams built for flood control can give people living downstream from the dam a false sense of security. During very large episodes of flooding, a dam may not be able to hold the large volumes of water; dams may ultimately collapse, possibly killing large numbers of people. For example, in the Italian Alps, after the Vaiont Dam, the fourth highest dam in the world, was built in 1960, occasional slippage of rock material occurred on the slopes behind the dam. In 1963 a mass of unstable rock debris, with a volume estimated to have been 700,000 cubic meters, broke away from the high valley walls and plunged into the reservoir, creating a wave that washed over the dam. Within two minutes a town 1 km downstream from the dam and a few smaller villages were inundated, killing 2,600 people.

As population increases, especially in urban areas, more dams will be needed to provide water for drinking, fire fighting, cooling air conditioners, decorative fountains, and lawn sprinklers. It is estimated that there are 40,000 large dams in the world, and the United States alone has almost 100,000 small dams.

More often than not these new dams flood wilderness areas and places considered sacred to native peoples, drown scenic landscapes and river valleys, cover productive farms, prevent the migration of fish to their habitats, and inundate forests and sites of historic, archaeological, and geological interest (for example, Three Gorges Dam, Yangtze River, China).

Dams and their reservoirs change river systems completely and for all time. Sediments that normally would be carried downstream are locked up behind the dam, even-

Norris Dam, Tennessee. Completed in 1936, Norris Dam was the first dam built by the Tennessee Valley Authority (TVA) and has the largest flood control storage of any TVA dam on a tributary of the Tennessee River. (Tennessee Valley Authority)

tually reducing the volume of water the reservoir can hold and thereby its efficiency. The additional weight of the sediments and water bearing down on the crust can cause earthquakes, as has happened at Lake Mead behind Hoover Dam, in Arizona. In Egypt little sediment is being carried to the Nile delta, making what was once an area fertilized naturally with silt carried by the river dependent on artificial sources. Even the fisheries off the coast have diminished because of the reduced amount of nutrients carried into the Mediterranean Sea. Impounded waters change chemically, especially in areas of aridity, where evaporation increases salinity, making the water less useful for irrigation. Surface evaporation off large lakes can alter local weather patterns by setting up convection currents (such as at Lake Nasser, behind the Aswan Dam, in Egypt). Not only are large volumes of water lost to evaporation, but, in addition, reservoirs sited in sandstone terrain lose large volumes of water laterally into the surrounding bedrock. Dams also change land use patterns and biological habitats downstream from the dam.

Because of the decrease of sediments, streams develop a greater capability to erode the valleys. Rapids become more dangerous, with large boulders no longer removed because of the elimination of large floods. Changes in river flow also cause changes in the distribution of vegetation, helping to establish new plants. Flooding no longer removes plants that have grown on the riverbed, and the more or less constant level of water changes the patterns of vegetation on the valley walls.

Building dams may have unexpected consequences. For example, in Suriname a dense virgin forest was flooded by a reservoir, resulting in the death and decomposition of a large number of trees. Their decomposition produced hydrogen sulfide that enveloped the people in the region. Workers at the dam had to wear gas masks for several years, until all of the trees decomposed. If that wasn't bad enough, the reservoir water became acidified, which corroded the metal works of the dam. Water hyacinth, which had been relatively rare, began to spread over the lake because of the nutrients released into the lake by the decomposed trees. Navigation was slowed because of the dense growth. Floating plants provide food, oxygen, and breeding sites for carriers of two devastating diseases, malaria and schistosomiosus. Mosquitoes breed in the puddles on the plants, and aquatic snails thrive in the slow-moving water and play host to the flatworm that causes schistosomiosus. Finally, the floating vegetation blocks out sunlight, diminishes the oxygen levels of the bottom waters, and kills plants that fish depend upon.

—Sidney Horenstein

See also: Freshwater; Lakes; Rivers and Streams

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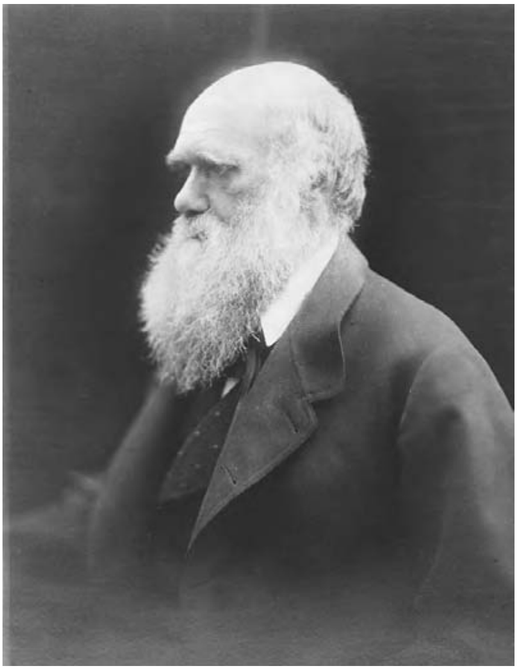
Darwin, Charles

Charles Darwin was born in 1809 at Shrewsbury, England. He was expected to follow in the footsteps of his father and grandfather, who were both prosperous physicians. (His grandfather, Erasmus, in addition to being a doctor, was also a famous philosopher, poet, and naturalist, and the first in Europe to publish a theory of evolution.) Charles was sent to study medicine at Edinburgh at the age of sixteen, but he was squeamish about the sight of blood and could not bear the screams of a strapped-down child in surgery. He soon rejected the pursuit of a career in medicine. To his father's disgust, Charles's only real interests seemed to be collecting beetles, shooting birds, and poking at rocks and plants—activities suitable only for an idle squire or a country parson. Doctor Darwin urged his son to become a clergyman instead and sent him to Christ's College, Cambridge, to prepare for a career as a country vicar.

Darwin was befriended by one of his Cambridge professors, the clergyman-botanist John Henslow, who instructed him in natural history. When Darwin was twenty-two, Henslow recommended him to a ship's captain, Robert FitzRoy, who was seeking a ship's naturalist and gentleman companion for a voyage around the world. FitzRoy (who was then only twenty-four years old himself) was taking the surveying ship HMS *Beagle* to chart the coast of South America, and then to explore the islands of the Pacific, Tasmania, Australia, and South Africa. Henslow expected that Charles would "snap at the opportunity." However, Charles's father proclaimed it a dangerous, hare-brained scheme that no "man of sense" would approve. He soon relented, however, and Charles abruptly quit his ecclesiastical studies to spend the years from 1831 to 1835 voyaging on the *Beagle*.

Darwin was thus able to explore the rain forests of South America, and he visited Australia, Tahiti, and South Africa, where he observed and collected thousands of plant and animal specimens. In Patagonia, he chipped a fossilized giant sloth from a cliff; and in the South Seas he discovered how coral islands and reefs were formed. It was a combination of adventure, hardship, scientific discovery, and unremitting hard work, all packed into five years. He galloped on horseback alongside Argentine gauchos, rode rough seas, survived killer storms and earthquakes, and wandered awestruck through creeper-laced rain forests teeming with gaudy birds and exquisite orchids. He habitually sought underlying connections and regularities, and eventually realized that the key was the shared history of life forms adapting to a changing earth.

After returning home, Darwin married his cousin Emma Wedgwood and settled down to family life near the village of Down, in Kent, some sixteen miles south of London. His first two books, *Journal of Researches aboard the H.M.S. Beagle* (1839) and "*The Structure and Distribution of Coral Reefs*" (1842), established him as a rising young scientist of talent and also as a popular author.



Portrait of Charles Darwin (Library of Congress)

For forty years, the Darwins and their children (they had ten, of which seven survived) lived in a spacious old house, complete with gardens, fields, a patch of woods, greenhouse, later a clay tennis court, and about fifteen servants. Darwin became a reclusive semi-invalid, devoted to writing, reading, and conducting experiments in his garden and greenhouse. A casual visitor would never have guessed that from this sleepy, idyllic retreat he was shaking the world.

Darwin had been strong and vigorous during the *Beagle* voyage, but he suffered ill health from a mysterious malady during most of his life thereafter. (Some scholars believe he was infected by a blood parasite from a beetle's bite in Argentina, giving him chronic Chagas's disease, coupled with debilitating anxiety from long-standing neurosis.)

Around 1837, Darwin began keeping notes on "the species question" in an ambitious attempt to discover "the laws of life." Building on the theories of his grandfather Erasmus (1731–1802), he became a "transmutationist" or evolutionist. (He used the terms *transmutation* or *the development hypothesis*. The term *evolution* was coined by philosopher Herbert Spencer and did not appear in Darwin's *Origin of Species* until the fifth edition, in 1869.)

Erasmus had believed that all living things arose by descent with modification from common ancestors over immense periods of time. During the early 1840s, he discovered a mechanism for evolution, which he called "natural selection." Organisms vary in nature, and those best adapted would survive and produce more offspring like themselves. But before he could publish his big "species" book, a younger naturalist, Alfred Russell Wallace, working alone in the jungles of Malaysia, came up with exactly the same theory and sent it to Darwin. There was an initial period of panic at being "scooped," after which Wallace's and Darwin's papers on natural selection were jointly presented at a meeting of the Linnean Society of London on July 1, 1858.

Although the Darwin-Wallace theory can be summarized in a few pages, how to use it to unravel nature's mysteries fills Darwin's 17 scientific books and more than 150 articles—an output that founded the modern research tradition. This incredibly productive life's work revolutionized every field he touched: botany, paleontology, physiology, taxonomy, comparative psychology, zoology, what we now call ecology, primatology, genetics, paleoanthropology, sociobiology, and all of the life sciences.

Current scientific theories of biodiversity, ecology, and evolution spring directly from the writings of Charles Darwin and his junior partner Alfred Russell Wallace, who independently discovered the theory of evolution by means of natural selection. Darwin's masterpiece, *On the Origin of Species* (1859), established the theory in science. Although Darwin's fieldwork predated Wallace's by more than twenty years, both had been impressed and influenced by the riotous diversity of plant and animal species they found in the Brazilian rain forests.

Divergence from common ancestors leads to biodiversity. Evolution is often pictured as a family tree or branching bush, bristling with divergent forks and twigs. Each lineage repeatedly splits and differentiates, and lines splay out, in Alfred Russel Wallace's image, "like the twigs of a gnarled oak or the vascular system of the human body." Some of Darwin's disciples, like German zoologist Ernst Haeckel, spent years working out detailed "trees of life," showing the divergence of families, genera, and species over time

Although today they may seem like inseparable concepts, evolution and divergence have not always been associated. Darwin sketched such a tree in an early notebook, but the principle of divergence occurred to him much later—about fifteen years after he had developed his basic theory of natural selection. Divergence was a crucial missing piece even during the writing of the *Origin*, and yet Darwin referred to its last-minute inclusion as "the keystone" of his book.

In the later views of both Darwin and Wallace, divergence serves a double function in evolution. First, it enables a given species under selection pressure to survive in modified form by exploiting new niches in the ecology. And second, the gain in diversity boosts the habitat's carrying capacity, enabling it to support a greater total amount of life. Typically, small, isolated habitats (such as Darwin's beloved Galapagos Islands, in the Pacific Ocean west of Ecuador) exhibit a startling diversity of closely related species, adapted for exploiting different foods or parts of the habitat.

Wallace's significant 1855 paper (the "Sarawak Law") began with this question: If one examines the numbers of closely related species within genera, geographic distribution of natural groups, and kinds of differences between species in a local area, what overall pattern (he called it a "law") would emerge? His answer was that the largest number of species seemed to be produced from those genera confined to a small area (such as islands), and their differences were related to feeding adaptations (sharp beaks, blunt beaks, long beaks, and so forth).

When Darwin read this paper, he scrawled on it: "Why should this law hold?" The answer, he later realized, was that under selective pressures, organisms evolve to fill "vacant places in the natural economy." He compared it to a division of labor, with efficient specialists exploiting the various food sources in a limited area. To test the theory in his own garden, he stripped the ground of turf in a square 3 by 3 feet and carefully monitored how many species would fill in the bare little plot. He was astonished when, after only a few weeks, he counted fifty-three varieties and species that had sprung up in his test square.

What is now taken for granted was then a startling insight: contrary to "common sense" expectations, the fierce struggle for existence does not reduce the overall number of related species in an area of limited resources. Instead, it has the paradoxical effect of allowing many more species and individuals to thrive there.

More than a century later, David Tillman, of the University of Minnesota, followed up on Darwin's experiments with biodiversity. Tillman directed a team of fifty workers to burn, plow, plant by hand, and tend 147 plots of grassland in the Minnesota prairie, each measuring about 100 square feet. In a few weeks, between one and twenty-one native species appeared in each plot. Those with more species, he found, retained nitrogen—the plant's most crucial nutrient—much more efficiently. Like Darwin, Tillman was struck by the fact that closely related species would tend to exploit slightly different resources in the same habitat, and that the resultant diversity would be beneficial to all (Tilman and Downing, 1994; Tilman et al. 1996).

The concept of diversity is related to Darwin's ecological view of nature, although the term *ecology* was not coined until 1869 by Ernst Haeckel, who was inspired by a passage from the *Origin of Species*. Darwin had marveled at a common riverbank "clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent upon each other in so complex a manner, have all been produced by laws acting around us."

This "tangled bank" expresses Darwin's view of nature as a web of interrelationships binding various plants and animals into a community. Not only is the visible vegetation entangled; the lives of different species are also intertwined. Ecological interdependence was one hallmark of Darwin's contribution to modern thought. He saw evolution as a lateral rather than simply an onward movement, whose power lies in multiple relationships as much as in selecting out.

When he first met the English zoologist Thomas Huxley, later to become his great friend and champion, Darwin was examining a tray of specimens at the British Museum. Huxley said something about what clear boundaries there are between natural groups. Glancing up, Darwin quietly replied, "Such is not altogether my view." Huxley later recalled that "the humorous smile which accompanied his gentle answer . . . long haunted and puzzled me." In the popular perception, Darwin is remembered best as a solitary observer and field naturalist. Actually, he excelled at two other modes of research for which he is not generally credited: collaboration and experimentation. He experimented constantly in his greenhouse and garden. To test whether certain plants that had evolved on continents could be the same ones found on distant islands, he soaked seeds for months in barrels of brine, then planted them to see which could survive long immersion in salt water. He measured the activity of earthworms in his garden by calibrating the rate at which a heavy stone sank into the turf.

Over the years, Darwin's books tackled the implications of his theory for human origins

(*The Descent of Man*, 1871), behavioral evolution (*Expression of the Emotions in Man and Animals*, 1872), coevolution of insects and plants (*The Varying Contrivances by which Orchids Are Fertilised . . .*, 1862), domestic breeding (*Variation in Domesticated Plants and Animals*, 1868), and botany and plant physiology (*Movements and Habits of Climbing Plants*, 1865; *Insectivorous Plants*, 1875; *Different Forms of Flowers on the Same Plant*, 1877). His first (*Structure and Distribution of Coral Reefs*, 1842) and last (*Formation of Vegetable Mould through the Action of Worms*, 1881) books were demonstrations of how great geological features may result from small, slow causes, acting regularly, over immense periods of time. It is remarkable that despite "never knowing a day of robust health" for forty years, Charles Darwin managed to write his 17 scientific books and 155 articles—a lifetime output of more than 10,000 published pages—working no more than two or three hours a day. "I have always maintained," he said, "it is dogged as does it."

When he died of cardiac disease in 1882, he expected to be buried in the local churchyard at Downe Village, but his powerful scientific friends petitioned for burial in Westminster Abbey, England's highest honor. His final resting place is a few paces away from that of Sir Isaac Newton, another scientific immortal.

Eulogizing his old friend, Thomas Henry Huxley said, "None have fought better, and none have been more fortunate than Charles Darwin. He found a great truth, trodden underfoot, reviled by bigots, and ridiculed by all the world; he lived long enough to see it, chiefly by his own efforts, irrefragably established in science, inseparably incorporated with the common thoughts of men. . . . What shall a man desire more than this?" (Huxley, 1893).

—Richard Milner

See also: Coral Reefs; Evolution; Evolutionary Biodiversity; Galapagos Islands and Darwin's Finches; Mass Extinction; Natural Selection; Wallace, Alfred Russel

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Deep-Sea Hydrothermal Vent Faunas

Biologists do not know how many species exist on earth (see Evolutionary Biodiversity), but the age of exploration for some groups is nearing an end. Although new species of birds, for example, continue to be found nearly every year, no one believes that vast numbers of birds new to science will ever be found again.

That is not so, however, for the creatures that inhabit the remoter, less accessible regions of the earth. And perhaps the deep sea is the least accessible of them all. Light cannot generally penetrate more than a few hundred feet of seawater; thus below that depth photosynthesis is impossible, and the kinds of ecosystems present in all other environments (including the upper levels of the sea, where the food chain is based on the photosynthetic activities of marine microplankton) can not exist. For the most part, the deep-sea fishes, the giant squids, and the sperm whales that prey on them—not to mention the brittle stars and other forms of invertebrate life that have been discovered living on the floors of the oceans miles below the surface—subsist on organic particles of dead organisms that rain down from the oceanic surface.

There is, however, one major exception: the so-called hydrothermal vent faunas, generally found in and near deep ocean trenches. Such trenches are the sites of colliding plates of the earth's crust, where subduction—the swallowing of one plate under another—is occurring (see Plate Tectonics). Heat from deep within the earth's mantle escapes, along with methane and sulfides that some forms of chemoautotrophic bacteria can metabolize, using energy derived from chemical oxidation reactions that enable them to synthesize organic compounds.

Such bacteria live in the tissues of species of large tube worms and clams commonly found around the vents; other species of marine life simply consume the bacteria directly. Thus hydrothermal vent faunas are the exception to the rule that ecosystems on earth are dependent on sunlight for photosynthesis to form the base of the food chain. Scientists speculate, however, that early in the history of life, such nonphotosynthesizing bacterially based ecosystems were relatively more common.

—Niles Eldredge

See also: Ecosystems; Evolutionary Biodiversity; Food Webs and Food Pyramids; Plate Tectonics

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Deposition

Not only do the agents of erosion—streams, wind, glaciers, waves, currents—wear away the land, they also transport the resulting rock debris, which eventually is deposited when their energy runs out and gravity takes over. The major sedimentary environments are eolian (wind), alluvial fans, glacial till and drift, fluvial (stream), and lacustrine (lake). Along the shore deposition takes place in evaporite basins, deltas, lagoons, and estuaries, and along barrier islands. Marine environments include continental shelves, reefs, submarine slopes, and the deep sea. Each one of these sedimentary environments has its own distinct chemical, physical, and biological conditions. This makes it easy to recognize the conditions under which ancient sedimentary rocks were deposited. The following are brief descriptions of representative examples.

The nature of fluvial deposits depends upon the source of the material, distance traveled, climatic regimes, and the amount of energy available—for example, velocity derived from slope steepness. These deposits contain particles that are angular to rounded and range from clay size to boulders. They are located in channels and on floodplains; climate determines the kinds of terrestrial animals and plants that live in and near the streams.

Lacustrine deposits form in low-energy freshwater environments. They usually contain fine particles, but in temperate and cold climates they could be varves—layers that form in pairs and are deposited yearly. Spores and pollen found within the deposits are tools helpful in determining past vegetation and climate. In deserts, where evaporation is brisk, water evaporates in the lake basin (playa lake), leaving salt-encrusted deposits.

Swamp and marsh environments contain slow-accumulating fine sediments, abundant plant life, and animals that are freshwater, estuarine, or marine. Most of the world's coal deposits were originally plant material that accumulated in freshwater swamps.

Eolian environments occur where wind-blown deposits accumulate, usually containing well-rounded, sorted fine sand that is cross-bedded. They form in deserts and along coastlines—almost anywhere there is a supply of loose material and prevailing winds. Stable dunes host a variety of plants and associated animals.

Glacial environments of deposition contain large amounts of unsorted, angular to rounded particles, from the smallest to house-size, piled in mounds and ridges, as well as layered material that has been reworked by meltwater. Along the margins of the ice, cold climate prevails, determining the type of plants and animals, but older moraines may be located in a variety of climates.

Shallow marine environments are found in estuaries, deltas, and along the inner continental shelves, containing clay, sand, and pebbles; their layers are sometimes disturbed by waves and currents. The skeletons of floating and bottom-dwelling animals are often mixed with these sediments, and they occur in any climatic zone.

Low-energy marine environments include the outer continental shelves; bathyal and abyssal environments are generally low-energy environments with abundant organisms, including floaters, swimmers, and bottom dwellers. They can occur anywhere in the oceans.

Pelagic environments contain sediments dominated by skeletal debris, almost entirely micro-organisms that have settled slowly onto the seafloor and have mixed with small amounts of wind-blown dust, volcanic ash, and other material. They are called oozes, and the shells of the organisms settle from open water in very large numbers; oozes may be calcareous or siliceous in chemical composition

High-energy deep sea environments contain turbidities derived from continental shelves and slopes, and are rapidly dumped on the deep seafloor. They are usually motivated by gravity, earthquakes, or both.

Organic reef environments are tropical and composed of living and dead corals and associated fauna. An apron of broken skeletons is located on the sea side of the reef, and fine carbonate sediment with abundant organisms is found behind the reef in the protected lagoon. If adjacent to a shoreline, tidal flats contain algal mats, stromatolite mounds, and limy sediments that are often mud-cracked.

The term *deposition* also refers to the accumulation of chemical precipitates in caves, lakes, and the sea. Water in embayments along the margin of the sea and freshwater lakes contains dissolved materials that are deposited when the water evaporates. Stalactites and stalagmites in caves are composed of calcium carbonate (calcite); they occur when water containing the mineral evaporates. Travertine, a type of limestone and also composed of calcite, is precipitated from warm- and hot-water springs. Precipitation occurs as a result of changes in temperature, pressure, solution concentration, or chemistry.

—*Sidney Horenstein*

See also: Abyssal Floor; Erosion; Estuaries; Freshwater; Lagoons; Lakes; Oceans; Rivers and Streams

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Deserts and Semiarid Scrublands

Deserts are characterized by very low rainfall; indeed, so-called true deserts receive less than 100 mm of rainfall per year. Because of the scarcity of water, vegetation is not abundant, and there is reduced chemical weathering of rock and thin soils.

Most of the world's deserts are located 30 degrees north or 30 degrees south of the equator. Air rising from the equator cools and releases moisture over the tropical latitudes. Some of the dried air moves north and some south, and it then drops downward about 30 degrees to either side of the equator. Moisture there evaporates from the surface, creating desert conditions. Most of the annual rainfall in these deserts occurs during the summer.

Hot deserts have richer and more diverse vegetation than the drier cold deserts. Cacti, for example, store large quantities of water in their expandable stems, and photosynthesis occurs primarily within stems rather than leaves.

Cold deserts are located in middle to high latitudes, 30 to 50 degrees, and they are usually in the middle of continents, where seasonal temperature changes are great. There is a relatively low diversity of plants and animals; rain usually falls in the winter, and plant growth is concentrated in the spring.

Some deserts lie in the wind shadow behind mountains. Moisture precipitates from air rising and cooling above a mountain; once over

Desert vegetation, Maricopa County, Arizona (USGS/Lee, W.T.)

the mountain, the now dry air descends, drying out the surface as it flows across the land.

Most of the processes that take place in the desert—weathering and erosion, for example—are the same as those elsewhere, but they are altered somewhat because of the lack of water. Today about one-third of the earth's land is arid or semiarid, with half of it so dry that it is uninhabitable. Characteristic of the desert floor is what is called desert pavement, which is developed as wind—a significant feature of desert areas—moves over the surface, picking up dust- to sand-size particles. Left behind is a lag deposit of coarser material, the desert pavement. The constant wind and supply of sand builds up dunes. Desert varnish, a dark coating on rocks large and small, forms from the slow precipitation of manganese and iron compounds, as well as minute clay particles. Large areas of dunes are called sand seas, or ergs; they are found in large deserts, usually taking up no more than 10 percent of the area.

Wind also builds deposits of loess, consisting of finely disintegrated rock debris that is very common, for example, in the north of China, where it is carried by the prevailing winds from the Gobi Desert in Mongolia. In northern China the loess covers extensive areas and reaches a thickness of more than 60 m. Easily eroded and carried away by streams, it is the reason that the Huang Ho (Yellow River) got its name. Although the weak loess forms vertical cliffs, it is easily excavated and provides a great number of people with shelter. Wind carries this material to cities such as Beijing, where the air is smoglike, and to adjacent countries such as Japan and Korea, and then out to sea. The wind-blown dust usually accumulates in semiarid regions along the edge of deserts.

Deserts expand and contract with climatic fluctuations. Their margins, where they are in transition to wetter ecosystems, are heavily exploited by humans. Grazing and trampling by cattle, the collection of firewood, overcultivation, and salinization caused by irrigation stress the environment, causing the deserts to expand, sometimes at a rapid pace. This process is called desertification. Today about 20 percent of the terrestrial surface is arid, and about an additional 15 percent is threatened.

—Sidney Horenstein

See also: Communities; Ecology; Hydrologic Cycle; Topsoil Formation

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Diatoms

See Protoctists

Dinoflagellates

See Protoctists

Dobzhansky, Theodosius

See Evolution

Dolphins

See Cetacea

Dragon Flies

See Arthropods, Terrestrial

Draining of Wetlands

Wetlands are those places in the world where water intergrades with land. They include such diverse areas as swamps and bogs, marshes, mangroves, vernal ponds, and riverside seeps. Although these transitional environments cover only about 6 percent of the earth's surface, they are among the most important of ecosystems. They cleanse polluted waters, help to prevent floods, protect shorelines, recharge groundwater aquifers, and provide habitat for a rich diversity of plants and animals. Yet for all their importance, wetlands have been drained, ditched, and filled over the centuries. In the past 200 years, more than half of the original wetlands in the United States have been destroyed. In some parts of the world, natural wetlands are nearly extinct. This loss has severely harmed wetland-dependent biodiversity.

Humans have directly and drastically altered wetlands for a variety of reasons. An estimated 26 percent of the world's wetlands have been drained and the land converted to agricultural purposes alone. Wetlands have also been filled for development and construction. Many of our major cities located in coastal areas or along rivers have been built on filled wetlands. In addition, people have destroyed wetlands, thinking that they were nothing more than breeding places for disease and vermin. In particular, ditching and draining for mosquito control has altered the hydrology of many wetland systems. The damming of rivers has also changed water flow, damaging wetlands adjacent to the rivers. Interestingly, many of these activities—such as agricultural conversion, irrigation, and dam construction—have been implemented with government support. Indirectly, development of surrounding uplands has also affected wetland quality and function, by introducing pollutants and sedimentation into wetland systems via runoff.

We now know that wetlands are critically important habitats, providing many ecological services for free that would cost billions of dollars to duplicate. Although wetlands are still under threat, today there are many worldwide efforts to protect and restore wetlands. Some countries have established legislation to protect wetlands as natural areas or to enforce the maintenance of water quality. Restoration—that is, the return of a degraded ecosystem to its former, undisturbed chemical, physical, and biological conditions—is also an important conservation tool. To accomplish this, dams are being reopened to restore river flow, which allows the natural cycles of flooding and sediment deposition to function in the adjacent wetlands. Tile drains that had been installed in agricultural fields to drain off water are being removed. Rivers and streams are being cleaned up by reducing point and nonpoint source pollution. (Point source pollution is contamination that originates from one place, such as a sewer pipe; nonpoint pollution comes from many sources, such as road runoff, lawn chemicals, and so forth.)

In addition to habitat restoration, wetland creation and mitigation are two other strategies being used to combat wetland loss. Wetland creation usually entails digging a completely new wetland in a nonwetland site, instead of restoring an existing one. Mitigation is a program whereby for each acre of wetland that is drained or filled another, comparable area is created anew, or restored to offset the loss. In general, wetlands are best protected in situ, where they are hydrologically and ecologically linked to the landscape—either by preventing their destruction in the first place, or by careful restoration.

—Elizabeth A. Johnson

See also: Coastal Wetlands; Dams; Interior Wetlands; Pollution; Rivers and Streams

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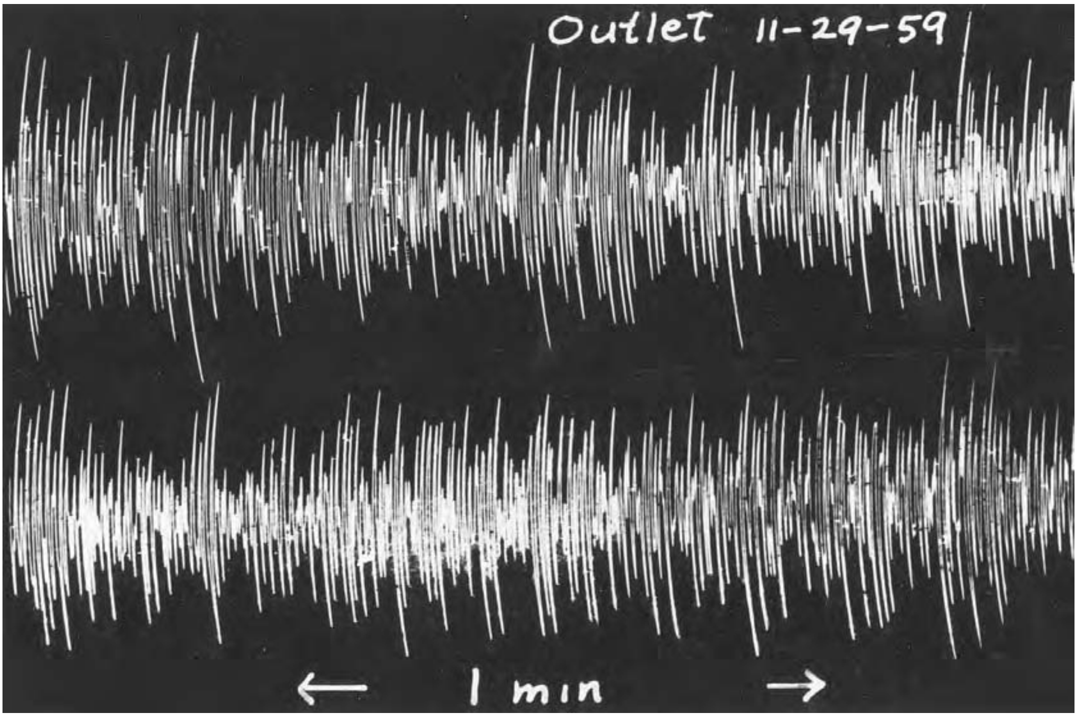
Earthquakes

Earthquakes occur when rocks are subjected to strain and rupture, moving past each other suddenly along a fault plane, forming seismic waves that move through the earth. What is called the focus of the earthquake is the place below the surface where the slippage occurred; the epicenter is the place on the surface of the earth, directly above the focus. When severe earthquakes occur, they can destroy buildings and other structures and cause great loss of life.



A record of an earthquake tremor, November 29, 1959 (USGS)

The shaking caused by earthquakes may trigger landslides, or cause certain types of clay to liquefy and flow down slope, causing damage to structures on its surface.

The magnitude of an earthquake is the amount of energy released; it is read directly from the seismogram record. On the Richter scale the magnitude is registered logarithmically, meaning that an earthquake of magnitude 3 is 10 times greater than one of magnitude 2; an earthquake of magnitude 4 is 100 times greater than a magnitude 2; a magnitude 5 is 1,000 times greater—and so on.

Another commonly used scale measures the intensity of the earthquake based upon its destructive power, as noticed by people and by observations of the effects on buildings, dams, and other structures. For example, a IV has occurred when dinner plates rattle on a shelf, and a VI when plaster falls. When buildings shift on their foundations, it is a IX.

Tens of thousands of earthquakes occur each year, most of them so small that only the most sensitive seismographs can detect them. Every few years, however, a severe earthquake occurs, killing, unfortunately, thousands of people. A Peruvian earthquake in 1970 killed 50,000 people when their adobe buildings collapsed. In mountainous regions like the Andes, earthquakes cause huge amounts of rock debris to move down slope, burying towns with little warning, as occurred in Chile in 1939, when 40,000 people died. Seismicity below the sea can generate large sea waves called tsunamis (or tidal waves), which cause heavy coastal destruction when they strike land.

Because of the loss of life and property caused by earthquakes, geologists and seismologists are trying to find a way to predict them. Chinese scientists have utilized the sudden change in the behavior of animals to predict earthquakes. In the United States and elsewhere, geologists monitor uplift and tilting of the land surface, changes in groundwater flow and level, and other physical characteristics. Most of the most severe earthquakes occur in narrow bands along plate boundaries; the goal is to find an accurate way to predict the timing and magnitude of an earthquake.

—Sidney Horenstein

See also: Geology, Geomorphology, and Geography; Mountains; Plate Tectonics

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Earthworms

See Annelida—The Segmented Worms

Echinoderms

The Phylum Echinodermata consists of at least 6,500 living species in six named classes, which include sea stars, sea urchins, and related animals. The beauty, appeal, and importance of living and fossil echinoderms have been recognized since ancient times. They have ranked among the most conspicuous marine animals since the Cambrian and are distributed today from the intertidal zone to the deepest ocean trenches, often in immense numbers; they are of considerable ecological significance. Echinoderms are most diverse in the tropics, but they are found in greatest profusion in productive temperate and cold-water ecosystems. They range in size from basket stars (*Gorgonocephalus*) 1 m in diameter and sea cucumbers (*Synapta*) 3 m in length to sea urchins (*Echinocyamus*) smaller than 1 cm. Perhaps the largest echinoderm and the most spectacular of all invertebrate fossils is a sea lily, *Seirocrinus subangularis*, with stems more than 20 m in length; it is found in massive groups attached to logs in Lower Jurassic shale.

The term *Echinodermata* was derived from the Greek for spiny (*echinos*) and skin (*derma*), and it refers to the prominent, flesh-covered skeletal structures of many species. The echinoderm skeleton is an internal system, unique in consisting of highly porous, calcium carbonate ossicles ("little bones"), each of which has the optical properties of a single calcite crystal. Another echinoderm characteristic and key to the group's success is the "mutable collagenous tissue" (MCT), which connects the ossicles, reinforces the integument, and enables echinoderms to transform nearly instantaneously from a rocky rigidity to puddinglike pliancy—and to just as quickly reverse the process. MCT is also capable of irreversible disintegration, giving echinoderms the ability to voluntarily sever appendages and to reproduce by fission.

The water vascular system (WVS), another exclusive echinoderm attribute, consists of a fluid-filled, ring-shaped canal that sends out five radial canals. Pairs of tube feet, which operate hydraulically, issue at intervals from the canals, protrude through the body wall, and serve in sensory reception, locomotion, feeding, and respiration. The radial canals and tube feet, accompanied by other coelomic systems, the nervous system, and specialized skeletal structures compose the ambulacra (Gr.: "walk, path"), which demarcate the radial, pentamerous (Gr.: "five-part") symmetry that characterizes the echinoderm body plan.

Among the traits that typify echinoderms is their ability for regeneration. It is widely believed that any piece cut from a sea star can reconstitute an entire individual, but in fact at least a portion of the disk is required for regrowth. All echinoderms have the capacity to regenerate damaged structures, and many can voluntarily sever their appendages in self-defense and then regrow them. The most extreme manifestation of regeneration occurs in echinoderms that reproduce asexually by dividing into parts and regenerating. That is also a faculty of some echinoderm larvae, which can clone themselves. In general, however, echinoderms reproduce sexually and produce planktonic larvae that undergo a dramatic metamorphosis, or they brood embryos and release crawl-away juveniles. The bilateral structure of echinoderm larvae is evidence that the pentamerous symmetry of the adult evolved secondarily.

Phylogenetic Relationships, Origin, and Fossil History

The ancestry of the extinct echinoderm lineages, and of the extant classes, has long been debated. At present, crinoids are generally regarded as a sister group to the other living echinoderms. Among the other classes, echinoids and holothuroids (=Echinozoa) are consistently viewed as sister groups. The connections between the asteroids, concentricycloids, and ophiuroids, however, and their precise relationship to the Echinozoa, are uncertain. Ideas are in flux regarding the relationship between echinoderms and other phyla, but it is clear that echinoderms, hemichordates (acorn worms), and chordates (tunicates, lancelets, and vertebrates) are the sole members of the animal branch Deuterostomia. Molecular systematic studies and other lines of evidence indicate that the echinoderms and hemichordates are each other's closest relatives.

The echinoderms probably evolved in the

Proterozoic, and the earliest purported representatives belong to the Ediacara Fauna. The first undisputed echinoderm fossils, however, are from the Early Cambrian, some 520 million years ago. These include small, squat helicoplacoids and edrioasteroids that lived anchored in sediment. By the end of the Cambrian they were displaced, probably by vagile organisms that destabilized the substrate, including such echinoderms as solutes and stylophorans, and by sessile, stalked, arm-bearing eocrinoids. Many of these ancient forms lacked pentamerous symmetry, and in appearance they were quite unlike modern echinoderms.

The radiation of the species and higher groups of echinoderms accelerated during the Ordovician Period, 505 to 440 million years ago, yielding a Paleozoic fauna with as many as twenty distinctive classes that was dominated by suspension-feeding rhombiferans and crinoids. These flower-shaped animals lived attached to the ocean floor in congregations that must have resembled underwater gardens. The classes surviving to the present day, including crinoids, holothuroids, asteroids, ophiuroids, and echinoids, were definitely in place during the Ordovician. The long stalks of Middle Ordovician crinoids put them in reach of plankton inaccessible to smaller organisms. Ophiocistioids and echinoids of that period were the first potentially herbivorous echinoderms. The appearance of inferred asteroid carnivores in the Ordovician and infaunal deposit-feeding holothurians later in the Paleozoic further presaged the mobility and trophic diversity characterizing modern echinoderms.

The number of echinoderm classes gradually declined during the waning of the Paleozoic, although great epicontinental seas of the Carboniferous Period supported vast populations of crinoids and blastoids. The Permo-Triassic extinction marking the transition to the Mesozoic Era 245 million years ago resulted in the demise of 90 percent of marine species including the Paleozoic crinoids and the other stalked echinoderms. Nevertheless, the Triassic marked the establishment of the lineage of articulates that gave rise to all living crinoids, and heralded the ascendancy of stalkless crinoids and other free-living echinoderms.

During the Mesozoic, echinoids replaced crinoids as the dominant groups of echinoderms. Remarkably, by the Permian echinoids had dwindled to just six known species, but the limited number of survivors seemingly saved the entire class from extinction. Similar bottlenecks affected the other echinoderm classes. Echinoid generic diversity peaked in the early Cenozoic and overshadowed the diversity of the other echinoderm classes, but at present the numbers of ophiuroid, asteroid, and holothuroid species exceed the species of echinoids. Although the current generic diversity among living echinoderms equals or greatly surpasses the diversity at any other point during the Phanerozoic, the disparity is probably an artifact of preservation in the fossil record.

Class Asteroidea (Sea Stars or Starfish)

There are 1,800 species of sea stars, which are stellate to spherical animals with a central disk and usually five, but as many as fifty, arms. The arms and disk enclose a spacious body cavity occupied by a complex digestive tract and reproductive organs. The ventral surface of the arms has an open ambulacral groove that can close to protect the tube feet.

Asteroids have a well-earned reputation as carnivores, although certain species consume sediment or plants. Carnivorous asteroids are by no means all detrimental, but asteriid species, sometimes numbering nearly 150,000 per hectare, have caused enormous damage to commercial shellfisheries. Their arms and tube feet are capable of exerting sufficient force to open bivalves, and a gap of only 0.1 mm is suf-

Red starfish (*Fromia indica*). There are 1,800 species of starfish. Starfish usually have five arms, but they can have as many as fifty. (Amos Nachoum/Corbis)

ficient for the asteroid to insert its stomach and digest its victim. Outbreaks of *Acanthaster planci*, the crown-of-thorns sea star (COT), have decimated Indo-Pacific reefs, which require decades to recover. Individual COT can release a remarkable 60 million eggs per year. There is evidence that their success has been enhanced by the anthropogenic release of nutrients and destruction of *Acanthaster*'s predators. Conflicting information, however, shows that numbers of COT have been comparable or greater over the last 8,000 years.

Concentricycloidea (Daisy Stars)

There are but one genus and only two species of daisy stars, which were discovered in waterlogged wood recovered from depths of 1,000 to 2,000 m. They are flat, round, small animals, no more than 12 mm in diameter, with quite distinctive features. Their water vascular system is configured in a double ring, and the tube feet are arrayed in single file on the edge of the body. They are sexually dimorphic, and males have copulatory organs and produce spermatozoa that are morphologically unlike those of other echinoderms. The introduction of the concentricycloids as a new class of echinoderms in 1986 has generated much controversy. Evidence including DNA sequencing has been marshaled to show that they are structurally modified asteroids, but additional attention to the systematics and the biology of these animals is still well warranted.

Class Crinoidea (Feather Stars and Sea Lilies)

There are 100 species of sea lilies, which are restricted to depths exceeding 100 m, and 600 species of unstalked feather stars. The globular crinoid body carries an upward-directed mouth and anus and downward-directed attachment structures in the form of the grasping, jointed cirri of feather stars and the long, segmented stalk of sea lilies. Crinoid arms, which have delicate, alternating side branches, are usually 10 and up to 250 in number. Although a stalk is absent in adult feather stars, one develops after metamorphosis in the juvenile and is discarded after the arms and cirri develop.

Crinoids are current-loving, and veritable suspension-feeding machines. They actively orient their arms to capture small animals, plants, and nutritive particles. Food is captured by the tube feet, bound in mucus, and carried to the mouth along the ciliated ambulacra. Feather stars and some sea lilies can crawl, and certain feather stars can swim; since they have muscles only on the oral side of their arms, however, they depend on the elastic properties of MCT ligament to generate downward power-strokes. The visceral mass and the arms of crinoids can regenerate, and even the stalks of some "decapitated" sea lilies can regrow most of the body and arms.

Class Echinoidea (Sea Urchins, Sand Dollars, and Heart Urchins)

The 900 species of echinoids have spine-studded, boxlike bodies composed of twenty columns of interlocking plates. Spherical "regular" echinoids have an anus at the apex and the mouth facing the substrate. In bilaterally symmetrical "irregular" echinoids the anus is located posteriorly. All echinoids, except some sediment-eating irregulars, have a mouth structure (Aristotle's lantern) with five teeth that continuously grow to compensate for dental abrasion.

Echinoids are of pivotal importance for embryological studies, since their copious gametes and transparent embryos are perfect subjects for experimentation on fertilization and development. Roughly 50,000 tons of echinoids are harvested each year for their edible roe, a largely unregulated fishery that has depleted or devastated stocks in several countries. In other regions, the grazing activities of enormous populations of echinoids have ravaged communities of algae, creating nearly sterile habitats called urchin barrens. The causes of echinoid population explosions are difficult to pinpoint, but disruption of natural ecosystems has frequently been implicated. Echinoids may succumb to pathogens, as did the *Diadema antillarum*, whose populations throughout the Caribbean dropped 93 percent in the 1980s. The extraordinary replacement of Caribbean corals by algae since that time points toward the formerly enormous impact of *Diadema*'s herbivory.

Holothuroidea (Sea Cucumbers)

Holothuroids are somewhat cylindrical animals with a horizontal axis of symmetry, and the mouth and anus at the extreme poles. Most of the 1,400 species have a degree of bilateral symmetry, but it is superimposed on a pentamerous body plan. Modified tube feet form eight to thirty finely branching tentacles around the mouth, which are specialized either for suspension or deposit feeding. Depending on the species, additional tube feet may be numerous or entirely absent. Holothuroids are typically soft-bodied because their ossicles rarely form a plated test, but rather are of microscopic size and complex shape. Although characteristically sluggish animals, some holothuroids are capable of swimming, and one gelatinous, deep-sea species is completely pelagic.

Holothuroids are the most numerous large animals on the vast deep seafloor, and therefore one of the earth's dominant animals. Their ecological impact is potentially enormous, since they can process sediment at a rate of more than 50 kg/square meter per year. A Chinese fishery for holothuroids dates back 1,000 years, and trade in sea cucumbers is still centered in Asia. Worldwide catches of about thirty species exceed 20,000 tons per year. Unfortunately, fishing pressure has increased considerably, and in many countries there are indications that holothuroid resources have been overexploited. Study and regulation will be required to sustain the fishery of these slow-growing and vulnerable echinoderms.

Class Ophiuroidea (Brittle Stars and Basket Stars)

The 2,000 species of graceful, agile ophiuroids have a disk containing a simple stomach (absent an anus), reproductive organs, and invaginated sacs used for respiration and reproduction. The jointed arms are sharply demarcated from the disk and nearly solid in construction, lacking an open ambulacral groove.

The basket stars have branching arms, and large individuals may have 10,000 or more barbed, terminal arm branches that swiftly curl around zooplankton prey. Many accounts have suggested that brittle stars lack eyes, can flex their arms only in a horizontal plane, and can move only by waving their arms. Some ophiuroids, however, have optically perfect lenses in their arm skeleton, which focus light on photoreceptors. The majority of ophiuroids can bend their arms in all directions, and one fish-eating species snares its prey in helical coils of its arms. Many ophiuroids crawl, some can swim by rapidly “rowing” their arms, and others advance using just their tube feet. Surprisingly, certain ophiuroids are capable of casting off and regenerating their disk and viscera. Ophiuroids are important in the diet of many fish and crustaceans, and sheer numbers ensure their significance in the economy of the sea, where brittle star densities of 7,000 individuals per square meter have been recorded.

—*Gordon Hendler*

See also: Evolutionary Biodiversity; Five Kingdoms of Nature

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Ecological Niches

Niche is a term that describes the relationship between an organism and its environment. This relationship is thought to be crucial in explaining why certain species exist where they do, and which other species they can coexist with. The constraints on coexistence that come from such niche relations are important in the development of theories about the regulation and the consequences of biodiversity. The niche concept has also been used to understand the functional dynamics (either evolutionary ones that involve genetic adjustments, or short-term adjustment via behavior or physiology) of species to one another. The niche has also been used as a conceptual way of describing how species contribute to ecosystem processes such as productivity and the cycling of materials.

As in all relationships, there are two possible components: the set of responses of the organism to the multiple factors in the environment, and the set of impacts of the organism on these factors. Mathematical theory indicates that in closed local communities, two aspects of niche relations are important in allowing for the stable coexistence of two species: (1) each species must be more sensitive to a different environmental factor (related to the response component), and (2) each species must have a greater net impact on the factor that it is most sensitive to (related to the impact component). The presence of both of these components is essential for theories of stable coexistence, because the absence of either component means that there is no feedback in the system, thus altering many aspects of ecological systems.

History

The niche concept has an origin that harkens back to the origins of the field, but one that has been characterized by some confusion—in part because the concept is perhaps too easily applied in the form of metaphor rather than in strictly logical terms. The confusion has centered on two issues: whether the focus was on biological aspects related to the response of organisms to the environment or to their impacts; and whether the focus was on descriptions of the habitats of the environment or on more detailed (within-habitat) factors.

Joseph Grinnell is the person most frequently cited as the originator of the term. His 1917 paper, "The Niche Relationships of the California Thrasher," is one of the first uses of the term. This paper focuses on the conditions that characterize the habitats used by a single species. Grinnell related these conditions (for example, the presence of chaparral for cover, certain temperature and humidity ranges, and the like) to the requirements of—or to factors that affect the fitness of—the California thrasher, thus emphasizing requirements and habitat perspectives. Intriguingly, Grinnell concluded with the statement that "it is, of course, axiomatic that no two species regularly established in a single fauna have precisely the same niche relationships." Since that was one of the first uses of the term *niche* and one of the first statements of this principle, one wonders how much theoretical work was being developed outside of print by Grinnell and his collaborators.

Charles Elton used the term *niche* ten years later in his influential *Animal Ecology* text in a substantially different way. His definition was vaguely stated as the "role of the species" and emphasized the functional role of species in food webs in relation to their impacts on other organisms and on the environment (that is, reducing food levels, supporting predators, modifying soil structure and so forth). It does not seem that Elton was familiar with Grinnell's use of the term, and this seems to be an independent derivation of the term. In contrast with Grinnell, Elton emphasized impacts and did not emphasize habitat descriptions.

Alfred Lotka and Vito Volterra developed basic mathematical models of species interactions (interspecific competition, and predator-prey interactions) that confirmed Grinnell's conclusions. In particular, the simple models they derived showed that Grinnell's "axiom" could be mathematically confirmed and made more precise by restating it as "interspecific competitors can only coexist if the average intraspecific effects are greater than the average interspecific effect." This theoretical work received strong empirical support in the early 1930s by the work of G. C. Gausse, who showed that laboratory populations of protists matched the quantitative predictions of these models remarkably well (the axiom is actually often called Gausse's Axiom). This theory incorporated both responses and impacts to make the predictions, although the links to the niche concept were not made explicit.

George Hutchinson (1959) was the first to provide a rigorous definition of the niche of a species as the n-dimensional hypervolume in which every point corresponds to a set of environmental conditions allowing the species to exist indefinitely. His definition is very strictly focused on the conditions allowing the population of a species to have a stable per capita growth rate of zero or more. Retrospectively, it is clear that this definition does not deal with the impact component of the relationship.

Robert MacArthur and, later, David Tilman developed models of resource competition using Hutchinson's definition to establish how consumers respond to resources. This component of the interaction in their models is defined by the mapping of so-called zero net growth isoclines (or ZNGIs), whereby the response of the species as determined by its per capita growth rate is equal to zero. They also showed that local stable coexistence required that such ZNGIs cross (allowing for a possible equilibrium point), implying the presence of a trade-off in the responses of different species to different resources, so that each species has a greater relative impact on the resource that is most limiting to it (see Leibold, 1995).

Robert MacArthur and his students also developed an alternative approach to niche relations using "resource use functions," one that focuses on using Gaussian distributions to model overlap in consumption of arrays of resources. These models were used to evaluate questions about similarity (as measured by overlap in resource use distributions) and coexistence, and about the evolutionary dynamics of niche adjustments. This body of theory was tremendously influential in the 1970s but has since come under criticism, and many (but not necessarily all) researchers feel that the conclusions are of heuristic use more than anything else.

Robert Holt, James Grover, David Tilman, Mathew Leibold, and J. Tim Wootton have extended the use of the isocline models of MacArthur and Tilman to interactions involving predators, omnivores, and disturbances. The conclusions again show that local coexistence of species requires that each species be relatively more limited by a different environmental factor (so that the ZNGIs that describe their responses to different environmental factors cross) and that each species has a proportionately greater impact on the environmental factor that it is most sensitive to. These extensions of niche theory to address multiple trophic levels and multiple types of factors are important because they allow the niche concept to be used to evaluate ecological processes and phenomena as well as the coexistence of species that simply share resources.

Richard Levins and more recently Peter Chesson (2000) have also used mechanistic models to address how temporal and spatial variability affects niche relations. They again emphasize that it is not only the relative responses to variability that matter but also the relative impacts on variability that affect conditions for coexistence.

Because of criticisms leveled at the niche theory developed with resource use functions, recent work in ecology tends to avoid use of the term *niche*, even though the underlying idea that relationships between organisms and environment are key to understanding the distribution of species is still critical. One of the more pressing issues is the extension of the concept at scales larger than the local community level.

Extensions of the Concept

Although the niche concept has a central place in theoretical community ecology, it permeates almost all aspects of ecology and evolutionary biology. Of key importance is how diversity of species originates and is maintained. The fundamental insight to arise from the work on the niche is that sustained coexistence of species at any scale depends on trade-offs among such species in their responses to different environmental factors and (at least at the local level) related trade-offs in their impacts on the environment.

The dynamics associated with evolutionary adjustments of species to one another can be evaluated in terms of such trade-offs. Hutchinson made a distinction between the "fundamental niche" of an organism, describing environmental conditions that allow a species to exist in the absence of competing species, versus the "realized niche," describing environmental conditions that allow a species to coexist with another species. The realized niche is thus a subset of the fundamental niche when interspecific competition between pairs of species is involved and the set of environmental habitat conditions that allows a species to coexist with a competitor is smaller than the set of habitat conditions that would allow such a species to exist in the absence of competitors. Much work has gone into thinking about the evolutionary dynamics that result. Especially intriguing was the idea of "character displacement," which argued that species could evolve in response to the presence of competitors to reduce how similar they are to each other by diverging in their niche relations. However, recent work has shown that convergence is also possible or likely.

Case Studies

One of the biggest problems with the niche concept is that it is very open-ended. Although one can study particular environmental factors, one often can't tell if there isn't some unsuspected dimension of the "n-dimensional" hypervolume that isn't important. In the lab, the environment can be controlled so that these problems are minimal. The classic work by Gausse on protists and a number of subsequent studies using protozoans, bacteria, or algae (Grover, 1997) provide good support for the conclusions of niche theories. They provide good support for the so-called Gausse's axiom; they show that more complicated models such as those using ZNGIs are useful in understanding interactions among multiple species; and they show how environmental conditions such as resource supply, predation intensity, and the effects of stressors (for example, temperature, pH, and harvesting) and variability can alter the outcome of species interactions.

Under field conditions rigorous application of these explicit niche models is much more difficult, and there are very few examples that even begin to match the rigor of the lab experiments described above. Instead, the concept is often used in a much more heuristic fashion to interpret data in the context of the theory (Giller, 1984). Such case studies include the classic work on intertidal barnacles by Connell, who showed that the distribution of two species along a stress gradient is controlled by competition between them, such that each dominates only a part of the gradient. More recent work has illustrated the role of niche relations in evolutionary dynamics, the role of predators in modifying niche relations among species, and the role of species interactions on regulating the relative amount of biomass in different trophic levels.

Two intriguing and important recent applications of the niche concept involve its application to coexistence in larger so-called metacommunities (sets of local communities linked by dispersal), and its application to evaluating the role of species in the functioning of ecosystems.

—*Mathew Leibold*

See also: Ecology; Ecosystems; Food Webs and Food Pyramids; Nutrient/Energy Cycling

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Ecological Status of Modern Humans

Human beings (species *Homo sapiens*) evolved between 100,000 and 200,000 years ago (see Human Evolution). We are an omnivorous species, which means that we are able to consume a wide variety of plants, animals, fungi, and even microbial foodstuffs, depending on cultural norms (that is, what local society deems appropriate to eat) and availability. Over at least the past 2.5 million years (the date of the oldest known tools in the archaeological record), human beings have come to rely more and more on culture—learned behavior—rather than purely anatomical biological adaptations for "making a living"—that is, for obtaining the sources of energy and nutrients necessary to life. Increasing reliance on culture over purely natural adaptations has greatly altered humanity's relation to the natural world.

Like all other species in the history of life, all early species of hominid were closely connected with the world's ecosystems. Specifically, all species in the entire history of life are divided up into small, localized populations that form parts of the local ecosystem. This means that local populations of, for example, squirrels will be relying on the acorn production of the local oak trees as one of their sources of food; in turn, local species of hawks and owls will be preying on the squirrels, and so forth. All the local populations of different species are interacting in different ways in a complex network involving the flow of energy and nutrients from one population to another. The way in which each population goes about obtaining matter and energy is what is meant by the expression "its ecological niche."

Generally speaking, the way that local populations obtain their energy, and the way that their adaptations match up with existing resources, determine the number of individuals of that species population that can survive in any local ecosystem (this is the so-called carrying capacity of the local ecosystem). All hominid species, including the earliest members of our own species, *Homo sapiens*, have lived in this fashion—that is, as local populations playing roles (having a "niche") in the local ecosystem. Indeed, peoples known as hunter-gatherers still exist on the planet, and their preagricultural mode of life corresponds closely to the original ecological mode of existence of early humans. It must be noted, however, that modern humans have driven most hunter-gatherers to extinction, and the few remaining groups (such as the San ["Bushmen"] peoples of southern Africa and the Mbuti ["Pygmies"] of equatorial Africa) no longer live purely hunter-gathering existences; they are, at least culturally speaking, poised on the brink of extinction.

The invention of agriculture some 10,000 years ago changed the ecological status of humanity in a momentous fashion. No longer limited by the available productivity of the local ecosystems, with the domestication of plants and animals, humans effectively took charge of the production of all their food and nutrient needs. Nor does the invention of agriculture represent a simple modification of the human ecological niche: for what the coming of agriculture really did was to outright abolish the human ecological niche. Consider what it is to plant a field with one, two, or at most three plant species: it means clearing of the land (chopping down trees, removal of shrubs, brush, and native grasses) and preventing their return, while the one or two desired crops are allowed to grow. Native plants attempting to reclaim the land are now considered "weeds," interlopers in what was once their own territory. Thus, in effect, with the arrival of agriculture, humanity declared war on the local ecosystem.

No longer relying on the productivity of the local ecosystem, humans in effect had also declared their independence of it. Thus, a mere 10,000 years ago, *Homo sapiens* became the very first species in the entire 3.5-billion-year history of life effectively to step outside of the local ecosystem. One result of that step was a rise, slow at first but ever accelerating, even now, in human population numbers: no longer controlled by the productivity (carrying capacity) of local ecosystems, and despite the occasional devastating bouts of famine in human history, human numbers have skyrocketed from some 5 or 6 million 10,000 years ago (at the dawn of agriculture) to more than 6 billion at the recent turn of the new century—one of the causes of the present-day Sixth Extinction.

But recently there has been still another change in the human ecological condition. Over the past 10,000 years, as our numbers have grown so extraordinarily high, as we have spread around the globe, and in particular as our capacity for communication has so dramatically improved, we find ourselves as the only species in the history of life that maintains economic connections with each other over truly vast distances. Some other species—such as some fruit flies—also have a worldwide distribution, brought about by the spread of humans around the globe. But while fruit fly genes can spread throughout the globe as reproductive connections are occasionally replenished, what fruit flies eat in Tokyo has little to do with what their relatives are eating in New York.

But we are different. We exchange more than $1 trillion worth of goods and services among ourselves every day. This too is very new, this economic integration of our species. It implies that, as an integrated economic entity, our species after all must be part of some larger-scale economic system—the first species in the history of life to be part of an economic system. And what is that system—as it clearly cannot be the local ecosystem? Some biologists and biologically inclined economists now believe that *Homo sapiens* is actually the first biological species to act as a component with the entire biosphere—the totality of all the earth's ecosystems.

In any case, the ecological status of our species is unlike that of any other species that has ever lived.

—Niles Eldredge

See also: Agriculture, Origin of; Ecology; Economics; Ecosystems; *Homo Sapiens;* Human Evolution; Population Growth, Human; Sixth Extinction

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Ecology

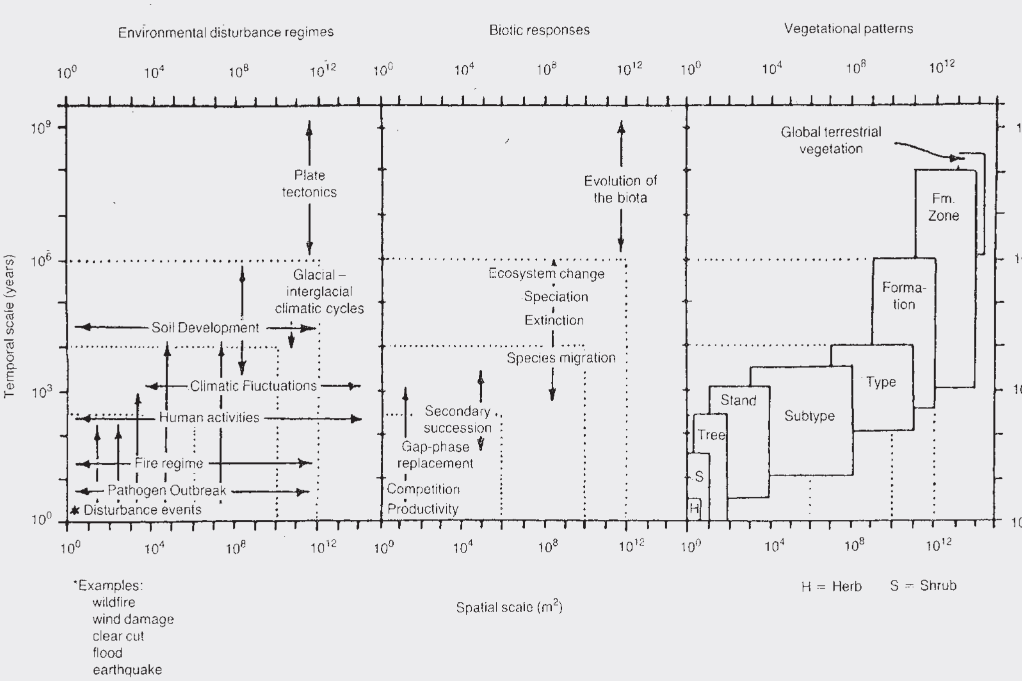
Ecology is usually defined as the study of interactions between organisms and their envi-

Composting garden waste. Ecology is associated with a political movement advocating government, business, and citizen involvement in taking responsibility for the ways that humans interact with life on earth. (Ecosystems/Corbis)

ronments, which nearly always includes other organisms. This definition covers a lot of territory: the function and adaptation of individual organisms of all kinds—from bacteria to gray whales—are included, as are the properties of population systems consisting of the local representatives of a single species, local ecosystems consisting of many different population systems, and larger, more inclusive systems at the regional up to the global scale. Some ecologists use an even broader definition: ecology is the study of interactions, distribution patterns, and abundance dynamics of organisms at varied scales of resolution. Ecology also is associated with a political movement that pushes for governments, institutions, and

Figure 1

Hierarchical Structure of Ecology



Source: Delcourt, Hazel, R., and Paul A. Delcourt. 1991. *Quaternary Ecology: A Paleoecological Perspective*. Figure 1.6, p. 18. London: Chapman and Hall. (Reprinted with kind permission of Kluwer Academic Publishers).

Note: A popular view of hierarchy in ecology, in terms of different disturbance regimes, forms of biotic accommodation and turnover, and traditional units used to describe terrestrial vegetation patterns. Other representations have been proposed, but this one is popular among terrestrial ecologists involved in developmental or historical studies of communities, ecosystems, and landscapes.

businesses, as well as individual citizens, to take responsibility for protection of endangered species, conservation of habitats, and, in general, the ways that humans interact with life on earth—to ensure the protection of biodiversity.

Scientific ecology is about different levels of interrelational organization within and among organisms, the past history of ecologic systems, the present and future composition and behavior of those systems, and the quest to identify generalizations about how life works. Or, one could simply use a definition introduced by the nineteenth-century biologist Ernst Haeckel: ecology is about the economy of nature. Although some ecologists are interested in purely scientific questions, most are now involved with the worsening problems created by the activities, by-products, and population expansions of humans, including habitat degradation and elimination, overharvesting of economically important species, intentional or unintentional introduction and spread of invasive species, and the associated collapse of modern biodiversity. Ecology can be seen as one of the two major divisions of biology, the other complementary and reenforcing division being evolutionary biology. In sum, ecology is the study of the way that organisms fit into the world.

Ecology, like all large scientific endeavors, can be divided into branches or subdisciplines that correspond to the different approaches used to study the economy of life. The branches of ecology correspond in most instances to the different organizational levels that can be studied. Although the grandest generalizations about how life works should apply to all levels of organization, sensitivity to scaling is one of the major concerns of modern ecology, because specific processes and patterns are associated with different kinds of ecologic units having characteristic sizes, time-related properties, and hierarchical positions. (The most important aspects of the ecologic hierarchy have to do with the fact that the systems of interest [individual organisms, populations, ecosystems] are divisible into component systems and at the same time are the components of more inclusive systems; interactions take place both within the different levels and between levels of organization.) The following list of subdisciplines illustrates both the diversity of approaches in ecology and the varieties of ecologic systems available for study.

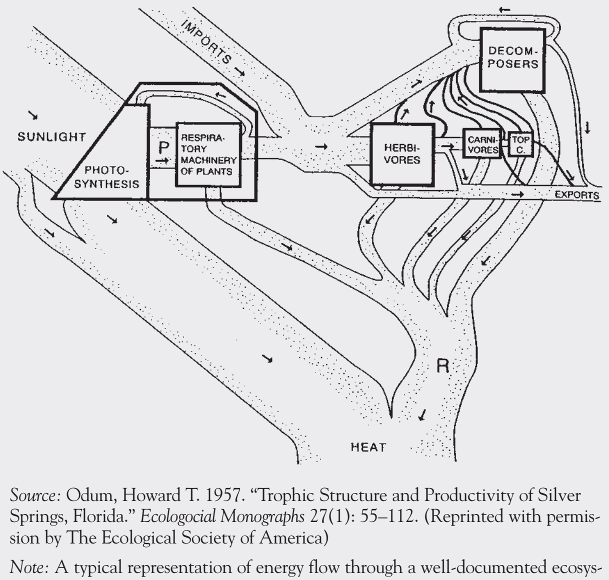
- *Chemical and physical ecology*—The description and interpretation of specific chemical reactions and physical processes occurring on a moment-to-moment basis and contributing to the survival and reproductive success of organisms of all kinds is called chemical and physical ecology. This is the most fundamental level of ecology. Chemical ecologists, for example, study the various chemical reaction pathways in photosynthetic plants having different ways of producing stable carbohydrates from the radiant energy of the sun. A physical ecologist would be interested in the physics of bird flight and might use computer models borrowed from mechanical engineering to help understand the processes involved.
- *Physiologic ecology*—Organization, function, and development of individual organisms and the chemical cycles and physical interactions of specific adaptations are studied at this level. Physiologic ecologists focus on the economy of individuals: the processing of food and respiration; fluctuations in functional properties during intervals of stress and ensuing relaxation; tradeoffs between moment-to-moment processes that support survival versus processes involved in production of offspring; individual costs or benefits from interactions with other individuals; and changes in physiologic properties caused by fluctuations in environmental factors such as temperature, salinity, or fluid pressure.
- *Behavioral ecology*—In the broadest sense, *behavior* is what an individual organism does; it is the way that organisms react to each other and manipulate their surroundings (including other organisms) to ensure survival and the leveraging of their genes into subsequent generations. Some organisms have rather minimal impact on their environments, while others appear to have the ability to re-engineer their surroundings to new specifications. Some make up social groups with complex internal behavioral processes. This branch of ecology is also called *ethology*.
- *Population ecology*—Localized groups of organisms belonging to the same species are *populations*. Populations are the natural divisions of local communities (from the point of view of patterns) or the working parts of ecosystems (from the perspective of processes), and they are sometimes referred to as avatars (local manifestations of the

same species). Colonizations, abundance changes, and local extinctions of these units are the things that interest population ecologists. Recent developments in this core discipline of modern ecology include the establishment of connections to genetics, the use of population studies to test evolution theories, and the widespread use of mathematical modeling techniques. The maturation of ecology as a rigorous scientific discipline resulted largely from the development of hypothesis-testing, laboratory and field experiments, a productive connection to evolutionary biology, and attempts to discover generalizations applicable to all kinds of organisms in this branch of ecology, beginning in the 1950s and 1960s.

- *Community ecology*—One of the fundamental observations of both ecology and of everyday experience is that different environments contain different groups of populations belonging to different species. Localized groupings may consist of organisms that co-occur for unrelated reasons, or that exist together in time and space because of shared environmental requirements or possibly obligate connections to each other. Describing and interpreting these groups of organisms is what community ecologists do. Some approaches to community study emphasize one important group of organisms (for example, a bird community, a deposit-feeder community), while other studies incorporate different groups (such as seasonal assemblages, or food chains). The basic method of study involves producing a list of species and estimating their relative abundances in a particular area or sample. Interestingly, few community studies have ever documented the entire biota of a specific area, because of time limitations on research projects and because no ecologist is an expert on all groups of organisms.
- *Ecosystem ecology*—Picture a local grouping of different organisms as consisting of living populations acting as the dynamic components that process energy and materials, changing through time on account of internal as well as external forces, influencing each other's abundance through interactions, and forming close connections with their surrounding habitats. This picture of

Figure 2

Energy Flow through an Idealized Ecosystem



Source: Odum, Howard T. 1957. "Trophic Structure and Productivity of Silver Springs, Florida." *Ecologocial Monographs* 27(1): 55–112. (Reprinted with permission by The Ecological Society of America)

Note: A typical representation of energy flow through a well-documented ecosystem (Silver Springs, Florida). Trophic (feeding) levels in the structure of the system are shown with boxes; amount of energy flowing between levels is represented by the width of the connections. P symbolizes gross primary production and R system respiration. Many ecosystems have energy flow networks that are more complicated than this one and have significant connections to adjacent systems.

connected, dynamic populations is a sketch of a *local ecosystem*. Ecosystem ecologists are interested in the function and development of local multispecies assemblies, and they often approach the description of such systems by identifying and quantifying the pathways of energy flow and nutrient cycling. In some studies, component populations are viewed as compartments or processors, and interactions between populations are the connecting pathways that give the system its structure. Whereas a list of species and the interpretation of how they connect to one another at a particular place are sufficient to draw an outline of a community, something like a circuit diagram is needed to document the organization and function of a local ecosystem.

- *Landscape ecology and macroecology*—The description and interpretation of systems of connected communities (*metacommunities*), networks of local population systems (*metapopulations*), regional ecosystems, and the large-scale patterns of species ranges, abundances, and body sizes all go into these branches of ecology. Viewing ecologic properties at the scale of regions is new and has grown out of a realization that the properties of local populations and communities have as much to do with regional processes as with local factors.
- *Global ecology*—The most ambitious attempts to generalize about the economy of nature come from very large scale studies that sometimes encompass the entire earth. Characterizations of major chemical cycles that involve organisms (for example, the carbon cycle), reciprocal interactions between life and global-scale environmental processes (such as the Gaia hypothesis), and large-scale pictures of productivity or the impact of humans on the biosphere fit into this branch of ecology.
- *Exoecology*—Interest in developing ways to detect life on other planets has grown rapidly in recent years because of the possibility of sampling the surface of Mars and because new planetary systems are being discovered by astronomers all the time—some of which may harbor life forms. Some of the same approaches used in global ecology would apply to the remote sensing of possible life on other worlds.
- *Conservation ecology*—This is the most active division of ecology, and it involves most of the approaches mentioned above in one way or another. Conservation ecologists study the impacts of human activities (including very large-scale problems of climate change, regional problems such as the spread of harmful invasive species, and more localized problems such as chemical pollution in a specific area) to understand the steps that need to be taken to preserve species diversity, habitat quality, and the integrity of ecologic systems. They are also actively involved in public education and the political activity needed to control or reverse these impacts, and they use ecologic methods and theory to propose remediation and preservation plans.
- *Paleoecology*—Paleoecology is the daunting task of doing ecology with fossils. Traditionally, paleoecologists tried to identify and interpret small-scale units such as populations and communities preserved in sedimentary rock formations. It is now appreciated that, owing to the way in which fossils accumulate in sediments, the paleoecologic record is not so much a document of short-term, small-area processes and patterns as it is a robust record of large, long-lived ecologic systems. Because some major taxonomic groups (such as bivalve and gastropod mollusks, articulate brachiopods, and corals with hard skeletons) are readily

preserved as fossils, the historical record of ancient metapopulations and regional ecosystems can be reconstructed in great detail. Recent developments include using paleoecologic patterns as baseline data in conservation ecology, using reconstructions of terrestrial plant assemblages to study climate change during the Quaternary Period, and the increasing awareness that ecology is not the backdrop but the driving force of evolution in many cases. In general, paleoecology is about large-scale, durable, inclusive units of organization; patterns in the history of life for which there is a fossil record but no modern counterpart to study; and the largest generalizations about ecologic processes and patterns.

- *Evolutionary ecology*—During the modern development of ecology, the connections between evolution and ecology were often ignored. Other than consideration of particular adaptations and niches of individual organisms or local populations, surprisingly little attention was devoted to the possible linkages between ecologic processes and evolutionary patterns. This is now a very vigorous branch of ecology that attempts to understand, among other things, the controls on adaptive radiations, the selectivity of extinctions, the nature of large-scale originations (for example, the "Cambrian explosion" of animal life) and replacements (such as mammals replacing dinosaurs after the end-Cretaceous extinctions), the perennial problem of latitudinal diversity gradients, and the reason that evolutionary rates at the level of populations observed in modern environments can be very fast but the evolutionary pattern of most species detected in the fossil record is one of morphologic stasis.

More effort than ever before will have to be expended in the early twenty-first century by new generations of ecologists to address the worsening biodiversity crisis, and it will seem increasingly difficult to justify purely documentational or theoretical work in ecology as the crisis unfolds. We must never forget, however, that progress in applied ecology depends on understanding fundamental properties of ecologic systems, proposal of new theories, ecologic interpretation of the fossil record, and on a thorough understanding of the natural history of organisms and the regions in which they live. It is also clear that the vigor of conservation ecology has both bolstered the importance and the workforce of ecology, and has quickened the pace and improved tremendously the quality of research on ecologic systems of all kinds. Ecology must continue to be a diverse endeavor, always ready with critical applications but continuing to illuminate the economy of nature in all of its forms.

—*William Miller III*

See also: Adaptation; Biogeography; Climatology; Communities; Conservation Biology; Ecological Niches; Ecosystems; Food Webs and Food Pyramids; Global Climate Change; Land Use; Nutrient/Energy Cycling; Succession and Successionlike Processes

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Economics

Economics is the study of human choices. Whether at the microlevel of the household or firm, or the macrolevel of nation-states, twentieth-century economics was primarily concerned with the choice of how best to allocate scarce resources to achieve individual, community, and societal goals. Maximizing efficiency has been the primary method of solving allocation problems at these varying scales. To do so, all units of a particular allocation problem must be valued in a common metric, most often money. This quest for an efficient, monetized allocation scheme led to the late–twentieth century dominance of market mechanisms and institutions in industrialized economies. Although originally conceived as the study of the "people's household," economics today is mostly concerned with the study of market choices in a variety of contexts.

Economics was not always so narrowly focused on the study of market behavior. The first economists of the industrial revolution were philosophers with broad interests and interactions with diverse pursuits of knowledge. The writings of Adam Smith, Thomas Malthus, and other classical economists are thought to have influenced Darwin in constructing his theories of evolution. However, a philosophy of economics grounded in contemporary knowledge of other disciplines and structured by physical resource scarcity and limits to technology has largely been abandoned in favor of a social science grounded in mathematical abstraction and a narrowly conceived theoretical architecture. Modern economic theory—applied to topics ranging from mate selection and stock market valuation to interest rate policy and environmental protection—is based on an axiom of efficiency by which optimal (the best) choice is determined at the point where marginal benefits of an action are equated with its marginal costs. The choice to produce or consume the next unit of a good or service is what economists refer to as a marginal choice, and it is argued as the basis for all efficient decision-making.

In a free market, in which consumers and producers are allowed to weigh their own marginal costs and benefits in making individual choices, the agglomeration of efficient individual decisions is argued as the social system that produces the most goods and services. This market distribution of maximum production—under constraints of labor, land, capital, and technology—does not consider allocation fairness, the scale of market activity, or any distinction between necessity and luxury goods. More is preferred to less in a system based on maximizing individual gains.

As economics is the dominant social science and preeminent advisor to nearly all levels of governance and policy-making, understanding its implications is paramount to protecting biodiversity. Economics as taught in most educational institutions has three major implications for the protection of biodiversity. First, decision-making based on principles of economics has no consideration for the scale of any activity. More goods and services are always preferred to less. Whether a particular resource allocation takes up more or less resources does not influence its adoption. A science of choice without self-imposed limits can be pursued only at the competitive exclusion of all other uses of energy and raw materials, and thus poses a fundamental threat to the biodiversity that all life depends upon.

The second major implication of economics on biodiversity has been its influence in the design of programs to manage and protect biodiversity in accordance with market principles. Many environmental protection policies must be justified on both economic and scientific grounds. Economic criteria revolve around measuring marginal costs and marginal benefits. This requires placing monetary value on nonmarket goods (such as biodiversity) in order to construct tradeoffs between conflicting resource uses. Economists have developed methods for imputing monetary value to natural resources and ecosystem services, including individual species. In this manner, the monetary value of a species or ecosystem can be compared with the monetary value of goods and services forgone for its protection. However, although such valuation can be a useful exercise for policy-makers in certain well-defined contexts, it cannot guarantee biodiversity protection. In fact, monetary valuation implies substitutability between market and nonmarket goods and services, a dangerous implication in the case of biodiversity that has no manufactured equivalent. A significant literature has demonstrated the “rationality” of driving a species to extinction under a market system of choice and a monetary measure of value.

A third implication of standard economic theory on biodiversity is the use of marginal units of analysis and continuous functions of change. Central to economic theory is the notion that optimal decisions must be made at the margin. In other words, it is only the next unit of a resource consumed or output produced that matters in the calculus of optimal decision-making. However, attention to the next unit fails to consider irreversibility, feedback loops, discontinuous change, and other complexities inherent in natural and social systems. A science of choice based on marginal change applied in a setting that does not respond predictably can result in unintended consequences.

Standard economic theory has come under intense criticism from both its practitioners and from natural scientists who seek to understand its implications on fundamental ecosystem services. Recent cooperative efforts between economists, other social scientists, and natural scientists have made gains in creating an economics for the twenty-first century that is more holistic in approach, broader in scope, and interdisciplinary in content. For instance, the transdiscipline of ecological economics argues for well-defined limits to substitution, minimum stocks of natural capital, preservation of ecosystem function, and a focus on resilience over optimality.

Jon D. Erickson

See also: Industrial Revolution/Industrialization; Sustainable Development; Urbanization; Valuing Biodiversity

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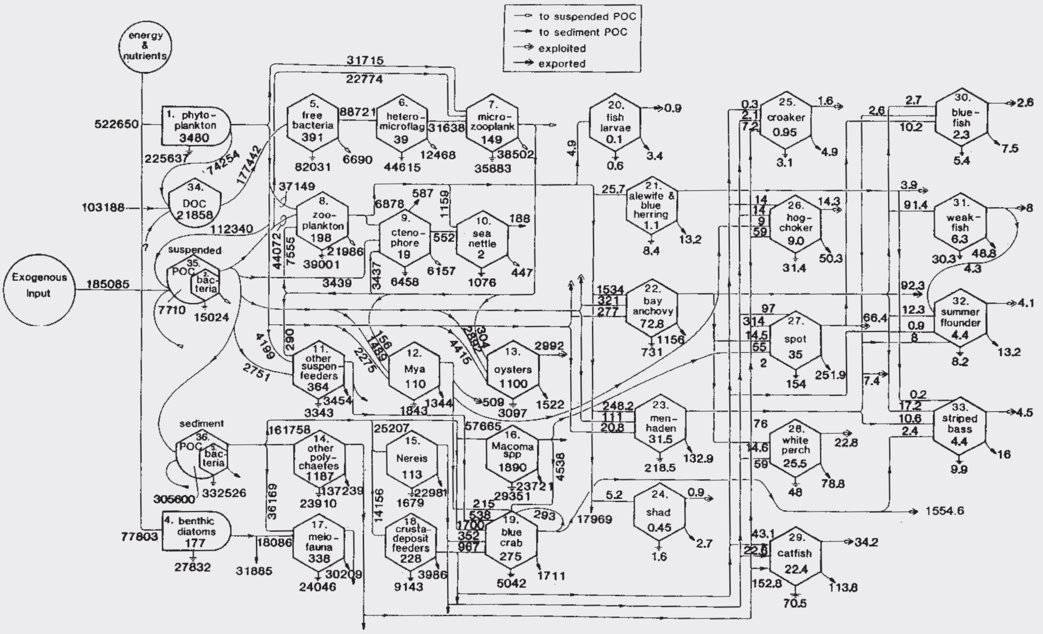
Ecosystems

Ecosystems consist of co-occurring organisms, their connections to each other and to surrounding environments, and the parts of their environments that are controlled or incorporated into their lives to such an extent that sep-

Figure 1

The Flow of Carbon among Components of the Chesapeake Bay Ecosystem



Source: Baird, Daniel, and Robert E. Ulanowicz. 1989. "The Seasonal Dynamics of the Chesapeake Bay Ecosystem." *Ecological Monographs* 59(4) 329–364, fig 2.(Reprinted with permission)

Note: The complex connections and the numerous components are typical of such systems, which may be much more complicated than this example. The "bullets" represent autotrophic system elements (plants); hexagons, heterotrophic taxa (fauna); and "birdhouses," nonliving storages. DOC = dissolved organic carbon; POC = particulate organic carbon. Numbers inside each box are the standing stocks in mg/m^2.

aration of the life-forms from physical-chemical factors becomes hard to justify. One way to look at ecosystems is to think of them as communities with all of the energy and materials pathways mapped out—communities, by comparison, would be the representations of the composition and structure of local ecosystems. An ecosystem, in a sense, is a dynamic picture of a community with the functional and developmental processes painted in, so that assemblages are seen as a kind of collective living entity. This viewpoint considers ecosystems to be natural, localized divisions of the biosphere. Another way to look at them is from a systems point of view, in which interacting populations are connected in a network of compartments representing the different organisms, with the connections being all of the quantifiable energy transfers or material cycles. This is a more pragmatic point of view that does not necessarily admit the natural reality of ecosystems but simply explores such systems using the perspective of a circuitry diagram or a flow chart. The functional identity of the ecosystem depends mostly on the flow of energy and chemicals. In ecosystem ecology, the emphasis is on processes. In community ecology, the emphasis is mostly on composition and pattern.

Although ecosystems are usually pictured as local functional networks of organisms together with their connections to environments, larger systems are often studied using the same systems approach. These more inclusive, regional systems appear to consist of smaller local ecosystems, the functional components of which are population systems (sometimes called avatars). This nested pattern of dynamic systems has led some ecologists to consider the economic aspects of life on earth as an ecologic hierarchy consisting of differently scaled entities that process energy and materials, undergo developmental changes over time, and simultaneously interact with other systems at the same level of organization, their own component parts, and their encompassing system. This is a complicated picture of the economy of life, but it is probably a more realistic one than thinking of ecosystems as simply the parts of nature that are interesting or significant enough to study using systems methodology and flow charts. This means that in order to understand how a local ecosystem functions and develops over time, one must investigate the patterns and processes at the focal level of the local system, properties of the component parts (providing what are called initiating mechanisms) that characterize each local system, and the processes going on in the surrounding larger system (providing what we call the boundary conditions). In other words, ecosystems do not function and develop in isolation: they are the products of their own internal dynamics and the larger-scale interactions taking place at local to regional levels of organization.

Some ecologists think that ecosystems can be studied adequately by dissecting the systems and measuring all the characteristics of organization and movements of energy and materials (this is referred to as the reductionist approach). Others argue that such systems display what are referred to as emergent properties: not only do the larger, more inclusive systems have process rates obviously different from the faster rates in the component sys-

Table 1
Major Divisions of the Ecologic Hierarchy

- Biosphere[1]
  - Provincial systems
    - Regional ecosystems
      - Biotope systems[2]
        - Local ecosystems
          - Interaction cells[3]
            - Population systems (avatars)
              - Individual organisms and colonies
                - Functional divisions of organisms[4]
                  - Cells involved in economic functions
                    - Molecular systems[5]

Each system in the hierarchy interacts simultaneously with similar systems at the same level, its component systems, and with a larger encompassing system. Systems at relatively higher positions in the hierarchy tend to be larger, longer lived, and exhibit slower process rates compared to systems at lower levels.

[1] All living organisms and their interactions; the most inclusive level of ecologic organization on Earth

[2] Constellations of closely connected local ecosystems

[3] Population systems ("entourage") within local ecosystems organized around a "hub" species that provides a significant resource (food, space, habitat structure)

[4] Includes organs and tissues involved in moment-to-moment survival of an organism

[5] When decomposed, this level reveals parts of cellular metabolic cycles and pathways of molecular synthesis

tems, but, in addition, differently scaled systems appear to be able to do different things. A single population system cannot form and maintain a food web or undergo succession, but a local ecosystem can; individual organisms may damage or destroy one another, but a predator-prey interaction results in a transfer of energy between processor levels, giving the overall system a part of its functional identity. In ecosystem ecology, ecologists probably have done more to own up to the complex organization of life than in any other branch of biology, because here they investigate various levels in the ecologic hierarchy simultaneously.

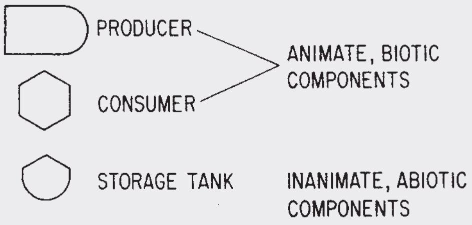
Components and Connections

The measurement and description of community attributes (see Communities) help to outline the framework of local ecosystems, but they reveal little about how such entities work. Instead of picturing the components as entries in an inventory of species that live together in the same place at the same time, the working parts of ecosystems are seen as energy-materials processors.

Interactions between population systems (primary consumption, predation and parasitism, commensalism and mutualism) are the channels that connect the processors, often in complex networks that change along environmental gradients and over time. Such systems also contain pools, or reservoirs, that temporarily store energy and chemicals. The component population systems undergo changes owing to natality-mortality and emigration-immigration dynamics, controlled both by intrinsic factors (such as the amount of primary production, competitive interactions, grazing/predation, and the products of habitat-altering organisms that re-engineer proximal environments) and extrinsic forcing or control (climate, hydrography, geology, disturbance regime, imported resources, and invasions). Action at each processor includes intake, metabolism/respiration/waste produc-

Figure 2a

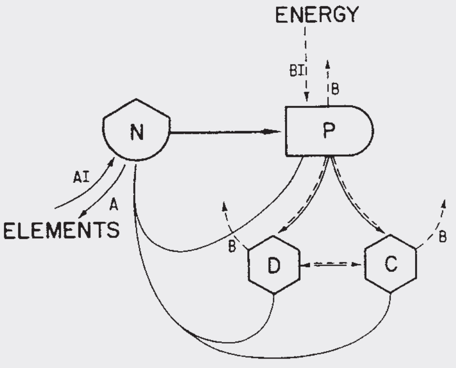
Howard Odum's Energy Symbols for Biotic and Abiotic Components



Note: The working parts of ecosystems are idealized as energy-materials processors. The components include organisms that function as producers and as consumers and also abiotic storage compartments.

Figure 2b

Generalized Static Model of Energy and Element Flows and Cycles in Ecosystems



Note: Solid lines = flow of materials (A). Dotted lines = flow of energy (B). N = nutrient pool. P = primary producers. C = Consumers. D = decomposers.

Source: Pomery, Lawrence R., and James J. Alberts, eds. 1988. *Concepts of Ecosystem Ecology*. New York: Springer-Verlag. figs 3.2 and 3.3, p. 45. (Reprinted with permission)

Mountains, forest, and pond in the American West. (USGS)

tion, leakage into the surrounding environment, and output to other processors or sinks. In terms of energy capture and transfer, ecosystems can be supported by either photosynthetic or chemosynthetic primary producers, or by detrital material imported from an adjacent system. In terms of chemical flow, ecologists usually focus on measurement of the most essential nutrients (C, N, P, Ca, K, and Fe in terrestrial systems, which have been studied extensively).

Kinds of Ecosystems

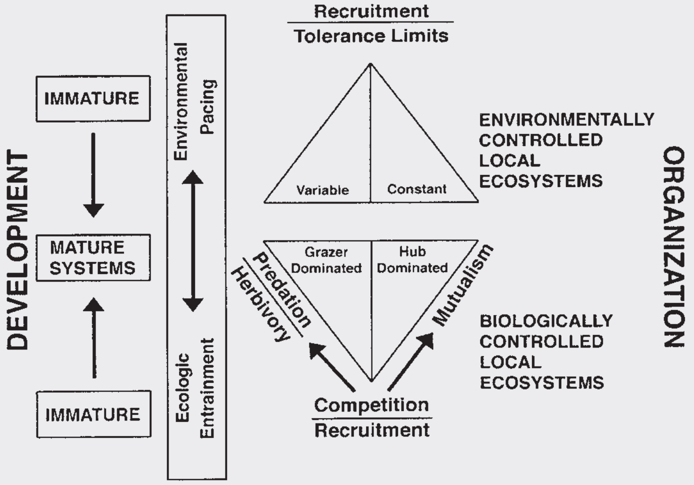
The simplest classification of local ecosystems involves associating such systems with unique environments—a biogeographic classification. An ecosystem inhabiting the floor of a submarine trench—receiving most of its resources from an adjacent landmass as phytodetritus and experiencing disturbances only from burrowing organisms bulldozing other organisms aside and from extremely rare turbidity currents—is strikingly different from a temperate forest system whose energy requirements are supplied entirely by photoautotrophic plants and that is subject to both seasonal fluctuations in climate and frequent storms. In other words, different environments support different kinds of ecosystems. This is one of the oldest observations of ecology.

A more general classification is based on whether function and development are shaped by extrinsic forces, or are mostly the result of internal dynamics—a classification emphasizing controls.

Ecosystems that are environmentally controlled are paced from the outside and are typical of rigorous, stressful settings. Such systems vary in structure and function with either aperiodic or seasonal change in environmental factors. These systems exist essentially at the whim of the surrounding environment. Adaptations have to do mostly with physical and chemical factors that define the environment. Biologically controlled ecosystems have structural and functional properties that result more from internal interaction of the population systems, resulting in habitat modifications, recuperation of resources, coevolutionary adjustments, and developmental self-regulation. Adaptations in this kind of system would have as much to do with biologic interaction as with the external environment, and could involve instances of incorporation (that is, exploitation of formerly deleterious aspects of the environment—for example, adaptation to fire in some terrestrial plant assemblages) or habitat engineering (that is, restructuring proximal environments—for example, beaver dam-lodge-pond complexes). The ecosystem of a mountain spring, which must endure dramatic changes in water availability and quality, a harsh climate, and must depend on the irregular recruitment of organisms from distant sources, would be environmentally controlled. A tropical forest, having an elaborate network of mutually compensating and regulating interactions among thousands of species, many of which are organized into cells consisting of a central species with an entourage of intimately associated organisms, and experiencing only small-scale disturbances from occasional tree falls, would be an example of a biologically controlled system.

Figure 3

Simplified Classification of Ecosystems



Source: Based on Miller, William III. 2002. "Regional Ecosystems and the Origin of Species." *Neues Jahrbuch Für Geologie Und Paläontologie, Abhandlungen* 225:137–156, fig. 1. (Reprinted with permission)

Note: Ecosystems can be classified based on whether function and development are caused largely by external or by internal processes. Environmental pacing (such as climate) could control local ecosystems that fluctuate irregularly in terms of vital functions and composition or remain stable or undergo regular cyclic changes. When internal processes become important, systems may be dominated by key predators or grazers, or by hub species that organize retinues of mutualists. Most of the local ecosystems that have been studied so far fit into one of the four major categories shown here.

Stability and Change

In many ecosystems that have been studied carefully, the networks of interconnected population systems are able to maintain the functional identity of the overall system during times of disturbance, as long as disturbances do not exceed some threshold beyond which a radical reorganization results. Holding the line against disruption is called homeostasis if systems are at equilibrium prior to the insult, or homeorhesis if systems were tracking a developmental trajectory instead of being in true

Sparse vegetation in Quatar (UN photo/P. Sudhakuan)

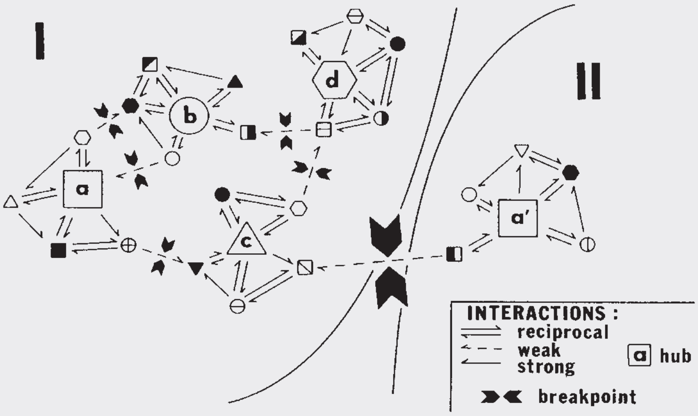
dynamic equilibrium. Systems consisting of interconnected dynamic subsystems (for example, populations of living organisms that form nodes in interaction networks) can maintain stability through what is called resilience, if they are capable of bouncing back to the original state or homing in again on their previous developmental trajectory. This is like a ping-pong ball being pushed below the surface of water in a tub, then being released to pop back up to the surface again. The rate of such a recovery is a quantitative estimate of the stability of a dynamic system; this is the kind of stability that most ecologists think about when they consider the durability of ecosystems.

Other systems display what is referred to as persistence stability by holding out for a long interval before finally succumbing to disruption, possibly owing to the special adaptations of key components of the system (body armor, special physiologic devices, versatile behavior, use of special structures as domiciles). This is like the strong wooden door of a fort that gives way to the battering ram only after application of repeated, energetic assaults. And still others, having developed an internal network of population systems that includes a kind of defense-in-depth resulting from a modular organization of functional parts around dominant species, show resistance stability by being able to sacrifice subunits but still maintain significant aspects of overall functioning. This is like a very complicated machine or information system that can partially break down but continue to perform its vital functions.

In any case, if the ability of an ecosystem to persist or rebound after disturbance is exceeded, the system degrades and collapses; it finally undergoes ecosystem replacement, as a new system is built up at the same location either from the durable remnants of the previous system (the physiologically robust species, resource generalists, organisms with resting stages) or from invading species able to exploit or tolerate the new environmental factors.

Figure 4

Resistance Stability in Ecosystems



Source: Miller, William III. 1996. "Ecology of Coordinated Stasis." *Palaeogeography, Palaeoclimatology, Palaeoecology* 127:177–190, fig. 3. (Reprinted with permission)

Note: Resistance is one source of stability in ecosystems. Systems that exhibit resistance stability have a "defense-in-depth" structure of subsystems that can be sacrificed during disturbances without causing the collapse of the encompassing system. The system cleaves naturally at breakpoints, as in this diagram showing local systems organized around hub species. The local systems are in turn connected to form a larger regional ecosystem, with breakpoints at a larger scale.

The Origin and Fate of Ecosystems

The first 3 billion years or so of life on earth were dominated by prokaryotes, life forms we collectively refer to as bacteria but that really include a vast array of simple organisms (for example, archaea, cyanobacteria, and other forms having a similar grade of cellular organization). Such organisms must have formed ecosystems, with possible early chemoautotrophy giving way to later photoautotrophy as the major forms of primary energy capture. Although the organization and function of these earliest systems is poorly known, we can be sure that the economic aspects of life were transformed radically with the appearance first of large-bodied animals in the oceans (at the Proterozoic-Phanerozoic transition, roughly 500 to 600 million years ago) and later with the appearance of large plants on the land (in the Silurian and Devonian periods, roughly 360 to 440 million years ago). That is when the level of complexity that characterizes modern ecosystems first appeared. There is a controversy among paleontologists about how explosive the "Cambrian explosion" of animal life really was: was it truly a time of extremely rapid evolutionary innovation and divergence; or were these processes taking place through the Late Proterozoic, with the "explosion" being more a sudden appearance of large, skeleton-bearing derivatives of previous evolution? The most reasonable interpretation is that the explosion was a major economic event more than anything else, involving the appearance of big, energy-hungry organisms, intricately organized networks of interactors, feedback loops with recuperators, storage sinks, and new ways to exploit opportunity, manipulate the environment, and maintain systems in equilibrium. The Cambrian explosion and the later appearance and spread of land plants were ecologic revolutions, and ecosystems were the things that were revolutionized.

Individual ecosystems are characterized by intervals of initial organization and establishment (called primary succession in local ecosystems), a life span that includes long periods of normal functioning and development punctuated by disturbances and recoveries of various magnitudes, and a final interval of degradation and collapse. Ecologists have been interested mostly in the function and development of local systems, and they have paid little attention to the "birth" and "death" of larger, regional ecosystems. These are the times when evolutionary and ecologic processes intersect in many crucial ways, as migration, speciation, and extinction rates are all accelerated to produce what is known as turnover pulses. Most of the characteristics of established ecosystems, such as composition, organization, and dominant processes, are "discovered" and "formalized" during these pulses, yet little is known about exactly how this works in terms of the interplay of evolution and ecology. The biodiversity crisis is spiraling out of control, providing many grim opportunities to observe and finally to make generalizations about how these events actually work. If conservation efforts are ultimately fruitless, and many different kinds of ecosystem are degraded and collapse simultaneously, there could be a "surrendering of the lease" from the large, varied organisms that have characterized complex Phanerozoic ecosystems to the previous owners/operators of the biosphere—the prokaryotes

—William Miller III

See also: Bacteria; Biogeography; Carbon Cycle; Coevolution; Communities; Food Webs and Food Pyramids; Global Climate Change; Nitrogen Cycle; Nutrient/Energy Cycling; Oceanic Trenches; Positive Interactions; Succession and Successionlike Processes; Tropical Rain Forests

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Embryology

Embryology is the study of how organisms develop from a single cell to a multicellular form. The term *embryology* is often used interchangeably with the term *developmental biology;* embryology, however, connotes a more classical approach to the field and is restricted to the study of the stages of development from fertilization of the egg to hatching, or birth. By contrast, developmental biology connotes a more modern approach and encompasses the entire life cycle of an organism, including the differentiation of egg and sperm, reproduction, embryogenesis, hatching or birth, metamorphosis, aging, and death. In spite of the different names, however, both embryology and developmental biology share a single common goal of unraveling the complex biological manner in which a multicellular organism is constructed.

Embryology can be divided into three major subfields. The first and oldest subfield of embryology is descriptive embryology. A descriptive embryologist is interested in understanding the basic structural patterns of the embryo. This can be accomplished by simply observing a developing embryo, using either a microscope or the naked eye. Often, however, the embryo will be preserved at different stages; it is analyzed by preparing thin cross-sections, mounting the sections onto glass slides, and observing the sections through a microscope. Modern approaches to descriptive embryology include using time-lapse cinematography or advanced microscopy to observe developing embryos.

Another subfield of embryology is experimental embryology. An experimental embryologist is interested in understanding how development works by posing hypotheses and testing them through the controlled manipulation of embryos. Experiments typically involve removing tissue from a developing embryo, grafting that tissue to another part of the embryo, and observing the effects. The study of developmental regulatory genes—genes that control developmental processes—also falls under the umbrella of experimental embryology. A genetic approach to experimental embryology includes locating or manipulating a particular developmental regulatory gene and observing its effects on the developing embryo.

The third subfield, comparative embryology, involves the study of two or more different species of organisms in order to gain insight into the similarities and differences in their development. Comparative embryologists are typically interested in investigating the embryo's role in evolution. The basic assumption behind comparative embryology is that new life forms must have evolved through changes in the developmental program of their ancestors, and insight into evolution may therefore be gleaned by comparing the development of diverse organisms. Understanding where and when the developmental programs diverge between distinct organisms has been a traditional approach to the subfield. More recently, understanding the role of developmental regulatory genes in diverse organisms has been the focus of comparative embryological studies (see Embryology Today, below).

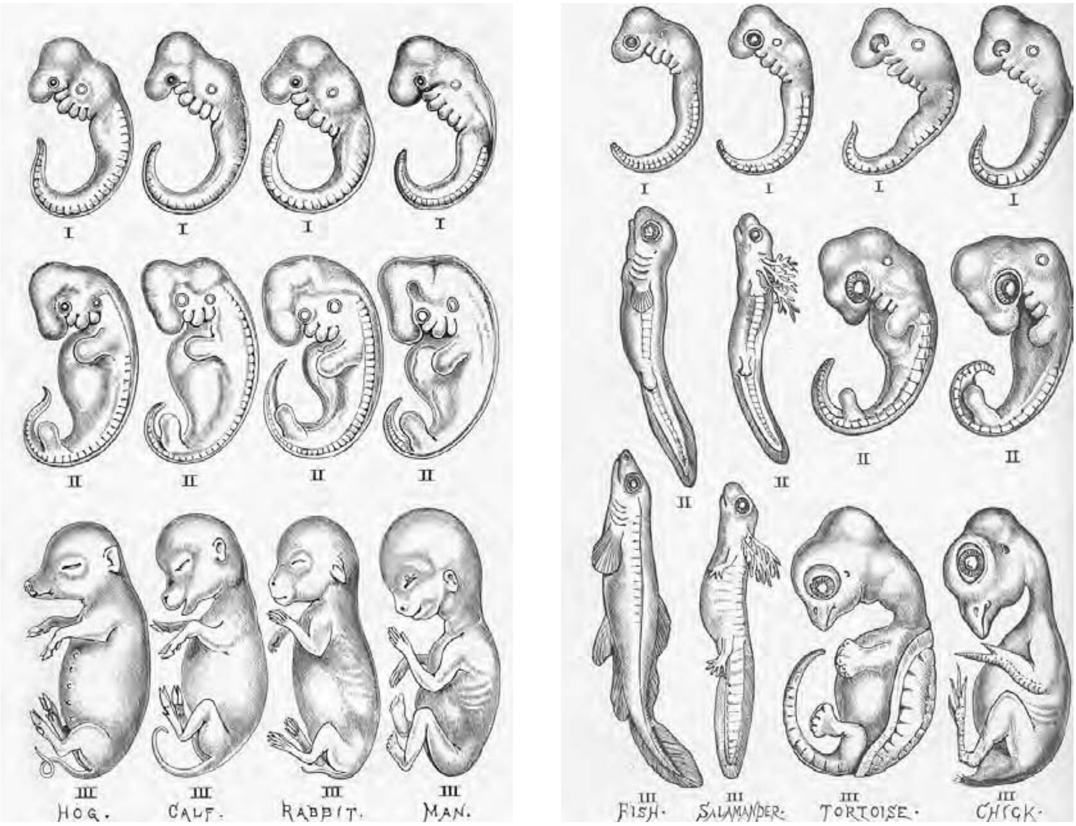
History of Embryology

Embryology has long been regarded as an important discipline for understanding the diversity of life forms. In the early 1800s, life was viewed as a continuous chain of increasing biological complexity, termed the chain of being. The development (or ontogeny) of an organism was in turn thought of as paralleling this chain of being, in that during its embryology, a higher organism passed through all of the adult stages of organisms found lower on the chain. This idea was termed the law of parallelism, and it dominated the field of embryology for the first part of the nineteenth century until it was refuted in 1828 by embryologist Karl von Baer.

Von Baer did not accept the notion that all of life formed as a single, continuous chain. He instead claimed that organisms are divided into four different groups, each of which shares similarities in its early development. Von Baer asserted that within a particular group, the more general features appear earlier in development than the more specialized features, and that the more specialized features develop from the more general ones. Using this concept, it would be impossible for an embryo to pass through adult forms of a lower animal, because development proceeds from the general to the specific, and not as a succession of specific adult forms. These ideas are today known as von Baer's laws (1828), and they remain valid as a framework for comparative studies in embryology. Following the publication of von Baer's laws, Charles Darwin addressed the importance of embryology for understanding evolution in his *Origin of Species* (1859), when he stated: "Community of embryonic structure reveals community of descent," which mimicked the ideas of von Baer in evolutionary terms.

Until the mid–nineteenth century, embryology was held to have a central role in revealing evidence for evolution, but its actual role

Figure 1
Illustration of Karl von Baer's Laws



Source: Romanes, G. J. 1896. *Darwin and after Darwin*. Chicago: Open Court Publishing, figs. 57–58, pp. 152–153.
Note: Early vertebrate embryos are indistinguishable, but as development proceeds the embryos develop characteristics unique to their species

in the evolutionary process remained vague. Ernst Haeckel (1866) was the first to actually suggest a mechanism for embryology in evolution; he asserted that ontogeny recapitulates phylogeny. This idea was referred to as the biogenetic law, and it was similar to the law of parallelism in that it proposed that during its development, an organism passes through all of the adult stages of lower forms. The major difference between the biogenetic law and the law of parallelism was that Haeckel cast his theory in evolutionary terms. He proposed that in evolution new features are added to the end of an organism's ontogeny, with the earlier stages being either condensed or deleted. According to Haeckel, careful scrutiny of an organism's embryology could reveal evidence of its evolutionary history.

The biogenetic law fell out of fashion in the late 1800s, when embryology transformed from a field that was mainly descriptive to one that was primarily experimental. This transformation was led by the embryologist Willhelm Roux, who in 1894 introduced a new journal, *Developmental Mechanics*. With the establishment of this journal, a new standard was set for embryological studies. Roux and others claimed that embryology must be explained mechanistically, and that can be accomplished only through experiments and not through observation. Evolution was viewed by this new generation of embryologists as too speculative and therefore no longer important for the field of embryology.

Evolution and development would not become reunited again until the late twentieth century, under the auspices of a new field called evolutionary developmental biology. Evolutionary developmental biology seeks to connect the mechanisms of development to the diversity of life forms. This new synthesis is now possible because of the recent conceptual and technical advances in embryology (see Embryology Today, below).

Homology and Embryology

One of the most important concepts to the field of embryology is homology. The term *homology* is often used to imply similarity by descent. The statement that a bat's wing is homologous to a human's arm implies that these two structures originated from a common ancestral forelimb. Because we cannot identify the exact ancestor to test this statement, embryological evidence is often used as the criterion for identifying structures as homologous. A bat's wing and a human's arm are homologous because developmentally they arise from the same tissues, are controlled by the same developmental regulatory genes, and produce anatomically similar structures in the same developmental order.

The concept of testing homology through developmental information can become obfuscated. For example, the eye of an insect and the eye of a vertebrate perform the same function, but they are not generally accepted as homologous structures, because they undergo distinct developmental pathways and are anatomically very different. Paradoxically, the vertebrate eye and the insect eye are both controlled by homologous developmental regulatory genes, *Pax*–6. It is now accepted that homologous genes can act on nonhomologous structures, and in turn the development of homologous structures can be controlled by nonhomologous genes. This new hierarchical view of homology reconciles some discrepancies that biologists encounter when using embryological data as a means of identifying homology.

Heterochrony

Heterochrony is a general term used to describe evolutionary changes in the timing of development. Heterochrony can produce subtle differences between organisms (such as the advance or delay in the appearance of structures) or huge differences (such as the evolution of a direct-developing salamander that lacks a larval stage from an ancestor that has a tadpole stage in its lifecycle). Many of the changes in development that are important to the evolutionary process are thought to occur through heterochronic processes.

Two major categories of heterochrony that occur during evolution are neoteny and progenesis. Both neoteny and progenesis are a result of the retardation of development such that the adult descendant resembles a juvenile of the ancestor. Neoteny refers to the general retardation of development, whereas progenesis refers to the truncation of development caused by the precocious onset of sexual maturation. Humans are thought to have evolved by neoteny, as many features of human adults appear to be retained juvenile characteristics of their primate ancestors.

Embryology Today

The current field of evolutionary developmental biology (or "evo-devo") seeks to understand the evolution of embryonic development and how modifications in development can lead to the production of novel features.

Through advances in systematics, there is a better understanding of the evolutionary relationships between organisms. Within such a framework, evolutionary developmental biologists can now address questions about what developmental changes might be important to evolution and how those changes came about. This once seemed like a daunting task to the mid-twentieth-century embryologist, but recent advances in developmental biology have created exciting new avenues of research for those interested in understanding the developmental basis for life's diversity.

The modern-day unification of embryology and evolution can be traced back to the mid-1980s with the discovery of a group of developmental regulatory genes called Hox genes. Initially discovered in insects, Hox genes were subsequently discovered in every major animal group. These genes were found to be highly conserved in their DNA sequence, chromosomal structure, and function. For instance, when the DNA sequences of these genes were compared, they were found to be remarkably similar in distantly related animals. In insects and mammals, these genes were found to be linked in groups along chromosomes, and expressed sequentially along the developing embryo. In addition, in insects and mammals, the Hox genes were found to play similar roles in providing cues for the proper placement of organs in a developing embryo. The remarkable conservation in structure and function of the Hox genes makes them particularly interesting for comparing developmental programs across distantly related animal groups.

In addition to the Hox genes, other developmental regulatory genes and gene pathways have been found to be highly conserved. For example, genes that control the development of limbs in insects also regulate limb development in mammals. Insects and mammals also share the same genetic controls for the development of eyes (see Homology and Embryology, above). From these discoveries, it appears that all of animal life shares a common developmental blueprint. Parallel discoveries have also been made in plant development. Genes that control how flowers develop are conserved across all of the flowering plants. These new insights into evolutionary developmental biology have revealed that the diversity of life evolved not so much from the evolution of new genes as from the application during development of ancestral genes in new ways.

—*Paulyn Cartwight*

See also: Evolution; Evolutionary Biodiversity; Evolutionary Genetics; Molecular Biology and Biodiversity; Zoology

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Endangered Species

Certain species of plants and animals have been officially recognized as being in particular danger—the danger of imminent extinction. An "endangered species," as defined by the International Union for the Conservation of Nature (IUCN), is one that is in danger of extinction throughout all or part of its range (Hilton-Taylor, 2000). The list of endangered species includes plants and animals of diverse types. Some endangered species are well known, and their plight garners a great deal of concern from the public. Other endangered species are nearly anonymous, but as members of the fragile web of life their survival is as significant as that of the most celebrated species.

Endangered species in the United States are protected under one of the most powerful environmental protection mandates ever enacted. The 1973 U.S. Endangered Species Act (ESA) expanded the definition of "endangered species" to include subspecies, and it specifies criteria used to determine the degree of the threat. These criteria include current or threatened habitat destruction, overexploitation, excessive losses caused by disease or predation, inadequacy of existing laws to protect the species, or "other natural or manmade factors affecting its continued existence." Restricted ranges and fragmented populations frequently make endangered species more vulnerable to the effects of climate change and stochastic events because of reduced genetic variability within the populations. Being listed as endangered provides legal protection from harm for individuals of the species and prohibits federal agencies from authorizing, funding, or carrying out any action that is likely to jeopardize its continued existence—including habitat destruction. It also mandates that recovery plans be developed. The Endangered Species Act also carries protection a step further, by including as one of its stated purposes the conservation of ecosystems upon which endangered and threatened species depend (U.S.F.W.S., 1989).

The Endangered Species Act has had some notable successes, including the bald eagle (*Haliaeetus leucocephalus*) and the peregrine falcon (*Falco peregrinus anatum*). These American bird species were listed as endangered in the late 1970s, when it became apparent that their populations had declined to perilously low levels. One of the key factors contributing to the decline of these raptor populations was the pesticide DDT, which caused the birds to lay eggs with weak shells and resulted in increased chick mortality. Pollutants like DDT accumulate within the food chain, and species at the top of the chain acquire the greatest burden. Habitat loss and persecution by humans were also significant factors in the decline of bird of prey populations. Bald eagles, forced to compete with humans for fish, were routinely shot by fishermen who were reluctant to share their catch. Peregrine falcons suffered from the encroachment of human populations on their habitats.

As a result of the ESA mandate, the use of DDT was abolished, vital habitat was protected, and heavy penalties were levied against those who harmed the birds. Also, intensive and successful breeding programs were established for peregrine falcons. As a result, bald eagle populations have made substantial recoveries, and the species has been down listed to "threatened" status; it has been proposed that it be delisted entirely. Eastern populations of peregrine falcons have rebounded from a low of a few hundred breeding pairs to 1,593 wild breeding pairs in 1998. Western populations have similarly increased. Peregrine falcons have taken up residence in urban areas, nesting on skyscrapers; they were formally removed from the endangered species list in 1999.

In contrast to the success of the protection efforts that made possible the recovery of the bald eagle and peregrine falcon, other endangered species have not fared well, despite a high degree of public awareness and concern. The tiger (*Panthera tigris*) is one example of an endangered species that has continued to decline despite all efforts at protection.

The tiger is the largest living representative of the cat family, and adult males can reach weights of more than 250 kg. These majestic animals once occupied a diverse array of habitats ranging across Asia and south to Iran and Indonesia. Several geographic subspecies were recognized, including three (Bali, Javan, and Caspian) that are now extinct. Although as

A dried tiger foot displayed by a vendor at a trading post in China's Sichuan province. Tiger parts are sold on the black market for use in traditional Asian medicines. (AFP/Corbis)

many as 100,000 tigers may have existed at the beginning of the twentieth century, it is estimated that today there may be fewer than 5,000 wild tigers left on earth.

The world's remaining wild tigers are threatened with extinction by the combined effects of human predation and habitat loss. Tigers are solitary predators, requiring large territories with ample prey. Forest destruction caused by logging and agriculture have isolated tiger populations and driven them into ever-smaller domains. As humans invade the tigers' habitat there is increasing human-tiger conflict over prey resources, and the fear of tiger attacks on humans prompts some to wish for their elimination. Efforts to protect tigers and their habitat are severely strained by a lack of alternative income sources for the local populations. Although captive breeding programs for tigers are very successful, without greater efforts to protect tiger habitat and to conserve the ecosystems that they depend upon, there will be no place for wild tigers in the future.

Illegal hunting has also been extremely detrimental to tiger populations. Since 1975 tigers have been protected under the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), which prohibits trafficking in endangered species and in products obtained from them. CITES protection has helped to curtail trophy and sport hunting, but it has failed to protect the species from poachers who sell tiger parts on the black market for use in traditional Asian medicines. Tiger protection will not become a reality until the local people are able to realize greater benefits as custodians of the species than they can as brokers of tiger carcasses.

For every species that has been recognized as endangered, there is likely to be an entire ecosystem of other plants and animals that is also vulnerable or is likely to suffer dire consequences if the endangered species becomes extinct. The recognition of endangered species such as the tiger and (formerly) the peregrine falcon is important not only for the survival of the species but also because they are sentinels for habitats and ecosystems at risk.

—Julie Pomerantz

See also: Conservation Biology; Conservation, Definition and History; Ethics of Conservation; Preservation of Species

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Equisetum

See Pteridophytes

Erosion

Erosion is a dynamic process by which running water, glaciers, winds, waves and currents, gravity and groundwater wear away the earth. These agents of erosion sculpt the earth's surface as they wear it down. Forces within the earth driven by internal heat raise the surface, and the agents of erosion driven ultimately by the heat of the sun wear it down.

As these agents of erosion do their work another process, termed weathering, takes place, the physical disintegration and chemical decomposition of rocks by gases and water in the atmosphere. Minerals in rocks, for example, react with water and oxygen, resulting in the formation of new substances that are susceptible to erosion. In climates where water freezes, the increase in volume in the conversion to ice produces powerful forces that can split rocks. Fractures in rocks are enlarged by tree roots growing in them, eventually splitting the rocks into smaller pieces. On steep slopes loose material becomes susceptible to being pulled down by gravity if the slope is undercut or rain increases the weight of the mass. The process of mass wasting, the downward movement of loose material (regolith) on the earth's surface, includes various types of slides, falls, and flows. Very slow movements called creep are a common process easily seen, for example, in cemeteries, where stone markers have moved downward even on gentle slopes. Much of the debris will end up in streams, the tools of the master sculptor of the earth's surface. Streams flow downhill confined within a channel and carry not only rock debris but also dissolved substances. The amount of material carried is dependent on a number of factors, such as the velocity and amount of water, amount and type of vegetation, nature of the bedrock (solid or loose), and steepness of the stream. Streams transport sediment by rolling and pushing, while hopping takes place with increased velocity and by suspension and in solution. This material becomes the grist for erosion. By a combination of down-slope movements, water running over the surface in sheets and within valleys, the surface is eroded. Rivers are the tools that cut down through the underlying rock and undercut their valley walls, producing spectacular features like the Grand Canyon. Drainage systems develop and evolve through stages controlled by climate and tectonics. Over the long term they constantly adjust to changing conditions, such as increasing or decreasing rainfall, rifting, uplift, subsidence, and volcanism.

Streams tend to be in equilibrium with their environment, and changes imposed by construction projects along valleys alter these dynamics, often increasing the amount of erosion. Deforestation removes a protective cover over the surface, making the surface more susceptible to the forces of erosion. Road-building in some areas can set up conditions that enhance the possibility of landslides. Essentially, road building undercuts steep slopes and makes them unstable, requiring extensive remedial action that may include netting, rock bolts, or simply terracing the cliff back, reducing the threat.

In cold climates or areas that have been subjected to colder climatic regimes in the past, glaciers have changed the landscape. At the present time about 10 percent of the earth's surface is covered with glacial ice, but during the recent glacial maximum, 18,000 years ago, one-third of the earth was covered with ice. As ice moves it picks up loose rock debris or plucks it directly from the bedrock, incorporating the material into the ice. The moving ice behaves like sandpaper, grooving, smoothing, and abrading the bedrock. Alpine glaciers begin their existence in areas protected from lots of sunlight, where snow accumulates in valleys high on the slopes. As ice forms the areas of accumulation enlarge, eventually forming large, bowl-shaped depressions called cirques. Ice moves out of the cirque and down the valley, deepening, widening, and converting the once V-shaped into the typically U-shaped configuration commonly seen in some mountainous areas of the United States such as the Rocky Mountains. Additional major erosional landforms formed by alpine glaciers are called horns (like the Matterhorn of Switzerland) and hanging valleys (such as Bridal Veil Falls in Yosemite National Park). Horns form where several cirques are formed around a mountain; as they enlarge and intersect, all that remains is a sharp central peak. Hanging valleys result from the fact that tributary glaciers do not erode as deeply as the larger main glaciers. As a result, after the glaciers have melted away the tributary valley terminates high above the main valley, marked by a waterfall.

Ice sheets move over parts of continents, altering the surface and profoundly modifying previous drainage systems. They gouge out valleys deep enough so that when they melt away, deep basins form that fill with water, creating lakes. Glaciers transport material, and when they melt they leave piles of rocky debris producing distinct land forms. Terminal moraines, for example, are ridges of debris deposited at the margins of glaciers; they can produce substantial features. Long Island in New York state owes its existence to two morainal deposits that extend the length of the island. Otherwise, the island would be just a string of small, muddy lumps off the coast. Glacial erosion produces distinct features, letting observers determine where glaciers once existed, implying a climate change for that area.

When the velocity of wind is sufficient, it can pick up small particles that then become an agent of erosion, blasting surfaces and alter-

A dust storm whips across the landscape in Namibia. (UN photo/Milton Grant)

ing their appearance. This sand blasting process is most obvious in desert environments. In areas where loose sand is at the surface, wind removes the material, forming shallow depressions called blowouts. Often, in desert areas, the wind removes finer material, leaving behind a lag deposit of coarse material—a striking desert pavement feature. Eventually, when the wind dies down, some of the sand will be piled up, building a variety of sand dunes.

Groundwater has a great capacity to create landforms, especially when the bedrock is composed of limestone. Water falling through the atmosphere picks up carbon dioxide, forming carbonic acid; with organic acids picked up from soil it dissolves limestone, creating most of the world's caves. Both the surface and subsurface features formed by solution of limestone are called karst topography, named for a region in Yugoslavia where caves are well developed. A large number of features such as sinkholes, caves, and disappearing streams are products of this process. Sinkholes form where the cave has enlarged to such a degree that the overlying roof rock is unsupported and caves in.

Along shorelines, waves and currents armed with sediment attack cliffs, undermining them, wearing them away, and producing such compelling shoreline features as stacks and sea arches. Along sandy low areas, the moving sand and gravel grind away at each other, reducing their size. As a result beaches along the coast have finer and finer sand as they get farther away from their source. Coastal erosion, destruction of cliffs, and the disappearance of beaches during storms are of great concern to

Rock erosion off the coast of California (USGS/Arnold R.)

people who live at and visit the shore. People and governments try to battle these erosive processes by building expensive structures to preserve what there is. Often the structures are inappropriate and actually enhance erosion.

—Sidney Horenstein

See also: Climatology; Deposition; Freshwater; Rivers and Streams; Topsoil, Loss of

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Estuaries

Estuaries are semienclosed indentations along the coast where salt water from the sea mixes with fresh water from the land. At any given place in an estuary, the amount of mixing depends upon the amount of runoff from the land, the tidal range, and the wind.

Salinity varies from that of normal seawater (35 parts per thousand) at the mouth to completely fresh, well upstream. The intermediate brackish water, mixed fresh and salt, occupies a large segment of many estuaries. During times of heavy rainfall the freshwater extends farther downstream, and during times of low rainfall saltwater moves farther upstream. Tidal action is also an important fac-

Gudsbranddal Estuary, Norway (Hubert /Stadler/Corbis)

tor in determining how far the salt water will go up the estuary. As a result of these factors, oceanographers classify estuaries into several types, based on the amount of mixing.

In the Hudson River estuary, a 5-foot tide occurs in salt, brackish, and fresh water for 210 km, until a dam upstream blocks it. The Native Americans used to call the Hudson the river that flows two ways: up and down, back and forth. Often estuaries are stratified as a result of the density difference, although mixing takes place during storms. During cold winters the upper freshwater layer can freeze over, and ice can be found at times at the mouth of the estuary. Net flow is to the sea, although floating organisms and other objects remain in the estuary for long periods, carried back and forth by the tide. Some estuaries are very long—such as Chesapeake Bay, where the tide takes a long time to reach the interior. As a result there are two high tides along its length.

Estuaries are young features on the earth, formed during the recent rise in sea level, a rise that began when glaciers started their retreat at the end of the Ice Age, some 15,000 years ago. Estuaries can also form as a result of tectonic activity causing blocks of the earth's crust to drop downward; glacial erosion's converting valleys entering the sea into fjords by deepening them; and the development of barrier islands. As sea level rises, estuaries within low-lying areas increase their life span as they widen laterally and extend upstream. Often this rise also enhances erosion, which destroys the low cliffs along the edge of the estuary. In some parts of Chesapeake Bay, for example, recent sea level rise has eroded the shoreline up to 3 m per year.

Brackish water charged with nutrients from freshwater inflow provides a rich basis for life, making opportunities for commercial and recreational fishing for finfish, molluscs, and crustaceans. In addition, many species inhabit the estuary for part of their life cycles. However, some large cities, such as New York and San Francisco, have been built up adjacent to estuaries, where pollution, diking, and filling along the estuaries' edges have caused a marked decrease in the abundance of many species; recent pollution controls in estuaries, however, have seen the return of a number of them, such as *Teredo,* the shipworm, in the Hudson estuary. This has had the negative consequence of destroying unprotected submerged wooden structures.

Where rivers discharge abundant sediment, estuaries may fill completely or partially, because the coastal processes, tides, long-shore currents, and wave action cannot remove the material fast enough, resulting in the growth of a delta at the mouth of the river.

Fjords are former river valleys that have been deepened by valley glaciers to below sea level, which, upon its rising, floods the trough. Fjords may be extremely long, extending hundreds of kilometers inland, as well as deep, in many instances exceeding 800 m; but generally they are very shallow, 10 to 20 meters, at their entrance. As a result, the flow of water in many fjords occurs at the top of the water column, while the rest of the water in the deep parts of the fiord has restricted circulation. As a result they are susceptible to pollution becoming trapped within the fjord.

—*Sidney Horenstein*

See also: Freshwater; Oceans; Rivers and Streams

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Ethics of Conservation

Ethics are the rules or standards governing the conduct of a person, or members of a particular society or profession. Ethics are based on values, or the worth that is attributed to something. Doctors are governed by medical ethics—the standards of their profession. We may consider it ethical to tell the truth, believing that honesty is beneficial to our interpersonal relationships and to society. We learn ethics from our parents, teachers, religious leaders, and friends, as well as through experience, study, reading, and thinking. Ethics are the underpinning of many of our decisions.

Environmental ethics are the standards that govern human behavior toward the nonhuman natural world. The ethics of biodiversity conservation are influenced and shaped by the value we place on biodiversity in relation to other human values. Biodiversity has instrumental value based on its worth as a source of goods, services, and information, as well as aesthetic and spiritual value. Some of these values can be quantified in economic terms, providing economic justification for conservation. Other values, such as a scenic vista or inspiration for human inventions (for instance, Velcro, inspired by the cocklebur), may be difficult to measure monetarily (although proxies do exist for valuing them); they nevertheless provide some recognized direct or indirect benefit to humans. It is widely held that human beings possess intrinsic value, meaning that they have worth in and of themselves, independent of any external evaluator. As a result, we also have duties to others, specifying how we should treat one another. Many conservationists also believe that like humans, other living things possess intrinsic value. The view that attributes intrinsic value only to humans is anthropocentrism, while a biocentric view attributes intrinsic value to both human and nonhuman life forms.

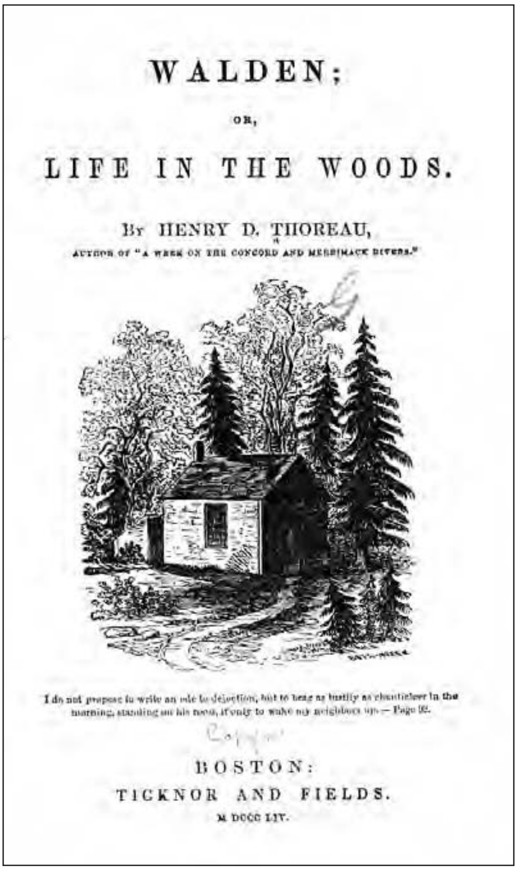
Extensive discussion has revolved around the question of what qualities confer intrinsic value. If humans have intrinsic value, what qualities give them this value, and do other beings possess those qualities as well? Prior to the rise of environmental ethics, philosophers tended to confer ethical standing on humans and not on other living beings. Because people can reason or speak (are rational), they alone were deemed worthy of moral consideration. Contemporary philosophers have objected to this justification, however, on the grounds that these criteria would exclude human infants, the mentally handicapped, and the profoundly senile. At the same time, some primates such as gorillas exhibit rudimentary capacities for communication.

One argument is that ethical consideration should be extended to all individuals that have sentience, or the capacity to suffer. Proponents of animal welfare such as Peter Singer (1975) and Tom Regan (1983) argue that ethical conduct toward animals requires that we avoid inflicting pain unnecessarily. However, Regan's conception of sentience includes a capacity to feel pleasure or pain but limits moral consideration to individuals that are self-aware. Kenneth Goodpaster (1978) argues for the moral considerability of all living things, based on the reasoning that sentience is not an end to itself but a means to any animal's survival: life itself is what sentience evolved to serve, so all living things should have ethical standing. Paul Taylor (1981) takes the view that all living things merit ethical standing and are of equal inherent worth.

Holmes Rolston (1988) agrees with Taylor that all living things have intrinsic value based on interests and a good (or worth) of their own, but he modifies Taylor's more extreme biocentric view by arguing that all are not equal. Those that are sentient, rational, and self-aware have greater intrinsic value than those that are not. This understanding gives greater value to humans and other "higher" animals than it does to invertebrates and plants, for example (but all are still valued according to the role they play). Rolston's view can be characterized as holistic: relative value is based on the good a thing provides to the whole. Species have value for their role in maintaining the integrity of an ecosystem. This emphasis on species value rather than individual value is most in line with conservation goals, because species continue and evolve, while individuals are temporary representatives of the species in each new generation.

Bryan Norton (1991) argues that whether instrumental or intrinsic value is attributed to nonhuman biodiversity, the same conclusion will be reached—that we should conserve it. Baird Callicott (1997) proposes that if the intrinsic value of biodiversity were widely recognized, the burden of proof in making conservation decisions would be shifted; sufficient justification would be required in order to put biodiversity at risk, rather than needing to justify why it should be conserved.

Although the basis for conferring intrinsic value on nonhuman biodiversity is a continuing subject of debate, there are ethical arguments for conservation with foundations in cultural and religious beliefs to which much of the world's population adhere. Traditionally, Western religion and philosophy have taken an anthropocentric view, according ethical consideration only to humans, with other beings regarded as means to human ends. However, with a knowledge of ecology and the



WALDEN;

OR,

LIFE IN THE WOODS.

BY HENRY D. THOREAU,

AUTHOR OF "A WEEK ON THE CONCORD AND MERRIMACK RIVERS."

I do not propose to write an ode to dejection, but to brag as lustily as chanticleer in the morning, standing on his roost, if only to wake my neighbors up.—Page 92.

BOSTON:

TICKNOR AND FIELDS.

M DCCC LIV.

Title page of* Walden; or Life in the Woods, *1854, showing Thoreau's hut at Walden Pond, Massachusetts (Library of Congress)

interdependence among living things, a conservation ethic based in this tradition requires fair consideration of how human actions that directly affect the environment will indirectly affect other human beings. The Judeo-Christian Stewardship Ethic that has emerged confers intrinsic value on all creatures. Because God declared his creation good, human "dominion" over nature makes us responsible for caring for God's creation. Similarly, Islam teaches that human beings have a privileged place in nature, contributing to a tendency to take an instrumental approach to nature because other natural beings are to serve humanity. However, there is a strong emphasis on stewardship, because an ethical relationship among people requires that there be an equitable distribution of resources among those of the present generation as well as among future generations. Other major world religions, such as Hinduism, Buddhism, and Taoism, invite humans to identify with other creatures and advocate sameness or oneness rather than separation between humans and others. Such beliefs lend themselves to an interest in environmental stewardship and conservation.

The conservation movement in the United States began as a moral movement, based in part on the biblical view of the natural world. Emerson and Thoreau wrote of the utility of nature as a temple and wilderness for the restoration of the soul. At the turn of the twentieth century, John Muir made this philosophy the basis for Romantic-Transcendentalism: a campaign for appreciation and preservation of wild nature that he believed was morally superior to exploitation of nature for industry or profit.

Gifford Pinchot, a younger contemporary of Muir, formulated a Resource Conservation Ethic with the objective of utilizing natural resources for maximum benefit: "the greatest good for the greatest number for the longest time." The principles of this ethic are equity (fair and just distribution in the present and future generations) and efficiency (natural resources should not be wastefully exploited, thus they should be used in the "best" way possible, ideally serving multiple purposes). This philosophy correlated well with the prevailing scientific worldview, and it gained support because of its relevance to the philosophical and political trends of the time.

Although Muir's and Pinchot's philosophies are both anthropocentric, a schism arose between them based on differences in their

John Muir, c. 1902. Muir and his fellow Romantic-Transcendentalists believed that appreciation and preservation of wild nature were morally superior to its exploitation for profit. (Library of Congress)

views of the benefits that humans may derive from nature. Romantic-Transcendentalists emphasized a transcendental reality beyond the physical world and valued psychospiritual above material uses, thus favoring environmental preservation. Resource conservationists were more materialistic and insisted on the democratic weighing of competing resource uses and the equitable distribution of the benefits of those uses.

Having begun his conservation career trained in Pinchot's utilitarian philosophy, Aldo Leopold came to realize by the 1940s that conservation must do more than maintain the flow of natural goods and services; it must protect the function and integrity of natural systems. Grounded in evolutionary and ecological biology, Leopold's Land Ethic helped to increase consideration for conservation ethics in scientific circles, and it continues to be a guiding ethic in conservation biology. Leopold recognized humans as members of the ecosystem along with other beings in the "land-community," thus including land and nonhuman beings in conservation ethics. The ecocentrism of the land ethic is famously encapsulated in Leopold's statement: "A thing is right when it tends to preserve the integrity, stability, and beauty of the biotic community. It is wrong when it tends otherwise."

Other views go beyond examining how we value nonhumans in nature, requiring that we rethink how we conceive of ourselves and our relationships with nature. Deep ecology and ecofeminism are examples of current philosophical viewpoints as well as political positions that drive some environmental ethics. Deep ecology, a term coined by Norwegian philosopher Arne Naess in 1972, emphasizes a deep level of questioning to examine the underlying values of our economic and political systems. The foundation of the deep ecology worldview is an ecological consciousness derived from a self-realization that expands the "self" to include all life. If this level of self-realization is achieved, it eliminates boundaries between the self and the rest of nature, and in effect, places deep ecologists outside of environmental ethics because a moral code is not necessary to show care for ourselves (which in this case includes all life on the planet).

Ecofeminism is the position that there are important connections between the domination of women and of nonhuman nature. Traditional rational approaches of Western patriarchal philosophy are the root of ecological problems and sexism, and have led to a human-nature dualism. Although ecofeminism recognizes the distinctiveness of humans from the rest of nature, it also recognizes the relationship and continuity of humans with it.

—Margret C. Domroese

See also: Organizations in Biodiversity, The Role of; Why Is Biodiversity Important?

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Ethnology

In anthropology, the term *ethnology* describes the social, cultural, and psychological study of peoples. The letter *s* in the word *peoples* is significant, indicating that the subjects of ethnology are treated as groups rather than as individuals. In ethnological work these groups are usually regarded as tribal, ethnic, national, or other corporate social entities. Ethnologists study culturally determined practices and environmental ethics as part of interactive social and behavioral systems. Ethnography focuses on the descriptive study of cultures; it analyzes, classifies, and interprets problems arising from ethnographic knowledge. These may be comparative, theoretical, economic, social, or other kinds of questions. Ethnology thus tends toward the systemic and theoretical, while fieldwork-based ethnography is more local and informational. In practice, however, there is considerable overlap between ethnographic methods and ethnological theory. Thick description, artifacts, and other ethnographic data provide the empirical foundations of ethnological analysis.

Lowie (1937, pp. 3–4) defined culture as the aggregate of customs, habits, beliefs, skills, practices, and norms that individuals acquire, not through their own creativity or actions but from their societies and kin. Culture in this sense is an omnibus term meaning all that people learn at a conscious or unconscious level from others in their surroundings; at the same time, culture itself is made by individuals acting in concert. Franz Boas shifted the ethnological usage of the term away from the nineteenth-century meaning of "culture" as a universal human condition found at differing stages of development, toward the plural "cultures" as historically particular, unique, local complexes. Talcott Parsons, following Max Weber, reinterpreted the concept of culture as a symbolic system. Methodological considerations of ethnography and ethnology include recognizing, gathering, and translating ethnoscientific knowledge to approximate a view of culture from the native viewpoint. Bronislaw Malinowski was the classic exponent of that approach, typically reached through fieldwork. Earlier Victorian "armchair" ethnology had been a museum-based discipline in which scholars usually stayed at home in Europe or America, analyzing collections of material culture and folklore brought back from "the field" by others. Following Boas and Malinowski, the emphasis shifted to the firsthand experience of fieldwork.

Classical ethnology placed particular emphasis on social organization through the study of kinship relations and analyses of myth and ritual. Originally conceived as an offshoot of the natural sciences, ethnology became a social science, but it tilted more toward humanism during the last three decades of the twentieth century. The discipline has frequently been caught up in the scholarly tension between a search for systematic conceptual theories, or predictive models of behavior, and inductive methodologies based on extrapolation from empirical data.

Ethnology, philosophically rooted in the eighteenth-century positivism of Auguste Comte, originally came to signify the discovery of psychological laws of humankind through the study of culture history. Nineteenth-century ethnologists such as Tylor and Morgan interpreted ethnology as a historical discipline. Although the remote past of antiquity was properly the domain of archaeology, these ethnologists focused on preliterate peoples in historical times in order to construct a natural history of man. To that end they adopted an evolutionary standpoint aimed at revealing successive stages of universal human development as observed in contemporary primitive societies.

One of the chief concerns around the turn of the twentieth century, when anthropology was becoming a professional discipline, was the explanation of similar cultural traits found in widely dispersed societies. For example, drills for making fire were formerly widespread throughout the world in countless local variations, working on the same principle. The diffusionists favored the spread of traits from a single origin as an explanatory principle over the possibility of independent invention. They regarded culture as contingent upon the particular migrations, explorations, intercourse, invasions, wars, colonizations, and other exigencies of history. Related languages, customs, behavioral traits, and material culture formed so-called culture circles (German: *kulturkreis*). These areal groupings were composed of associative bundles of related traits. Traits radiated outward in successive waves, from centers of so-called high civilization to the outer margins of their spheres of influence. The diffusionist principle of centrifugality held that these centers generated dynamic cultural changes internally; as their influence spread, the traits moved farther from the center, widening the circles like concentric ripples in a pond. Diffusionists postulated that the oldest cultural forms would thus be found as archaic remnant traits located at the periphery of the culture

Eskimos from Port Clarence brought to the United States by the Reindeer Commission, Bureau of Ethnology, 1894. (Library of Congress)

circle. For example, postcolonial Francophone societies in Quebec, Louisiana, and the Caribbean have maintained many distinct local elements of language and culture rooted in old French forms that died out in Europe centuries ago.

The weaknesses of diffusionism as an ethnological theory and historical method included its bias against the possibilities of independent invention and its insistence on a top-down model of imperial cultural drift from the so-called high civilizations to the rest of the world's peoples, rather than a dynamic, interactive model of mutual influence and exchange. Diffusionists were unable to fully recognize human agency and the ingenious adaptive creativity that produces similar solutions to fundamental problems in widely varying environmental circumstances.

Adolf Bastian was a major figure in late nineteenth-century German ethnology. Bastian's concept of an underlying psychic unity of mankind was used against the polygenist racial formulations of the time, which sought to prove that human races were descended from different species. Boas, who had been schooled in the German tradition, was key to the development of an American style. He defined ethnology as "the science of the psychical phenomena of man considered as a member of society, not as an individual" (from the Franz Boas archives, American Philosophical Society Library, Philadelphia). When British anthropology was established as an academic discipline during the first decade of the twentieth century, it distinguished ethnology from sociology. Ethnology was to be the psychological branch of anthropology (also called anthropogeography), as the study of environmental influences on humanity and culture. Its purpose was the comparative classification of the world's peoples based not on physical characteristics but on "conditions of material culture, language, and religious and social institutions and ideas" (Kuper, 1996, pp. 2–3). This school tended to favor diffusionist ideas, opposing the neo-Darwinian social evolutionists who schematized races of man in taxonomic hierarchies.

Twentieth-century British and French ethnology (or social anthropology) developed along somewhat different lines from U.S. ethnology (or cultural anthropology). Structuralism, functionalism, and structural-functionalism stripped away the past-oriented approach of historical reconstruction in favor of present models of living cultures as integrated systems. Cultures are represented as approximations of internally defined idealized social forms suspended in a timeless ethnographic present. This method has the advantage of self-contained explanation, not needing to refer to factors outside a culture to make sense of its practices and beliefs. Among its disadvantages are the possibility of yielding static, ahistorical representations. There is also the ever-present possibility that these ethnological categories, as abstract idealized forms, are in fact more the mental constructions of the anthropologist than internally verifiable ideas or principles indigenous to the cultures under scrutiny. The structural-functionalism of Radcliffe-Brown and Evans-Pritchard, at first closely tied to colonial administration, was a link between knowledge and power in Africa and throughout the British empire. This approach elaborates the conceptual underpinnings of societies and cultures, stressing the importance and complexity of social organization, kinship relations, exchange, and ritual. During the 1960s the French structuralism of Claude Lévi-Strauss, intellectually rooted in the sociology of Durkheim and Mauss and the semiological approach of Saussurean linguistics, brought a systemic, cognitive approach to the study of myth, ritual, and kinship. Structural analyses are based on principles of binary opposition in form and in psychological symbols.

American culture-historical ethnologists, led by Boas, relied on the inductive methodology of carefully observing and accumulating empirical data. They developed methods of delineating the unique aspects of each particular culture, without constructing broad, overarching, comparative theoretical frameworks. This resulted in a wealth of ethnographic knowledge, while limiting the synthesis of ethnological knowledge beyond the specific data pertaining to each society. The influential culture and personality school, which included Boas's students Ruth Benedict, Margaret Mead, and Edward Sapir, focused on psychological factors in the individual's development in society, emphasizing the study of childhood, learning, family, and socialization. Sapir emphasized that the environment affects each person individually, and that culture is not a reified entity but the aggregate of separate human-environment interactions. Gregory Bateson was the son of William Bateson, a nineteenth-century biologist who coined the word *genetics*. The younger Bateson advocated the adaptation of deductive natural science methods to the elusive problems of understanding psychological forms. Bateson's cybernetic model of communication applied natural biological principles of symmetry, as found, for example, in the morphological segmentation of arthropod limbs, to the formal analysis of continuously regenerated social structures.

The postwar theory of cultural evolution centered not on species evolution in the biological sense but on the view that progress in technology and the conversion of environmental resources into energy are deterministic of culture. Its founder, Leslie White, critiqued the Boasian paradigm for its lack of either grand synthesizing statements or a comprehensive ethnological theory of social organization. Boas's defenders countered with the argument that the lack of such generalization is precisely the strength of historical particularism, which seeks difference, or what makes each people and culture unique. Only after taking into account the diversity of human experience, knowledge, and practice, they contended, could broader principles of human society and culture be formulated. Cultural ecology, founded by Julian Steward, was an influential postwar school of ethnology. It ascribed a greater role to creative adaptation to environment, natural resources, and social factors than did the technological determinism of the cultural evolution school. Steward's theory of multilinear evolution made for a more open-ended and nuanced view than the nineteenth-century teleological formulas he called linear evolution, allowing for polyvariate results from similar causes and a more diverse branching of human cultural forms. Both cultural evolution and cultural ecology extended the capabilities of the type of environmental ethnology begun during the early twentieth century by Alfred Kroeber, Robert Lowie, and Clark Wissler. They drew on the materialist economic determinism of Marx (although uncited during the height of the cold war), in a return to the primacy of environment and economy over psychological and religious factors. This lineage led to several divergent tendencies, including cultural materialism, a highly deterministic neo-Marxian paradigm that considered all cultural effects to be explicable as superstructural responses to base environmental and economic conditions. The Malinowskian emphasis on economics and ecology returned to the forefront of ethnology during the 1960s.

For much of the twentieth century, the Chicago school was closely allied with British structural-functionalism and the main rival to the various Boasian offshoots. Marshall Sahlins (1972) integrated structuralism with historical particularism, environmental constraints, and the theory of economic exchange. Raymond Firth applied modern economic theories to preliterate societies. Edmund Leach synthesized an analytic model of culture in which norms of customary behavior approximate ideal concepts of social structure, while ecology governs practical economics and rational choices. For example, Leach (1954) reasoned that, in highland Burma, the organization of village life could be understood as a specific adaptation to the environmental constraints of agricultural fields and irrigation canals.

In his ethnographic writings on Indonesia and Morocco, Clifford Geertz (1973) helped set standards for particularized rigor in moving ethnology away from abstraction toward thorough local knowledge and thick description.

Beginning in the 1960s and acutely since 1980, the field has undergone arduous self-examination and critique of its own colonial past. Some ethnologists have moved away from science models toward an ethnology of reflexive and literary turns. The ever-expanding field of ethnographic inquiry has led to the proliferation and accelerating fragmentation of ethnological subdisciplines. Poststructuralism, visual anthropology, cultural studies, subaltern studies, feminist anthropology, and queer theory are some of the many ethnological subdisciplines now coexisting as integrated environmental approaches to the study of culture and society.

Human ecology and various historical so-called new ecologies, stressing the interaction of people with nature and the role anthropogenic environmental landscapes play in social organization and cultural memory, continue to gain currency at the turn of the twenty-first century. Biocultural diversity is a relatively new paradigm combining linguistic and sociocultural methods with environmental science and preservation policy studies. In its interdisciplinary relation to environmental and conservation science, ethnology plays a crucial role in understanding traditional ecosystems and involving local communities in preservation and development.

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See also: Anthropology; Coloniality; Ecosystems; Ethnoscience

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Ethnoscience

Ethnoscience is a somewhat broad term for the study of local systems of knowledge and classification. The incorporation of the term *science* in *ethnoscience* refers to indigenous knowledge of plants and animals and classification systems, including culturally specific techniques of cultivation and animal husbandry. Originating in linguistics, the concept and practice of ethnoscience has spread to ecology and ethnology, spawning many subfields. It is of growing importance in conservation biology and environmental policy making. Ethnobotany in particular has powerful implications for pharmaceutical research and the genetic engineering of crops. Emphasizing the mental systems of a group of people, ethnoscience is sometimes called cognitive anthropology. It delineates heuristic (knowledge-based), linguistic, and cultural categories of environmental information that differ cross-culturally.

Native classification systems operate according to principles that are often internal to the specific culture-history of the people in question. Overlapping categorizations can arise situationally. Thus the same set of entities or phenomena might be arranged in multiple ways by different sets of criteria, according to varying cultural contexts and social circumstances. For example, plants may be divided into categories of edible versus nonedible, seasonal versus year-round, or medicinal materials versus construction materials. These classifications can cut across the morphological or genetic conventions of Western scientific taxonomy and nomenclature, resulting in closely related biological species occupying very different ecological and cultural niches. Furthermore, such concrete distinctions are situationally determined, so that different classification systems might be invoked by the same people according to differing circumstances or applications. Thus the same set of trees may be sorted at different times in mutually nonexclusive ways into hard versus soft woods, leafy trees versus conifers, light versus dark colors, tall versus short trunks, or other familiar groupings arranged according to specific biological criteria, depending on the applicable cultural context. These overlapping conceptual categories are not necessarily hierarchical, but may be based instead on relative degrees of, and pragmatic or intellectual conceptions of, similitude and difference.

Berlin, Breedlove, and Raven (1973) elaborated the concept of rank in folk biological classification. Using empirical evidence compiled from a widespread but limited number of samples, Berlin and subsequent researchers have contended that folk taxonomies tend toward general congruity with the Linnaean hierarchical system of classical biology. In Linnaeus's scheme, progressively narrower categories are each subsumed within nested levels of classification. From the most general to the most specific, these categorical levels are kingdom, phylum, class, cohort, order, family, subfamily, tribe, genus, species, and subspecies. In folk taxonomies, the ostensively universal ethnobiological ranks, from most to least generic, are unique beginner (for example, plant), life-form (for example, tree), generic (for example, oak), specific (for example, white oak), and varietal (for example, northern white oak). Within any given system, categorizations at the life-form level are postulated to be invariably few in number. There is a sixth class called intermediate, residing between life-forms and generics (such as evergreen tree, encompassing the generic categories of pine, fir, and larch), but its instantiation at the linguistic level is held to be rare.

Nomenclature is a key indicator of taxonomic and conceptual groupings, but other factors such as biological features, adapted uses, and psychological associations can override naming as the salient organizing principle of a folk system. Named categories (or lexemes) typically characterize the more general levels of classification within a domain (for example, animal, fish, trout), while the secondary categories or binomial labels that modify them are found at more specific levels (for example, brook trout). There is some evidence to suggest that secondary named categories might be more common among agricultural peoples than among hunter-gatherers. Morphological characteristics are just one aspect of a word, and not always the most relevant criteria. Intellectualists adhere to the principle that naming and taxonomic conventions are conceptual, based on observation of plant or animal characteristics and distinctive features. Structural anthropologist Claude Lévi-Strauss argued for the intellectualist position as the basis of totemic systems of classification and mythic symbolism. Utilitarianists, on the other hand, argue that such classifications are primarily adaptive, for example in the categorization of species by use—for food, fuel, medicine, or construction materials. There is a wealth of variety and inherent flexibility in different ecologies, adaptive mechanisms, linguistic parameters, individual creativity, and human thought. This diversity suggests that an operative combination of intellectualism and utilitarianism might work best for determining salient distinctions among living things. Ethnoscientific approaches extend beyond the plant and animal worlds to include systemic environmental qualities and larger cycles of nature.

Neoevolutionary stereotypes of traditional peoples as "primitive" act as blinders to many in the developed world, with the result that these cultures are unfairly derided, their contributions devalued or ignored. Mainstream scientists began to seriously credit the value of traditional indigenous wisdom around the 1970s, when habitat destruction, pollution, heedless large-scale development, overgrazing, and the threat of cultural ethnocide had reached crisis proportions in many parts of the world. The !Kung San of the Kalahari desert, for example, are frequently acknowledged as a people bearing important ways of discerning environmental resources of moisture and nourishment in many hidden forms, including underground water and buried ostrich eggs, as a means of survival.

The term *ethnobotany* was coined and defined in the late nineteenth century by John Harshberger, a botanist at the University of Pennsylvania. This understanding basically restricted the concept of folk classification to so-called primitive or preliterate peoples. In postwar anthropology, the notion of ethnoscience was broadened to apply to any local situation as "the system of knowledge and cognition typical of a culture" or "its particular ways of classifying its material and social universe" (Sturtevant, 1964, pp. 130–131). Nancy Turner's work on the ethnobotany of the Salish Indians of the interior plateau of British Columbia is exemplary of the genre, using fieldwork to exhaustively inventory and describe their knowledge, categorization, conservation and resource management, and traditional uses for endemic plant species such as saskatoon, soapberry, and camas (Peacock and Turner, 2000). In India, the study of ethnobotany has been taken broadly to signify the entirety of human-plant relationships, with many subdisciplines such as ethnopharmacology, ethnoecology, and even ethnolinguistics subsumed under this heading. Jain (1987) divides the human-plant relationship into the abstract (folklore, magic, sacred plants, taboos) and the concrete (material uses, domestication, conservation, improvement of species).

The now conventional Western view of indigenous peoples as universally living in harmony and balance with nature seems to be based partly on historical reality and partly on romantic fantasy. Although many traditional societies have achieved and perpetuated sustainability within their ecosystems, patterns of production and consumption are necessarily based on a certain amount of destruction of resources. Their manageability and renewability are keys to continuing exploitation of local environments by local communities. Despite the timeless depictions of early ethnographies, however, it is rare for a people to live in stasis with their ecosystems over many generations without adaptation and change. Flexibility and creativity in the face of shifting climatic conditions, cyclical natural phenomena such as floods or drought, population pressures, migrations, desertification, and a host of other ecological factors are keys to historical survival for many cultures over long periods of time. Nevertheless, the prolonged existence of human-plant-animal interaction in circumscribed environments indicates that there is much traditional conservationist wisdom among indigenous groups that could be usefully applied to large-scale and local development. Industrial and postindustrial societies, living off the entire biosphere rather than a single local ecosystem, pose a threat to these traditional ways. Cultural values are intrinsic to conservation and sustainable resource management. Ethnobotanists look for the ways in which people perceive, conceptualize, and utilize the plants in their environment, including naming and classi-

Margaret Mead with a Manus mother and child in 1953 during a visit to the Admiralty Islands (Bettmann/Corbis)

fication, the cultural significance of plant species, their varieties, physical properties, economic value, and utilitarian applications.

The pharmacological uses of plants in traditional healing practices constitute a vast repository of locally conditioned knowledge regarding the curative properties of certain plants. Modern drugs derived from traditional herbal medicines include ephedrine (*Ephedra sinica)* from China; quinine *(Cinchona)*, curare *(Strychnos*, *Chondodendron)*, and cocaine *(Erythroxylum coca)* from South America; morphine *(Papaver somniferum)*, atropine *(Atropa belladonna)*, and codeine from Europe; and colchicine *(Colchicum autumnale)* from Eurasia. Ethnobotanical inventories can reveal pharmacological, psychoactive, and medicinal properties of plants previously unknown to Western science.

The many ethnoscientific subdisciplines include ethnoecology, ethnozoology, ethnohistory, ethnoarchaeology, and ethnoastronomy. At the metalevel, ethnoscience—a science that categorizes types of systems—is a classification of classifications. The ethnosciences themselves thus constitute a heuristic system of the type they categorize, in this case the realm of cross-cultural studies. Ethnoscientific methodology represents a disciplinary attempt to achieve an anthropological point of view, or a construction of the world as the "native" sees it, following the ethnographic tradition of Malinowski. Perhaps it is best conceptualized as the science of ways of knowing, in the ancient and modern senses of "science" as knowledge and method, empirical data, and systems of thought. As a cognitive anthropological category, ethnoscience reveals ecological differences in ethnographic relief. Malinowski was a pioneer of the technique of ethnographic fieldwork as a means to the collection, translation, and classification of particular ethnoscientific knowledge in his studies of western Pacific categories of plant, bird, and ocean life. Harold C. Conklin's work (1957) on the Hanunoo system of ethnobotanical classification in the Philippines was a widely imitated model of determining systematic nomenclature and folk categories within a cultural ecosystem. Studies of Navajo classification by Gladys Reichard and others also developed this approach.

Ethnoscientific data tend to reinforce the reality of species. Berlin's system of six universal ranks, described above, is widely used by biological and social scientists as a basis for formulating native biotaxonomies. Brown (1984) surveyed the nomenclature of folk classifications for animals (based on a sample of 144 languages) and plants (based on a sample of 188 languages) and proposed the existence of a set of universal encoding principles for defining and delimiting biotic taxa. Limitations and distortions are liable to be introduced by an overly rigid cross-cultural application of Berlin's schema of ranks roughly corresponding to Linnaean taxonomic hierarchies. For example, Morris (in Minnis, 2000, pp. 83) reports that among the Chewa of Malawi, "folk concepts do not constitute logical or inclusive categories, for their folk classifications are inherently flexible, with many ambiguous or overlapping categories." Frequently, such categories might be viewed more productively as functional rather than taxonomic.

Hierarchical schemes arranged according to inferred folk taxonomic principles sometimes fail to take into account the variability of conceptualizations that arise from the exigencies of culture history. Lévi-Strauss illustrates this trap of misinterpreting classificatory logic according to surface evidence with the hypothetical example of a society organized into a trichotomous division of totemic clans (bear, eagle, turtle), of which one lineage (bear) gradually dies out. A resultant population explosion among the surviving groups and subsequent ecological changes in their environment may then cause one of the remaining pair to split into two moieties (yellow turtle, grey turtle). Over time, these two turtle subdivisions would tend to take on the formal characteristics and essential attributes of clans, the historical fissure becoming in effect the organizing principle of a new trichotomy (eagle, yellow turtle, grey turtle). Without historical knowledge of its true origin, the actual basis of the societal division as expressed in the later classification system cannot be known with any degree of certainty. The lesson drawn by Lévi-Strauss is that since the irreducible contingencies of historicity can be rendered invisible to an outside observer, "*the principle underlying a classification can never be postulated in advance*. It can only be discovered *a posteriori* by ethnographic investigation, that is, by experience" (1966, p. 58, emphasis in original).

Totemism, religion, ritual cycles, and other psychological and symbolic structures and events provide keys to the management of seasonal resources and their cyclical cultivation and distribution. These systems act upon the environment and embody the integration of nature and culture in unique ways that are as important to ecosystem maintenance as to cultural survival and the continuation of ethnic traditions, the ties of generationally transmitted knowledge and behavioral practices that sustain a people as a group. In recent years there have been a growing number of studies of environmental inventories and use of plant and animal resources. Adaptations and new models of sustainable forestry, agriculture, and maritime resource management seek to list and apply ethnoscientific databases to rational schemes of sustainable development, drawing on existing stocks of biocultural diversity and linguistic specialization. The Mayan territory of Mexico and Central America is considered a biocultural megadiversity site, containing a large number of anthropogenic plant systems. Anthropologists are applying the ethnoecological technique of "ground-truthing" to the Peruvian Amazon and highlands, interviewing local indigenous people about their environment as an empirical check on scientific estimations of biodiversity in the region. The Matsigenka people's large repertoire of biological categories suggests underestimation by environmental scientists. Their classificatory system resembles those used by ecologists, but their deeper knowledge of the variety of forest species has yielded at least three times the amount of biodiversity known from satellite images.

The traditionally maintained ecological interdependency of traditional societies, in the Amazon for example, strikes a delicate balance between human activity and the environment. This balance is being disrupted and threatened by changes in climate, land use, economic development, and other factors. Ethnopharmacology is a subfield in which industrialized society is showing an increasing interest. Many modern medicines are derived from indigenous precursors; curare and quinine, for example, were introduced to Western science by the Shuar rain forest people of Ecuador and Peru. Increasingly rapid species loss could mean that untold numbers of unknown cures for human and animal diseases will disappear forever. As a familiar traditional saying usually attributed to one or another African people reminds us, "Every time an elder dies a library burns down."

The incommensurability of loss of traditional environmental knowledge (sometimes referred to in the literature as TEK), with the difficulty of reconstituting past ecological wisdom, makes preventing the further disappearance of tradition one of the most urgent tasks facing the world in the twenty-first century. The emerging concept of biocultural diversity is an anthropological and biological approach emphasizing the integration of linguistic and cultural systems with biota spheres. Issues of cultural survival have become critical in relation to issues of the environment. The codependence and mutual influence of human societies with their environments are shaped everywhere by such forces as cultivation practices and pathogen vectors. International efforts are required to create stable environmental regimes in the fragile circumpolar Arctic, for example, working in cooperation with native peoples and drawing respectfully on their ecological knowledge, acquired over centuries. The urgent development of fair and equitable intellectual property rights is a crucial step to protecting indigenous communities—especially in the Third World—who have developed pragmatic knowledge of plant life over centuries of practice. Profits from medicinal and other uses of laboratory-based adaptations have yielded little return to the mostly impoverished peoples who cultivated the foundations that make new varieties of food and medicine technologically possible. International covenants and agreements granting corporate patents over valuable genetically modified life forms derived in laboratories from species bred by indigenous peoples have so far produced little benefit to these local communities.

—Thomas R. Miller

See also: Anthropology; Botany; Classification, Biological; Cultural Survival, Revival, and Preservation; Ecosystems; Ethnology; Extinction, Direct Causes of; Indigenous Conservation; Land Use; Endangered

Species; Linnaean Hierarchy; Organizations in Biodiversity, The Role of; Preservation of Habitats; Preservation of Species; Species; Subsistence; Sustainable Development; Systematics; Tropical Rain Forests; Valuing Biodiversity; Zoology

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European Plant Species

See Alien Species

Evolution

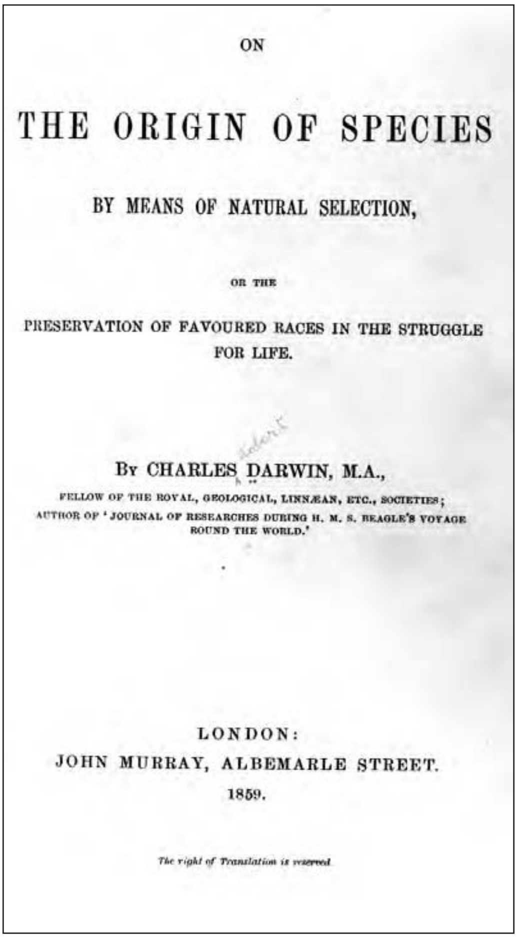
Evolution, in biology, is the idea that all organisms are descended from a single common ancestor that arose in the deep geological past. Estimates of the number of species currently on earth vary between 10,000,000 and 100,000,000, and many more have succumbed to extinction over the 3.5-billion-year history of life on earth. According to the idea of evolution, all those species, past and present, are related by the process of ancestry and descent known as "evolution."

The terms *theory of evolution* and the closely similar *evolutionary theory* refer to two separable aspects of evolution: (1) the very idea that all organisms are descended from a single common ancestor (our general definition of evolution, above); and (2) ideas about how the evolutionary process operates. This article deals with both aspects.

The word *theory* in common language is often associated with guesswork or vague ideas; for example, each of us may have our own "theory" of why the Yankees lost the 2001 World Series to the Arizona Diamondbacks. In science, however, the word has a more formal meaning: a scientific theory is a body of one or more hypotheses that have been rigorously analyzed and tested, and rather than being "falsified" (that is, demonstrated to have been incorrect), the idea has so far appeared to have stood all tests—and therefore is the strongest explanation so far available for a particular set of natural phenomena. Thus plate tectonics is a theory, as are quantum mechanics, special relativity, and a host of related, well-confirmed ideas in science.

In biology, evolution in the first sense—that all organisms are descended from a single common ancestor—has been tested over and over again, and has been repeatedly confirmed. Biologists agree that life has evolved—the very few exceptions being creationists, who refuse to accept the idea of evolution, based on their religious views. Creationists are especially common in the United States, Canada, and Australia; creationism is usually, though not exclusively, associated with some aspects of conservative Protestant Christianity. “Scientific creationists” attempt to disprove evolution with supposedly scientific evidence and argumentation—though their arguments have long since been disproven by scientists. One of the standard creationist claims is that the very idea of evolution is not scientific, as no one was there in the remote past (many creationists, however, dispute the 4.65 billion year age for the origin of the earth and follow an interpretation of Genesis that sees the earth as only some 10,000 years old). If no one was there to observe the evolution of life, and if evolution cannot be tested in the laboratory (but it can!—see below), then, creationists claim, the idea is not a truly scientific one.

To be scientific, an idea must be testable, which means that if an idea (“hypothesis”) is true, we must be able to make predictions from it regarding what we would expect to observe. Failure to make these predicted observations would “falsify” the idea—the cardinal procedure of hypothesis testing in all of science. So we ask: What observations would we expect to make in the natural world if the hypothesis that evolution has occurred—that all organisms are descended from a single common ancestor—is correct?



ON

THE ORIGIN OF SPECIES

BY MEANS OF NATURAL SELECTION,

OR THE

PRESERVATION OF FAVOURED RACES IN THE STRUGGLE
FOR LIFE.

Robert

BY CHARLES DARWIN, M.A.,

FELLOW OF THE ROYAL, GEOLOGICAL, LINNÆAN, ETC., SOCIETIES;
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ROUND THE WORLD.’

LONDON:
JOHN MURRAY, ALBEMARLE STREET.
1859.

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Title page of On the Origin of Species *by Charles Darwin, 1859. (Library of Congress)*

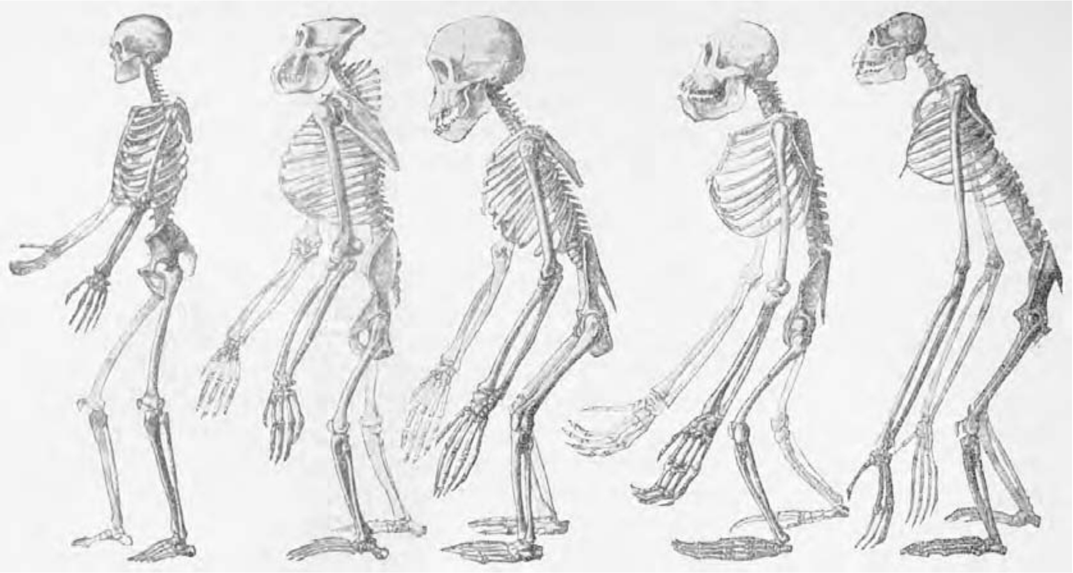
There are two such predictions. The first one, pointed out by Charles Darwin in his epochal book *On the Origin of Species*, published in England in 1859, is that if all organisms are descended from a single common ancestor, we should expect to find a pattern of progressive similarity linking up all of life. In other words, closer relatives should resemble each other more (that is, share more features in common) than either one does with more remote relatives. Like the ever-widening circles in a pool after a rock is thrown in, we should find features that link up small groups of close relatives with their remoter kin, and so forth, until we find features in common that link up absolutely all kinds of organisms on earth.

And that, in fact, is what we observe. Another way to look at it (as Darwin did in his only diagram in his book) is to see that as the tree of life grows up and branches out, new features acquired in evolutionary history are shared only with subsequent descendants—and not with other organisms belonging to groups that had branched off earlier. Indeed, a century before Darwin wrote, the great Swedish naturalist Karl von Linné (Linnaeus) showed that life is organized in a hierarchical fashion; organisms seem to fall into natural groups based on their appearance, and these natural groups seem to cluster together into more inclusive natural groups, and so on. Linnaeus—along with nearly everyone else in the eighteenth century—thought that a supernatural Creator (God) had fashioned life this way. Darwin was able to suggest a natural explanation for these "nested sets" of organisms that we see in the biological realm—and to suggest that these sets of similar organisms must be there if the fundamental idea of evolution is true.

It is the experience of more than 150 years of research in systematic biology ("systematics") and paleontology that life is indeed organized into progressively nested sets of species. Although these repeated observations do not prove the truth of evolution—absolute proof of anything in science is in principle impossible—failure to falsify the idea means that evolution is as well corroborated a notion as any other in science.

Here is an example of how life is nested into increasingly larger groups, eventually including absolutely all of life. You can start with any species you want: a dog species, a whale, a species of grass, a fungal species, anything. Let's start with our own species, *Homo sapiens*. We look very much like extinct fossil species that go back some 4 to 5 million years, looking more like the younger fossil species, and sharing fewer features the farther back you look in the fossil record. Confining our gaze, however, to living species, we find that we share more than 98 percent of our genes with chimpanzees; we share other similarities with the tail-less great apes. Great apes and humans (collectively, the hominids, Family Hominidae) share still more resemblances with monkeys—and all together, the hominids, monkeys, lemurs, and a few other groups belong in the Order Primates. Primates, though, are linked with rodents, whales, bats, carnivores, and others into the Class Mammalia, all of whose members have hair and mammary glands. Mammals, though, share with fishes, amphibians, reptiles, and birds a basic body plan that includes a vertebral column—forming the Vertebrata. Vertebrates are animals. Animals share with plants, fungi, and certain kinds of micro-organisms a basic structure to their cells, in which DNA and RNA (the "nucleic acids" of heredity) are isolated from the rest of the cell in a distinct nucleus set off by a double-layered wall. But DNA is found in most bacteria, while the similar molecule RNA is found in absolutely all of life. So there you have it—a nested set of groupings of organisms that link human beings up with all other forms of life on earth. Had we started with any other species, we would have found the same pattern of progressive inclusion based on shared possession of similar features—shared features that arose in the course of evolution.

The other great prediction that comes from the basic idea that all species are descended from a single common ancestor is that the fossil record of the history of life ought to show a progression from simple to more complex organisms. Assuming that life arose by natural chemical processes more than 3.5 billion years ago, we would expect the earliest life forms to have simple DNA or RNA strands covered by a simple protein coating. (Whether DNA and RNA, which carry the instructions for protein assembly, arose first, or rather proteins [whose component amino acids can be formed and strung together into chains in simple laboratory experiments] came first, is still a matter of debate among scientists who study the origin of life.) The simplest forms of life we know are bacteria, assumed to be much more complex than the earliest life forms. But



Skeletons of five primates (Bettmann/Corbis)

among the organisms that we know living around us today, we would predict that the simplest of them, the bacteria, would be the first to show up in the fossil record. We would not predict that, say, elephants would have come first, and fungi and microbes later!

This second prediction is also abundantly confirmed by our observations of the fossil record. The oldest fossils are some 3.5 billion years old—and are indeed bacteria. Bacteria were the sole forms of life for at least a billion years. The next big step in life's history was the appearance of more complex (eukaryotic) cells, the kind with a distinct nucleus. And, as we would predict, the first evidence of such cells (more than 2 billion years ago) shows them to belong to relatively simple, single-celled micro-organisms, not the more complex, multicellular forms of life we know as animals, fungi, and plants.

Although the famous Cambrian explosion showed a very rapid proliferation of forms of animal life over a 10-million-year period beginning some 540 million years ago, evidence of even earlier fossils shows that the more simple kinds of animals—such as the group to which corals and jellyfish belong—did indeed come before the more complex, advanced animals such as arthropods (which include crustaceans, insects, and the extinct trilobites). If we consider our own group, the vertebrates, we encounter, as we would predict, various forms of fishes first in the fossil record, followed by amphibians, whose reproduction is still tied to the water. The appearance of the "amniote egg," with membranes that retain water and nutrients for the developing embryo, came later. The oldest, most primitive amniotes were scaly reptiles. Birds arose later from a specific group of reptiles (dinosaurs, apparently), while mammals arose from a separate lineage of reptiles, as is beautifully shown by a sequence of fossils in South Africa that are more than 200 million years old. Primates arose later, and advanced primates—such as our own lineage—arose only about 4 to 5 million years ago.

Thus the second prediction of evolution is also well corroborated. The basic idea of evolution, that all life has descended from a single common ancestor in the remote geological past, is thus abundantly confirmed. Evolution is as well corroborated as any other scientific theory—such as plate tectonics or special relativity. It is as well confirmed as the notion that the earth is round, spins on its axis, and revolves around the sun. For that reason, most biologists are content to call evolution a "fact"—for that is what facts really are, well-confirmed ideas about the nature of things.

The Second Meaning of "Evolutionary Theory": How Does Life Evolve?

Darwin's *On the Origin of Species* (1859) immediately established evolution as a serious scientific issue in the minds of scholars throughout the Western world. Although others before him (going back, some would say, to the ancient Greeks) had entertained notions of the interconnectedness of all life, nonetheless it was Darwin's book that finally forced the thinking world to take the idea of evolution seriously. And although Darwin presented biological patterns, especially of the nested groupings of organisms, it is clear that he succeeded where others had failed in establishing the probable truth of evolution because he was able to suggest a mechanism—a causal theory of just how it is that the features of organisms can be modified over time. (Indeed, Darwin used the term "descent with modification" throughout his text instead of the term *evolution*.)

That mechanism was natural selection, an idea developed simultaneously by the naturalist Alfred Russell Wallace. Natural selection remains the prevailing explanation of why biological nature appears to be so well designed—that is, how giraffes came to have their long necks for browsing leaves from high shrubs and trees; how bats attained the ability to echolocate (that is, navigate and find insect prey by emitting ultrahigh-frequency sounds that bounce back to the ear in radarlike fashion): in short, all the adaptations of the biological world. Natural selection has been observed occurring in the wild, has been the subject of many laboratory experiments, and has been analyzed mathematically in great detail.

Natural selection results from the simple fact that resources are limited in the natural world, so that those organisms best able to obtain energy and nutrient supplies (as well as survive disease and predation) will tend to survive longer and produce more progeny than those less able to cope. Because organisms tend to resemble their parents, what we now realize to be the underlying genetic information for successful living is passed on in relatively greater amounts to the next generation. But Darwin reasoned that if the environment should change, the natural variation in a population might very well include organisms with other features that then might have an advantage in the new conditions—and thus natural selection would favor the other variants that were not selected for in the past. In that way, the features of an entire species of organisms would be changed to meet the new conditions.

Darwin was frustrated, however, in not knowing how, exactly, offspring tend to resemble their parents, or how new variant features arise from time to time. The science of genetics had yet to be born. But during Darwin's lifetime, the Austrian monk Gregor Mendel performed simple experiments breeding peas in his garden, and in so doing discovered that features seem to be inherited through particles that could be separated and recombined, important rules that lay the foundation of the modern science of genetics.

Mendel's work was largely ignored in his lifetime, but several individuals and teams of biologists all rediscovered Mendel's work just at the turn of the nineteenth century—thus jumpstarting the serious scientific study of heredity. Most of the early progress came from the laboratories of Thomas Hunt Morgan at Columbia University in New York. There, experiments on fruit flies soon revealed that the particulate nature of inheritance discovered by Mendel was caused by the existence of such particles, soon dubbed "genes," arranged in a linear fashion along strands in the cell nuclei, called "chromosomes." Also, sudden changes in heritable information—called "mutations"—were soon discovered. Here, at last, was sound knowledge of the mechanisms of both heredity itself and the origin of novel genetic information.

At first, however, the findings of the new science of genetics seemed to be at odds with the Darwinian notion of evolution through natural selection. One botanist, Hugo Devries, for example thought that the sudden appearance of mutations in the flowers of the evening primrose was in itself sufficient to explain how organisms change through time in evolution. Geneticists came to assume that the sort of natural history practiced by Darwin and Wallace was old fashioned, and that natural selection itself was no longer necessary as an explanation for how evolution occurs.

Some of the conflicts between the idea of natural selection and the early results of genetics included the observation that most mutations are deleterious—that is, harmful to organisms—including some that are downright lethal. Also, Darwin had talked of selection gradually modifying traits—such as hair length in mammalian coats, for example—whereas genetics stressed the particulate either/or nature of inheritance, such as the yellow/green or smooth/wrinkled dichotomies in Mendel's original data of pea genetics. It took thirty years before geneticists observed mutations that were small scale and either neutral or even beneficial in their effects. Eventually, too, geneticists learned that many genes can combine to determine a trait, allowing them to reconcile their new theories of inheritance with the sort of continuous variation in size and shape on which Darwin had focused.

Thus the way was finally cleared, by the 1920s, to reconciling genetics with the concept of natural selection. This work was achieved by three mathematically inclined geneticists: Sewall Wright in the United States, and Ronald Fisher and J. B. S. Haldane in England. Their approach essentially founded the mathematical study of evolution—a discipline still known as "population genetics."

The reconciliation of natural selection with the newer science of genetics inspired still more work in evolutionary theory. The Russian-born geneticist Theodosius Dobzhansky migrated to Morgan's lab at Columbia University and launched into a brilliant series of studies of evolutionary processes in natural (wild) populations of fruit flies. Dobzhansky, along with the ornithologist Ernst Mayr (also in New York, at the American Museum of Natural History), became intrigued at a pattern they thought had been overlooked by Darwin and all his successors up to the 1930s: discontinuity in the natural world. In particular, they saw that species—especially those living in the same regions—are almost invariably different from each other, and, in particular, do not interbreed with one another.

Dobzhansky, in particular, observed that, at the genetic level, genes are particulate and discrete. But at the level of the population, characteristics tend to be continuous: a spectrum of variation in the size and shape of the antlers of deer, for example, or the tails of humpbacked whales. But at the level of species, discontinuity once more seemed to be the rule. And, he supposed, this must be the result of some additional evolutionary factors—as natural selection would be expected to produce a continuous array of variation within a species.

Thus was born the notion of speciation—that is, the circumstances leading to a new species evolving from an ancestral species, from which it becomes reproductively isolated. Developed at first by Mayr and Dobzhansky and still a subject of ongoing research in evolutionary biology, speciation is generally thought to occur when a portion of an ancestral species becomes physically isolated from the main part of the species. If natural selection modifies that population sufficiently so that mating no longer is possible, then we say that a new species has evolved. This is very different from Darwin's original view, as Darwin thought that new species were just the consequence of long periods of gradual change within a species, such that, given enough time, we would recognize that an ancestral species had slowly evolved into what we would call a new species. We now know that new species can evolve very quickly—on the order of hundreds or a few thousands of years.

The 1940s, despite the outbreak of war, saw a remarkable coming together of evolutionary disciplines in what came to be called the Synthetic Theory of Evolution. Paleontologists (led by American Museum paleontologist George Gaylord Simpson), botanists, ecologists, systematists, cytologists (biologists who study cells), and developmental biologists all more or less agreed that the new integration of genetics with Darwinian selection was sufficient to explain all the major features of the evolution of life. By 1959—the centennial year of Darwin's publication of *On the Origin of Species*—many biologists firmly believed that a complete theory of the mechanisms of evolution was at hand. They were mistaken.

Events since 1959

The molecular revolution that began with the discovery of the structure of DNA in the 1950s had a profound effect on evolutionary biology. Not only have molecular mechanisms that bias the transmission of heritable information to the next mechanism been discovered, but, in addition, the mere fact that so much has been learned about the structure and function of DNA and RNA has reintensified focus on the gene.

Thus one major movement that began as early as the 1960s was to recast Darwinian selection more expressly in terms of genes—a movement perhaps best exemplified by the notion of the "selfish gene" promulgated by British biologist Richard Dawkins. Dawkins and colleagues developed a picture of the biological world centered around the importance of transmission of genetic information to the next generation: even genes compete with one another to be transmitted to the next generation.

One aspect of this line of research has been the development of sociobiology and its even more recent offshoot, human "evolutionary psychology." One problem plaguing Darwin from the very beginning was the existence of so-called altruism, whereby, instead of competing with one another for food and other resources, including mates, organisms within many species actually are observed to cooperate. British biologist W. D. Hamilton, in the 1960s, showed convincingly that the degree to which organisms cooperate is proportional to the number of genes that they share; close relatives cooperate, because cooperation in this case fosters the transmission of each individual's genes. From these critical observations, sociobiology (named and first thoroughly discussed by American biologist Edward O. Wilson in the 1970s) was developed—an evolutionary biological account of social systems from the perspective essentially of the gene.

On the other hand, paleontologists were

making further discoveries on their own. In the early 1970s, for example, paleontologists Niles Eldredge and Stephen Jay Gould pointed to the long-neglected phenomenon of stasis—the tendency of most species as seen in the fossil record to remain pretty much unchanged, often for millions of years, in stark contrast to the standard expectation, going back to Darwin, that species will almost inevitably change slowly and gradually through geological time. In their notion of punctuated equilibria, Eldredge and Gould combined their observations on stasis with the Mayr/Dobzhansky theory of speciation.

Still further work in paleontology has revealed the importance of mass extinctions in evolution. The net effect has been a reemphasis on the importance of the physical environment in causing extinctions and in triggering renewed bursts of evolution as an aftermath to extinction. *Turnover pulses,* a term coined by paleontologist Elisabeth S. Vrba, are episodes of sudden extinction of many species within a regional ecosystem, followed by bursts of speciation—all triggered by pronounced regional environmental change leading to disruption of entire biomes. Such turnovers are an essential ingredient of the Sloshing Bucket theory of evolution.

Much remains to be done; science never rests, and no answers are final. Although biologists agree that life has evolved, they still disagree about some of the details of exactly how evolution actually occurs. Creationists point to this disagreement as evidence that evolutionary biology is not true science—as if chemists and physicists did not openly and actively disagree with one another! Much progress has been made in understanding how the evolutionary process works. The task now, for even further progress, is to integrate the gene-centered view with the environmentally oriented views set forth above. There still is plenty to be done in evolutionary biology!

—Niles Eldredge

See also: Adaptation; Darwin, Charles; Evolutionary Biodiversity; Evolutionary Genetics; Human Evolution; Linnaean Hierarchy; Natural Selection; Paleontology; Punctuated Equilibria; Speciation; Species; Systematics; Wallace, Alfred Russell

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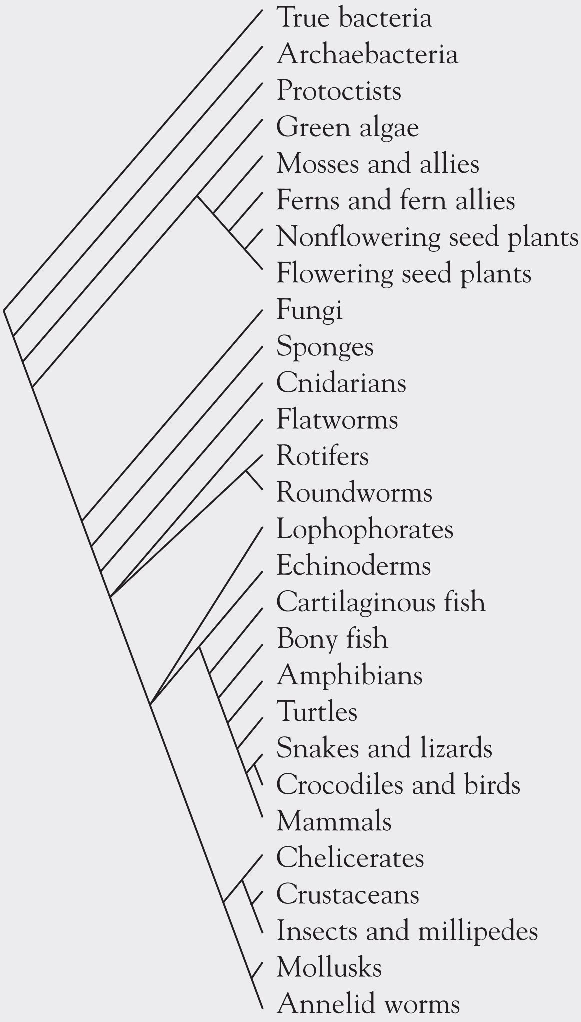
Evolutionary Biodiversity

Biodiversity is the term that embraces all the species represented in all the ecosystems of the world. Thus there are two complementary aspects to biodiversity—both necessary for understanding the earth's biodiversity in all its richness. One is ecological biodiversity, which is all of the world's local ecosystems. The other side of biodiversity is evolutionary biodiversity: the roster of species on the planet, mixtures of which supply the living components—the local populations of organisms—that compose the world's ecosystems. One can think of the evolutionary spectrum of the world's species (that is, everything ranging from bacteria and more complex microbes up through fungi, plants, and animals) as the roster of players in the game of life, while the ecological side of biodiversity (the world's ecosystems) is where the game of life is actually played. One important aspect of the general biology of each group of organisms is the characteristic roles that they play in ecosystems the world over.

Each of the major groups of organisms that, together, compose the evolutionary side of biodiversity is treated in a separate article in this encyclopedia; for more details, consult the appropriate entry. The purpose of this article is to develop an overall picture of evolutionary biodiversity, and in particular to show how all of life, from its very beginnings more than 3.5 billion years ago, is interrelated. For all of life has descended from a single common ancestor, and all of life on earth—at least 10,000,000 species, and possibly as many as 100,000,00—is interrelated in a way that can be shown as a great "tree of life." Figure 1 reveals the latest scientific thinking on how all of the major groups of life still living on the planet are related in an evolutionary (phylogenetic) sense. The diagram omits all those groups that have already become extinct and are known only through the fossil record. For more on how this form of evolutionary biological research is conducted, consult the articles on Systematics and Phylogeny, as well as the general entry on Evolution.

Figure 1

Evolutionary Relationships among the Major Divisions of Life



Source: Based on Eldredge, Niles. 1999. *The Pattern of Evolution*. New York: W. H. Freeman.

Bacteria are the simplest forms of life—and, not surprisingly, the first to appear in the fossil record. Bacteria are prokaryotes—that is, they lack the complex organelles and a distinct nucleus housing DNA typical of the more complex forms of life (the so-called eukaryotes). It has recently been shown that there are two major, distinct forms of bacteria: the so-called eubacteria (or "true" bacteria) and the archaebacteria, which are considered by many biologists to be more closely related to eukaryotes than are the eubacteria. Currently there are nine major groups, or phyla, of bacteria on earth.

Ecologically speaking, bacteria still pretty much run the world: it is possible to see the eukaryotes (especially the complex forms of animal and plant life) as forms of life that not only came later in evolution but also in a sense very much depend on the microscopic bacteria for their very existence. Different kinds of bacteria are responsible for a variety of ecological roles; for example, some bacteria, living in conjunction with the roots of leguminous plants, can "fixate" nitrogen. Nitrogen is a vital component of the proteins of all animals and plants, and nitrogen makes up roughly 70 percent of the earth's atmosphere. Yet only a few forms of life—all of them bacteria—are able to take up free nitrogen and fix it so that it can be utilized by plants, and therefore by the animals that eat the plants. Still other bacteria are essential for the digestion of cellulose; together with some forms of fungi, they are the only organisms that can break down this material, which forms the cell walls of plants. Without the breakdown of cellulose, life would have ceased long ago—clogged as the earth would have been with undecayed vegetable matter. It is true that bacteria cause disease—anthrax being one of the more notorious examples. But the bacterium *Escherichia coli*, which lives by the billions in every human's gut, is absolutely essential for normal human digestion. The invisible bacteria truly are the key chemical engineers of the planet.

Biologist Lynn Margulis has proven that more complex cells—eukaryotes—are the products of the permanent evolutionary symbiosis of at least two distinct forms of bacteria. The telltale evidence for her conclusion is that both the mitochondria of animals and the chloroplasts of plants have their own separate complement of DNA, in addition to the DNA housed in the eukaryotic cell's nucleus. That is what might be expected if two different kinds of bacteria, each with its own supply of DNA, had fused to create a more complex form of cell. Mitochondria and chloroplasts are in effect the powerhouses of the cells of animals and plants, respectively—the places where stored energy is converted for use (mitochondria) or, in the case of chloroplasts, the site of photosynthesis, the conversion of water and carbon dioxide in the presence of chlorophyll and sunlight into sugars, a form of trapped solar energy. Without photosynthesis, no animal life would be possible. It is important to note that certain kinds of bacteria, such as the blue-green algae, developed photosynthesis billions of years ago.

The most primitive forms of eukaryotic life are the protoctists—of which there are some twenty-seven different phyla currently recognized. These include amoebae, the shelled diatoms and formaniniferans, as well as ciliates and the flagellated protoctists. Some, like the euglenids, photosynthesize and are rather like one-celled plants. Others, such as the flagellates, are very animal-like, and derive their nutrient and energy supplies by absorption of tiny particles. It has been clear to biologists for more than 100 years that the root of each of the "higher" multicellular forms of eukaryotic life extends down into this mixture of plant-like and animal-like single-celled eukaryotes. Further research, increasingly using the techniques of molecular biology, will no doubt continue to separate which of the protoctists would be classified with the fungi, which with the plants, and which with the animals. There is still a great deal of research and analysis to be done in the systematics (that is, the analysis of evolutionary relationships) among these primitive single-celled forms of life.

Although biologists have traditionally

thought that fungi were the most primitive forms of multicellular, eukaryotic life, recent studies comparing DNA sequences of samples of fungi, plants, and animals have yielded the surprising result that we animals are more closely related to fungi than to plants.

Plants (Kingdom Plantae) of course are essential to the workings of all terrestrial ecosystems. There are some five major divisions of plant life recognized on the tree of life (Figure 1), including green algae (some biologists include these with the single-celled protoctists), mosses, ferns, gymnosperms (conifers), and angiosperms.

Photosynthesis, as we have already noted, is essential not only to the plants themselves but to all animal life as well. As producers of their own energy source from the simple ingredients of sunlight (the energy), carbon dioxide, and water, plants are autotrophic. But in addition to their ecological role as primary producers, plants play further crucial ecological roles: their roots fix soil, thus combating erosion. Trees in cities have been found to have a powerful effect in filtering chemicals from the air. And trees regulate the water cycle, especially in tropical rain forests. When vast tracts of tropical rain forest are cleared, not only does erosion set in but, in addition, rainfall cycles are disrupted. It takes, for example, some 52 million gallons of water to flush a single ship from the Pacific side to the Caribbean side of the Panama Canal; the water comes from the great artificial Lake Gatun, flowing downward by gravity to keep enough water in the canal for the ships to pass through. Without daily rainfall for much of the year—all supplied by the surrounding rain forest (which itself has been increasingly under threat to development in Panama), the Panama Canal would soon dry up.

Fungi—considered, like plants and animals, to be their own separate kingdom of life—are saprophytic, meaning that they absorb nutrients and energy from dead organic matter. Thus fungi are essential to the full cycle of life that makes it possible for new generations to replace the old. They include the familiar mushroom as well as yeasts (so useful in fermentation) and molds (such as penicillin). Only fungi and certain bacteria are capable of breaking down cellulose. Some species of termites in the tropics have huge fungal gardens deep within their mounds; the termites bring back pieces of wood fiber and leave it to the fungi to break down into a form that the termites can eat and digest, thereby obtaining the nutrients and energy they require.

Animals (Kingdom Animalia) are heterotrophs—they need to eat something else organic simply to stay alive. Some animals (herbivores) eat fungi and plants exclusively, while others (carnivores) eat the plant-eaters; still others eat the animals that eat the plant-eaters, and so forth through a complex chain of matter-energy transfer that is the “food-chain” and lifeblood of every local ecosystem. Some animals (omnivores) eat a wide range of foods: fungi, plants, and many kinds of animals; our own species, *Homo sapiens*, is an omnivore par excellence.

There currently are some thirty-seven separate phyla of animals living on earth. Sponges are among the most primitive of the animal phyla (so much so that most people do not even realize that they are animals). Sponges have only a few different kinds of cells, some arranged into channels in which they can filter food particles from currents of water, others for constructing their often massive skeletons.

Animals of the Phylum Cnidaria (including corals and most jellyfish) are a bit more complex, their cells being arranged into a two-layer system of tissues, though they lack the true organs (such as gills, brain, and heart) found in more complex animals. Flatworms have excretory organs and eyes, but roundworms and certain other animals lack the internal body cavity that ranks among the defining features of the higher animals.

The coelomate phyla—those with true organs systems and body cavities—are divided into two main branches, first recognized by biologists in the nineteenth century: the protostomes and the deuterostomes. *Protostome* means "first mouth," and the word refers to the fact that the first opening (blastopore) in the round ball (balstula) that cells form early on in embryonic development becomes the mouth of the adult animal. Protostomes include such important phyla as the annelid worms, the mollusks, and the arthropods. Those phyla, plus some other, less prominent groups, also share many aspects of body organization and details of embryological development that mark them distinctively as a main branch of the animal evolutionary tree—and one that we now know has been separate from the other great branch, the deuterostomes ("secondary mouths"—that is, the blastopore becomes the anus and a new opening is created later in development to form the mouth), for at least the past 540 million years.

Echinoderms (meaning "spiny skins"), a phylum that includes starfish and sea urchins (as well as many extinct groups), are very strange animals indeed. None of them have anything even remotely resembling a head—and no eyes or brain, either. They have a complex hydraulic system (that is, "water vascular system") that operates their tube feet, which they use for locomotion and (in the case of starfish) for grasping prey.

Yet, odd as echinoderms are, their DNA and aspects of their embryological development clearly show that echinoderms are among the closest relatives to the Phylum Chordata—our own phylum! We belong to the Subphylum Vertebrata—all chordates with a spinal column. The vertebrates include the cartilaginous fishes (sharks and rays), the bony fishes (salmon, tuna, and bass, plus some other more primitive forms), amphibians (frogs and salamanders), reptiles (turtles, crocodilians, lizards, snakes, and some others), birds (everything from ostriches to hummingbirds), and mammals: insectivores, probably the most primitive mammals (shrews, moles, and hedgehogs are insectivores), rodents (rats, mice, squirrels, and many others), rabbits, bats, whales, perissodactyls (horses, tapirs, and rhinos), artiodactyls (hippos, pigs, sheep, deer, antelope, giraffes, and so forth), carnivores (for example, bears, dogs, cats, hyenas, weasels, and seals), elephants, and, of course, primates—our own group. Primates include lemurs and lorises, New World monkeys, Old World monkeys, the great apes, and ourselves, *Homo sapiens*.

Human beings are very much a part of the great "tree of life." And though our species is listed last in this brief kaleidoscopic overview of earth's evolutionary biodiversity, this is not to say that we sit alone atop some sort of pinnacle of evolution. Each and every kind of organism on earth, no matter how simple or complex, so humble as a bacterium or regal as an American bald eagle, is beautifully adapted to the life it leads.

—Niles Eldredge

See also: Entries on all major groups of life mentioned in this article, as well as: Classification, Biological; Ecosystems; Evolution; Food Webs and Food Pyramids; Linnaean Hierarchy; Species; Systematics

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Evolutionary Genetics

Evolutionary genetics studies the patterns and mechanisms of genetic changes underlying evolutionary change. Because biological diversity at all levels (including population, species, and ecosystem diversity) has a genetic basis and is a result of evolution, evolutionary genetics provides insight into the ultimate mechanisms creating biodiversity. Evolutionary genetics utilizes empirical tools and mathematical methods and models. Evolutionary genetics has an important impact on many other fields, including medicine, anthropology, psychology, agriculture, conservation, economics, and philosophy.

Major Questions of Evolutionary Genetics

Among the most important questions that evolutionary genetics attempts to answer are these: What are the patterns of genetic variation within and among populations and species? What are the forces responsible for maintaining genetic variation within populations? What are the forces driving evolutionary change and, ultimately, the origin of new species? Why are there so many (or, perhaps, so few) species? How did they become so well adapted to their environments? What is the time scale for evolutionary change? What is the correct evolutionary tree for a set of species? What is the correct evolutionary history of life? Where do new genes and characters come from? Why do sex and recombination occur at all, and what are their evolutionary consequences? Where did humans come from? To what extent are humans different from other organisms?

Experimental Tools of Evolutionary Genetics

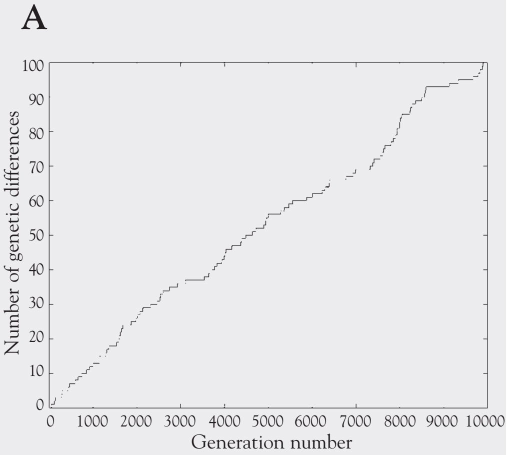
The most common empirical tools and techniques of evolutionary genetics are (1) classical genetic analysis of the distribution of specific genes and traits among offspring of particular crosses, (2) artificial selection experiments in which only organisms possessing certain characteristics contribute to the next generation, (3) studies of variation in enzymes in natural populations (enzymes are proteins that act as catalysts in biochemical reactions), and (4) studies of variation in molecular sequences (such as amino acid sequences, RNA and DNA sequences) between different organisms, populations, and species. Molecular methods have become the most powerful tool of modern evolutionary genetics. Experimental evolutionary genetics allows one both to quantify the extent of genetic differences and to estimate important evolutionary parameters (for example, mutation rates, the distribution of effects of mutations on different characteristics, including fitness components, strength of selection, rates of migration, and so forth).

Theoretical Population Genetics

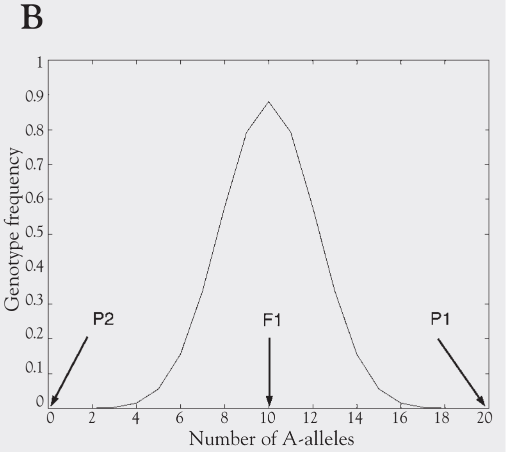
The effects of different factors (such as mutation, random genetic drift, and selection) on biological populations within one or a few generations are typically very small, and the time-scale for most evolutionary change is rather long. This makes it very difficult to observe or measure these changes directly. Moreover, even the simplest biological organisms, such as bacteria, have thousands of genes that can be in many different states (alleles). This results in an enormous potential for genetic diversity. For example, the number of different genetic combinations that are possible with L genes, each with just two alleles, is 2^L. If $L = 1{,}000$ (which is a reasonable estimate for simple bacteria), there are $2^{1,000} \approx 10^{301}$ genetic combinations. This number is much larger than estimates of the number of elementary particles in our universe. In many cases biological intuition is not helpful in evaluating the quantitative or qualitative effects of different biological factors on genetic systems that are that complex. Difficulties in direct observations and enormous genetic complexity make it necessary to use mathematical models and methods to analyze evolutionary change at the genetic level.

Figure 1

Effects of Mutation and Recombination



Dynamics of genetic divergence (by mutation) between two isolated populations.



Distribution of the number of A-alleles among the offspring of F_1 organisms achieved by recombination. Arrows mark genotype F_1 and its parents, P_1 and P_2.

Theoretical population genetics provides a mathematical foundation for the study of evolutionary genetics. The common procedure of theoretical population genetics is to start with some simple mathematical models that, although not fully realistic, can be completely analyzed and then refined into more realistic models that can be used to answer specific evolutionary questions. There are two general areas of theoretical population genetics: a prospective theory and a retrospective theory. The prospective theory takes the current state of a population (species, ecosystem) as given and tries to predict the relevant biological properties in the future. The prospective theory mostly uses methods developed within the mathematical theory of the dynamical systems (deterministic and stochastic). In the retrospective theory, one observes the current state of a population (species, ecosystem) and asks how it got here. The retrospective theory relies heavily upon statistical methods. Theoretical population genetics is essential for interpreting genetic variation, for predicting evolutionary change, and for reconstructing evolutionary history. It also provides a foundation for understanding the evolution of different characteristics, such as life histories and genome structure.

The Effects of Major Evolutionary Factors on Genetic Variation

Evolutionary genetics has established that most natural populations have very high levels of genetic variation. A number of evolutionary factors control both the maintenance of genetic variation within populations (species, ecosystems) and the rates of genetic divergence between different populations (species, ecosystems). Among the most important factors are mutation, recombination, random genetic drift, gene flow, and natural and sexual selection. Mutation and recombination are the primary factors introducing genetic variation into populations. Random genetic drift, gene flow, and natural and sexual selection act on this variation and control which genetic variants will be preserved and which will be removed from the population. Sufficient genetic divergence (cumulative or in specific traits or genes) results in the emergence of a new species.

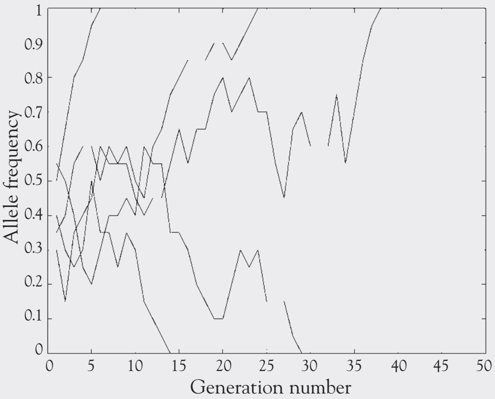
Mutation and Recombination

Mutation is a sudden, heritable change in the genetic material, most often appearing as an alteration of a single gene by replacement, duplication, or deletion of a number of DNA base pairs. Mutation can sometimes alter the structure or number of genes or entire chromosomes. Most mutations are harmful, but some are advantageous. Mutations occur naturally at low rates (10^{-5} to 10^{-6} per gene per generation). Mutation is considered to be the major factor limiting the speed of evolution. Isolated populations tend to accumulate different mutations diverging genetically. This is illustrated in Figure 1A, which describes the dynamics of genetic divergence by mutation between two hypothetical populations that were identical genetically before their physical separation. It is assumed that a new mutation is fixed in one of the subpopulations with a small probability, 0.001 per generation. The graph gives the number of mutations that differ between the populations as a function of time. Note that the number of genetic differences ("genetic distance") increases approximately linearly with the time since separation; thus genetic distance can serve as a proxy for time (a "molecular clock"). This property allows one to calculate the time to a common ancestor on the basis of genetic distance. This technique is widely used for reconstructing phylogenetic relationships between different groups of organisms.

Recombination is the exchange of genes between paternal and maternal chromosomes that occurs when reproductive cells are formed. Recombination results in offspring that have a combination of genes (characteristics) different from that of their parents. Recombination can potentially produce an enormous variety of new genotypes. This is illustrated in Figure 1B using a hypothetical example. It is assumed that one diploid parental organism, P1, has alleles A in ten specific loci (*locus* is a position on a chromosome occupied by a gene; *loci* is the plural form of *locus*). Because each diploid organism has two copies of each gene (inherited from its father and mother), the overall number of A-alleles is twenty. Another parental organism, P2, has A-alleles in these

Figure 2

Effects of Random Genetic Drift on Allele Frequencies in an Asexual Diploid Population



Different lines describe the changes in the frequency of allele A in five simulated populations that had the same initial frequency (equal to 0.4). The frequency of A quickly reaches 1 (in populations 1, 2, and 3) or zero (in populations 4 and 5) meaning the disappearance from the population of allele a or A respectively.

loci. Thus the overall number of A-alleles here is zero. Their offspring, which we denote as F1, will all have an intermediate number of A-alleles (which is ten). Figure 1B describes the distribution of the number of A-alleles among the offspring of F1 organisms, assuming that these organisms mated among themselves and that the loci are unlinked. This distribution includes genotypes with many different numbers of A-alleles at relatively high frequencies.

Random Genetic Drift

Random genetic drift means random changes in genotype frequencies that result from variation in the number of offspring between individuals and (in sexual organisms) from the inherent randomness of the process of production of reproductive cells. Random genetic drift affects biological evolution in two important ways. First, it tends to remove genetic variation from populations. This is illustrated in Figure 2, using five hypothetical populations of diploid organisms each with one locus with two alleles (A and a). It is assumed that the population size is twenty individuals and that initial frequency of allele A is 0.4. In Figure 2 different lines show the dynamics of the frequency of allele A in each population. Allele frequencies fluctuate from generation to generation until genetic variation is completely lost (that is, the allele frequency becomes equal to one or zero). Under random genetic drift, this happens in a time span comparable with the population size. Second, random genetic drift affects the probability of survival of new mutations in the population (see the section on natural selection, below). The effects of random genetic drift are inversely proportional to the population size, so that it is most important in small populations and is negligible in large populations. If mutation and random genetic drift are the only forces acting on a population, the population will continuously accumulate new mutations with the rate equal exactly to the mutation rate.

Gene Flow

Most species are composed of many local populations that occasionally exchange migrants. Gene flow between local populations is the exchange of genetic material by interbreeding between migrants and members of a local population. Gene flow increases the variation in the genetic composition of a population (because migrants bring “foreign” genes into the population) and decreases genetic differences between the populations exchanging migrants. In the absence of other factors, the time until the populations exchanging migrants become genetically similar is proportional to the inverse of the migration rate. Gene flow prevents continuous genetic divergence of populations that would happen by mutation and random genetic drift. The joint action of mutation, random genetic drift, and gene flow results in complex genetic variation within geographically structured populations.

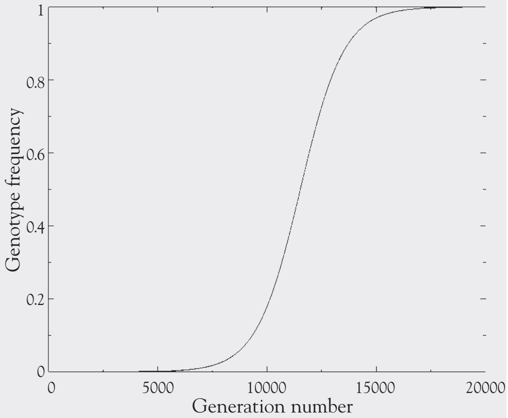
Natural Selection

Natural selection is the nonrandom and consistent differences between different genotypes (that is, in survival and reproduction). Natural selection acts to preserve genotypes that have higher fitness (that is, viability or fertility) and to eliminate genotypes that have lower fitness. Natural selection is viewed as a creative force that directs the course of evolution by preserving genotypes or traits best adapted in the face of environmental conditions and competition. Natural selection causes adaptation that is improvement in function, and it can act on tiny differences in fitness. This is illustrated in Figure 3a, which shows the changes in the frequency of a slightly advantageous mutant that is initially rare in a hypothetical asexual population. It is assumed that the ancestral genotype has a relative fitness of 1. (In this example, "fitness" means "viability"—that is, the probability of surviving to the age of reproduction.) The mutant genotype has slightly higher fitness (w = 1.001) and a very low initial frequency (p = 0.00001). Figure 3a shows that by approximately generation 18,000, the mutant genotype replaces the ancestral genotype.

Another illustration is provided in Figure 3b using a hypothetical asexual population that initially has five different genotypes at equal frequencies. In this figure, five different lines describe the frequencies of five different genotypes with fitnesses w^1 = 0.96; w^2 = 0.97; w^3 = 0.98; w^4 = 0.99; and w^5 = 1.00. Here, the differences in fitness between different genotypes are larger than in the previous example, meaning that natural selection is stronger. The least fit genotypes (genotypes 1 and 2) practically disappear from the population by generation 100. The fittest genotype (genotype 5) dominates by generation 500. Figure 3b shows that if natural selection is strong, biological evolution can be very rapid. In large populations, natural selection will quickly establish advantageous genotypes and eliminate disadvantageous ones (as illustrated in Figure 3). In contrast, in small populations random genetic drift will interfere with natural selection, resulting in the possibility of a stochastic loss of advantageous genotypes and establishment of slightly deleterious genotypes. Accumulation of deleterious mutations in small populations may result in their extinction.

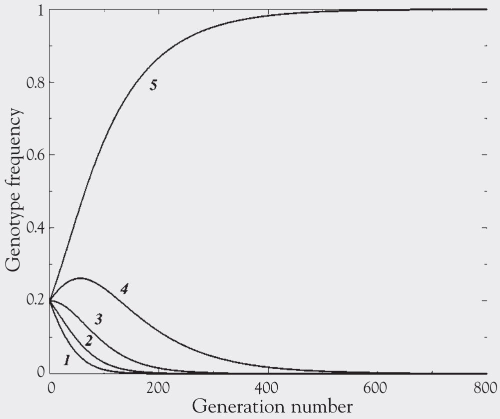
Figure 3a

Effects of Natural Selection on Allele Frequencies in an Asexual Population



Establishment of a slightly advantageous mutant that is initially rare

Figure 3b



Strong selection in a polymorphic population

Sexual Selection

Sexual selection is the nonrandom and consistent differences between different genotypes of the same sex in their ability to mate with (or fertilize) the organisms of the other sex. Sexual selection can be as strong as natural selection and can result in rapid genetic divergence of different populations. Sexual selection is the cause of the evolution of many secondary sexual characteristics, particularly in male animals, such as bright colors, elaborate ornaments, and conspicuous songs that are not useful or may even be deleterious for survival. Sexual selection is thought to be a major cause of speciation in some groups of organisms.

Implications for Biodiversity

Two major evolutionary mechanisms creating biodiversity are speciation (that is, the origin of new species) and divergent evolution. Evolutionary genetics has identified the most important factors affecting these mechanisms and their time-scales. Mutation, recombination, spatial structure and gene flow, natural and sexual selection are all very important in generating and maintaining biodiversity. The level of biodiversity depends on a delicate balance of deterministic and stochastic forces acting on biological systems. Evolutionary genetics has shown that although under certain conditions biodiversity can be created rapidly, under the most likely conditions the processes of generating biodiversity are very slow.

—Sergey Gavrilets

See also: Evolution; Molecular Biology and Biodiversity; Natural Selection

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Extinction, Direct Causes of

Extinction—the total loss of a species or higher taxonomic grouping—occurs for a wide variety of physical and sometimes biological reasons. Extinction should be regarded as a normal process in the history of life: much like the death of individual organisms, species are destined eventually to become extinct. Some species become extinct shortly after they have evolved; others may last for thousands, hundreds of thousands, or in many cases even millions of years (see Species). The vast majority of species that have ever lived are now extinct. Many biologists and paleontologists are beginning to think that extinction actually plays a vital role in the evolutionary process: in many instances, new species tend to appear rapidly after extinction has claimed species that had been formerly living in a region (see Evolution).

Scientists distinguish between what is called background extinction and events when extinctions of many species occur more or less at the same time in a pronounced extinction "event." The term *background extinction* simply means that a certain percentage of species are likely to fall prey to extinction as time goes by. For example, if the favorite food source of a species begins to disappear, the size of the species will diminish—and if it shrinks too far, the entire species may disappear—a victim of extinction.

In general, however, species become extinct through environmental change that occurs too fast, or too strongly, for species to survive through habitat tracking or evolution. And when such changes occur, they tend to affect many species within the regional, or even global, ecosystems at the same time. Thus it has become clear in recent years that most extinction is not background but rather is concentrated in regional or global events—often (at least in the case of the global events) called mass extinctions.

Habitat destruction is the single leading cause of extinction. When habitat disappears, the animals, plants, fungi, and microbes dependent upon it for nourishment and shelter will also tend to disappear—to become extinct.

There are many ways that habitats can become disrupted or destroyed. Climate change is a leading cause of habitat destruction (see also Habitat Tracking). For example, in one well-documented example from eastern and southern Africa, global climate change starting around 2.8 million years ago radically transformed the environment. From warm, moist tropical woodlands, within the space of 300,000 years, grasslands, indicative of a cooler, drier climate, replaced the woodlands in most places, driving many woodland-adapted species to extinction.

Climate change alone, however, is often insufficient to cause extinction: many of the Pleistocene (Ice Age) animals and plants—including those living on land, as well as marine invertebrate species—simply migrated southward, ahead of the advancing glaciers; when the climate warmed up and the glaciers retreated northward, so did the species living in the various ecosystems that had been displaced to the south. Mere loss of habitat in one region is not enough to cause extinction—if similar habitat occurs elsewhere, and species are able to migrate to it.

Yet global climate change is thought to have played a role in at least some of the five major mass extinctions of the past—most notably, perhaps, the Late Ordovician and Late Devonian mass extinction events.

Global cooling has another related effect on habitats: when seawater is locked up into huge, expanding sheets of continental glaciers a half-mile thick or more, sea level drops. The ice caps today are relatively large—not as great, of course, as when glaciers came as far south as Illinois and southern New York state (as recently as 18,000 years ago), but nonetheless greater than they were for most of the past half-billion years. This means that, for most of the past half-billion years, shallow seaways covered substantial parts of the interiors of North America, Eurasia, and, to a somewhat lesser extent, the continents of the Southern Hemisphere.

These shallow epicontinental (epeiric) seaways usually teemed with life—species of brachiopods, corals, rooted echinoderms like crinoids, corals, and mollusks, as well as many kinds of fish in the Paleozoic; mollusks (clams, snails, and ammonoids) as well as mosasaurs (marine lizards) and fishes in the Mesozoic and Cenozoic. But when the seas dried up and their natural habitats disappeared, species abruptly became extinct—all at about the same time.

Perhaps the most famous cause of mass extinction is the collision between the earth and one or more comets or asteroids from outer space. Extraterrestrial impacts are well documented as the probable cause of the fifth major mass extinction—the one at the end of the Cretaceous Period that ended the Mesozoic Era, some 65 million years ago; it took out the nonflying dinosaurs as well as the last of the ammonites and many other terrestrial and marine species. It is thought that bolide impacts may have been involved in the great Permo-Triassic extinction of 245 million years ago, as well, perhaps, as the extinction event at the close of the Triassic Period some 210 millions of years ago.

Collision of major extraterrestrial objects with the earth would have had the force of many hydrogen bombs—obviously obliterating all life forms within hundreds of miles of impact. But how could such an impact cause a wave of extinctions that engulfs the entire planet—as apparently happened 65 million years ago? The general theory of extinction-through-impact is profoundly ecological. We know from large volcanic eruptions in the past 200 years (such as the great explosion of Krakatoa in the strait between Malaysia and eastern Java in 1883) that large amounts of fine dust particles can be sent up into the highest reaches of the earth's atmosphere—coloring sunsets and, more important, blocking enough sunlight to lower the earth's temperature by 1 or 2 degrees centigrade. The Krakatoa eruption not only colored sunsets but is also thought to have triggered the great blizzard of 1888 in New York, and to have prompted snow to fall in the summertime in the northeastern United States; 1888 became known as the "year without summer."

These volcanic events provide a clue as to what might have happened immediately after a major impact event. Huge amounts of particulate matter and vapors would be sent up into the atmosphere, blocking sunlight sufficiently to interfere severely with photosynthesis in land plants—and in the planktonic marine microorganisms that photosynthesize near the surface of the oceans. Photosynthesis provides the very base of the food chain on land and in the sea, so a die-off of photosynthesizers would soon be followed by the loss of many of the species that depend upon them. Extinction comes about, then, by major disturbance to the flow of matter and energy through the world's ecosystems. Moreover, wildfires broke out after impact, followed by a major cooling event. Habitats were severely altered or destroyed, causing the great loss of species that we have come to call global mass extinction.

Biologists, including Charles Darwin, have speculated that biological factors can also cause extinction. Although difficult to prove, it seems likely that, especially in times when species become able to invade new habitat, very often resident species—species already adapted to and living in a particular region—will become extinct. For example, when the Isthmus of Panama was raised to form a direct land bridge between North and South America—an event that was completed by about 2.5 million years ago—some animal species (many of which were marsupials, like opossums) from South America were able to move north, while placental mammals from the north were able to move south. Although still a matter of study and some dispute, it appears that, on the whole, more species in South America were driven to extinction by the arrival of alien species than vice versa. In all instances, the cause of extinction is thought to be failure to survive given the competition with alien species.

The current Sixth Extinction is, in one sense, very different from the extinction events of the past—especially those that happened through physical causes. The difference is that the current extinction event (the "biodiversity crisis") currently gripping the word's species and ecosystems is caused virtually entirely by the behavior of a single species: *Homo sapiens*. On the other hand, the current extinction event is very like those mass extinctions of the past, because humanity is disrupting habitats and driving species extinct in a manner very reminiscent of extraterrestrial impacts and other physical causes of mass extinction.

Humans drive other species extinct in several ways. One is the conversion of land for agriculture. Over the past 10,000 years, since the invention of agriculture, people have cleared land—forests and grasslands—to plant one or two crops where normally many species of plants and animals would exist. We have drained swamps and marsh lands for cultivation, made deserts bloom through irrigation, and even regained farmland from the sea—as in the Netherlands. The negative effects (that is, in terms of driving species extinct) of such

Mexican official walks amid deforestation in the Lacandon rain forest, Montes Asules, which is on the verge of total destruction. (Reuters NewMedia Inc./Corbis)

human-caused habitat transformation are more pronounced in the tropics than in the higher latitudes, simply because there are more species in the tropics and many of them are restricted to smaller regions than is the usual case in the higher latitudes. In other words, there is a far greater chance of driving one or more species extinct by chopping down ten acres of forest in the tropics than there is in clearing ten acres in Ohio. But it all adds up, and conversion of natural habitat to farmland has been a leading cause of extinction in recent times.

But people destroy habitat for reasons other than the purely agricultural (which includes raising livestock on range land as well as growing crops). Especially in the past few hundred years, as human population has skyrocketed, cities and suburbs, with their malls, streets, and tract housing, have destroyed an enormous amount not only of natural habitat but also, increasingly, of the farmland we need to feed ourselves.

Warfare, too, has contributed increasingly to the damage that humans have caused to the landscape. We continue to cut down forests for the wood itself—for building, or even, in many instances especially in the Third World, simply for firewood to provide fuel for cooking and heat. Overharvesting of timber—where far more trees are cut than are being replaced in a sustainable manner by reforestation—remains a major source of habitat destruction.

Overharvesting of certain animal species by humans also has driven animal species to extinction. Many of the large mammalian species of the great Ice Age are thought to have been driven extinct by overhunting by humans. Twelve of the thirteen major oceanic fisheries, by the same token, are now so severely depleted by overfishing and harmful fishing practices that many fish species are now on the very brink of extinction. Pollution, too, poses a major threat to habitats—and directly to individual species of plants and animals.

Finally, the introduction of alien species (see Alien Species) is a major cause of extinction—just as it seems to have been in certain instances in the geological past. Humans bring domesticated animals (not to mention parasites and disease-causing micro-organisms) as they spread around the planet. Possibly a contributor to the first wave of the Sixth Extinction, the spread of alien species has reached shocking proportions in recent centuries, as opportunities for travel and trade have expanded. The brown tree snake, for example, is responsible for driving nine species of native birds extinct on the island of Guam in the South Pacific. The snakes arrived on airplanes as troops moved about during World War II, and they remain a major menace to this day. Aircraft in Hawaii are inspected daily, and some brown tree snakes have already been detected. It is felt that, should this aggressive snake ever become established on Hawaii, it would be the final death knell for many of Hawaii's endemic birds and other species already hard hit by extinction since the arrival of humans, human pets, and domestic animals, as well as by the ravages of cultivation.

—*Niles Eldredge*

See also: Agriculture, Origin of; Alien Species; Darwin, Charles; Evolution; Habitat Tracking; Pollution; Sixth Extinction; Species; Urbanization

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Five Kingdoms of Nature

Five Kingdoms Taxonomy and Its Logic

The five kingdoms of life is a modern taxonomic scheme, based largely on the work of R. H. Whittaker (1924–1980). Its main virtues are its fidelity to life's morphological and chemical diversity, and evolution. It is widely, though not exclusively, considered to be the most logical way to group organisms, based not only on their likenesses and differences but also on their evolutionary history. The five kingdoms are the Kingdom Monera (bacteria, also known as prokaryotes); the Kingdom Protoctista (eukaryotes or organisms consisting of cells with nuclei, excluding plants, animals, and fungi); the Kingdom Fungi; the Kingdom Plantae; and the Kingdom Animalia. These last two kingdoms, plants and animals, were long considered dichotomous opposites, two great groups into which all living beings could be nicely divided. However, the discovery of microbes (which include organisms that have both plantlike and animal-like characteristics) and an increasing awareness by biologists since the nineteenth century of evolution made the ancient plant-animal division untenable.

Microbial Evolution and the Inadequacy of the Plant-Animal Divide

Unlike many previous taxonomies of living organisms, the five kingdoms taxonomy reflects current understandings of evolutionary history. Both paleontological evidence in the form of microfossils, as well as biochemical (metabolic) and genetic comparative studies of living organisms, show that the first organisms for which there is evidence on earth are bacteria. The biggest division between types of organisms is not between plants and animals (as an ancient perspective cognizant of green growing, and breathing moving, living things suggested before knowledge of cells or evolution) but rather between prokaryotes and eukaryotes. Prokaryotes are all organisms without nuclei (*pro* = "before"; *karyon* = "kernel") in their cells; eukaryotes (*eu* = "true"; *karyon* = "kernel") all organisms with nuclei in their cells. Additional differences are the lack of true chromosomes in prokaryotes and the differential presence, in eukaryotes only, of gene-containing plastids (for example, the chloroplasts of plant cells) and gene-containing mitochondria (in virtually all eukaryotes) outside the nuclei. Eukaryotic cells also are generally much larger in size.

The difference between prokaryotes and

eukaryotes is really striking for anyone positing a gradual view of evolution. In this case, however, there is no "missing link": abundant genetic, comparative metabolic, microbial ecological, and other studies show, beyond a reasonable shadow of a doubt, that bacteria came together in symbiosis to produce the larger eukaryotic cells with nuclei, chromosomes, and, more often than not, mitosis (and sometimes meiosis)—characteristic chromosomal pairings and separations during cell division. Bacteria, by contrast, divide by simple cell division. The mitochondria and plastids (which may be purple-brown phaeoplasts or red rhodoplasts as well as the more familiar green chloroplasts) have an independent bacterial origin: the reason they continue to possess separate DNA, their own timetable of reproduction, and their own binary fissionlike mode of reproduction outside the nucleus is that their ancestors were bacteria. The symbiotic origin of eukaryotic cells thus shows neither plants nor animals, but rather bacteria, to be the primeval form of cell. Not all bacteria merged by any means, and free-living bacteria today have descended from bacterial ancestors assumed to have first evolved on earth more than 3.5 billion years ago. But among those bacteria that did merge were cells with nuclei and mitochondria (descended from aerobic, oxygen-metabolizing bacteria)—the first eukaryotes.

Circumstantial and genetic evidence suggests that the ancestors to the host cells were heat-resistant, oxygen-poisoned fermenting cells similar to the modern *Thermoplasma,* which survives the heat and acid of geysers in Yellowstone National Park. Although evidence is not definitive, these hosts of the ancestors of mitochondria had probably already established still another symbiosis—with highly motile spirochetes, known to feed on, attach, and sometimes inhabit other cells—before becoming a breeding ground for oxygen-breathing bacteria. The hosts preferentially survived because the surface of the planet, as geological evidence such as red beds of rust (iron oxide) shows, was becoming much richer in oxygen. Oxygen, produced by photosynthetic bacteria, the ancestors to plastids, as a result of microbial evolution to use water (H_2O) for hydrogen to build cells, is a highly reactive gas still toxic to many cells (called anaerobes). The ability to metabolize oxygen thus conferred an evolutionary advantage on anaerobes containing oxygen-breathing (and thus detoxifying) mitochondrial ancestors in their cells. The host-mitochondrial ancestor assemblages were the first O_2-respiring (or aerobic) protoctists, amoebalike cells. They were the ancestors to animals and fungi. Meanwhile, photosynthetic bacteria, when they were eaten but not digested, joined the host-respiring bacteria assemblage and created another sort of eukaryotic cell—one ancestral to algae and plants.

The upshot of all this microbial evolution, from a taxonomic standpoint, is that plants and animals are not an ancient all-encompassing division but relatively recent branches on the tree of life. Our ideas about how life has evolved have changed how life is best divided. The bacterial symbiotic ancestry of eukaryotic cells renders obsolescent older forms that continue to be used out of ignorance combined with linguistic momentum. (Language also has its rudimentary organs.) Thus it is now, for example, inaccurate to speak of "one-celled animals"; you are more a giant colonial amoeba, because amoebalike cells were your ancestors, than are amoebas (protists, one-celled protoctists) one-celled animals: protoctists evolved not only into animals but also into fungi and plants. A more technical term, protozoa, is also best avoided for similar reasons: *protozoa* comes from the Greek words for "first animals." Microbes such as *Chlamydomonas*, a single cell with green plastids that swims through the water, shows the inadequacy of the plant-animal divide.

Carl Woese's Competing Three Kingdom Taxonomy

Although the accumulation of knowledge tends to create redundancies and contradictions in classifications, the five kingdoms taxonomy enjoys a position as the most up-to-date classification scheme based on morphology, cell biology, and genetics. Its main rival, the three kingdom scheme innovated and championed by biochemist Carl Woese at the University of Illinois, Urbana, is based almost entirely on genetic sequences of ribosomal RNA. Since genes may jump and change, and spontaneously mutate without necessarily causing changes in the proteins of the bodies of organisms, however, the three kingdom system is less well rounded in its informational base.

Moreover, while genetic studies will certainly alter future classificatory schemes, one of the main insights of Woese's three kingdom taxonomy (in which two of the kingdoms are bacteria) supports the five kingdoms scheme. That is the distinction between two kinds of bacteria, the archaebacteria and the eubacteria. (All nonbacterial organisms in the Woese system—that is, plants, animals, fungi, and protoctists—are lumped into the Eukarya.) This distinction supports the five kingdom notion of a common, symbiotic origin to bacteria and visible life forms. That is because gene sequences in RNA show similarities between archaebacteria—"old bacteria" in Greek, a group that includes prokaryotes inhabiting extreme environments such as salt flats and tolerating extreme conditions (similar to those thought to prevail on the early earth) of high heat and acidity—and the cells of modern plants and animals. This makes sense if we assume that the ancient *Thermoplasma*-like forms joined in an earthly partnership with the predecessors to mitochondria (and, later, the predecessors to chloroplasts and plastids) to make cells with nuclei. Indeed, in the three kingdom taxonomy, animals and archaebacteria are about as related as archaebacteria and eubacteria. Such solely genetic-based classification, however, chafes against the naturalist's sense, based on morphology and paleobiology as well as molecular biology, that plants and animals are more closely related to each other than either is to bacteria. Nonetheless, both the modern three kingdom and five kingdom systems of taxonomy are more reflective of evolution than the antiquated (but highly persistent) plant-animal dichotomy.

A Brief History of the Five Kingdom Scheme

"Some people dismiss taxonomies and their revisions as mere exercises in abstract ordering," writes Stephen Jay Gould, "a kind of glorified stamp collecting of no scientific merit and fit only for small minds who need to categorize their results. No view could be more false and more inappropriately arrogant. Taxonomies are reflections of human thought; they express our most fundamental concepts about the objects of our universe. Each taxonomy is a theory about the creatures it classifies." Early humans did not distinguish well between alive and not alive, considering moving astral bodies alive, and wind and other aspects of nature to be inhabited by unseen spirits (here we can see the origins of religion). A primordial tripartite division, into plants, animals, and minerals, is still a norm among educated people. (That is despite the fact that plants and animals have mineral parts, such as the calcium phosphate of bones, and that many minerals, such as limestone, were once produced in or by the living tissues of organisms really neither plant nor animal.) With increasing study, living things have become divided into more subtle categories. French zoologist Georges Cuvier classified all animals, including microbes, into four phyla. The Swiss taxonomist Linnaeus, who invented the Latin binomial nomenclature still used and familiar to us as species names (for example, *Homo sapiens* [humans], *Canis familiaris* [dogs]), put all simple animals together into Vermes—that is, worms. In the nineteenth century photosynthetic protists were still considered one-celled animals by zoologists, while botanists claimed them for their own as tiny plants.

The imaginative German champion of Darwin, Ernst Haeckel (1834–1919), proposed a new kingdom to make room for the microbes, which he correctly saw were more general than plants and animals rather than specialized versions of them. First he lumped them together into the Kingdom Monera; as his ideas developed, he alternately included, then excluded, cells with nuclei (eukaryotes) within the Monera. Later, in 1956, H. F. Copeland, a biologist at Sacramento City College in California, clearly separated bacteria and cells with nuclei in a four kingdom system. In Copeland's taxonomy, initially overlooked, the first organisms to evolve, bacterial cells, were split apart from their symbiotic evolutionary products, the amoebas and other cells with nuclei collectively known as protoctists (familiar today in forms such as algae, *Paramecia,* and slime molds). Not until the 1960s and 1970s, with the arrival of molecular biology and more powerful forms of microscopy, did it become clear that microbes are distinct not only from plants and animals but also from the smaller nucleiless bacteria. The first essentially modern taxonomy to be accepted long after he suggested it in 1956 was put forth by Cornell University biologist R. H. Whittaker. Whittaker, a student of desert and forest ecosystems, found bacteria and fungi to be so distinct from plants that treating them as such was intellectually unacceptable. He argued for the five kingdom system with Protista (single cells) rather than Protoctista as his kingdom of miscellaneous microbial eukaryotes. The modern five kingdom system is essentially identical, except that multicelled eukaryotes that do not develop from embryos and are not fungi are now called protoctists, with the informal term "protist" being reserved for single-celled and other microscopic organisms in the kingdom. (The term *protoctista,* for "organisms that are clearly neither animals nor plants," was first coined by British biologist John Hogg.)

Differentiating among the Five Kingdoms

The biggest distinction used today in classifying life is the presence or absence of a nucleus and other membrane-bounded cell organelles such as mitochondria. Free-living organisms lacking such structures, and true chromosomes, are bacteria, or prokaryotes. They belong to the Kingdom Monera (Prokaryotae). Protoctists, the next kingdom of life to evolve, are composed of organisms that are either nucleated cells or colonial aggregations of such cells. As colonies of cells with nuclei, protoctists evolved on their own and into fungi, animals, and plants. The cells of these organisms have nuclei and mitochondria, and thus seem to come from a common microbial ancestor with nuclei and mitochondria in its cells. Perhaps the second biggest distinction to classify life forms, at least in the macroscopic kingdoms (fungi, plants, and animals), is nutrition. Fungi absorb their food, plants produce it, and animals consume it. (For a more detailed analysis of fungi, protoctists, and bacteria, see individual entries for those groups.) Additionally, plants and animals develop from embryos. Diverse embryo-forming animals, which range from beings smaller than protoctists to giant blue whales, show diverse forms of intelligence and behavior. Plants and animals (except for the sponges and Placozoa) possess tissues and organs. Algae and seaweeds are protoctists because, although green and plantlike, they do not form embryos.

Plants also all develop from multicellular structures enclosed in maternal tissue—that is, from embryos. Since embryos are sexually produced (or asexually produced in beings whose ancestors were sexual), all plants and animals may be regarded as being sexual or having sexual ancestors. The differentiation into specialized tissues, whether leaves and flowers of angiosperms, or the skin and lung tissues of primates, may be a legacy of sexual activities that evolved in protoctist ancestors. The prevailing plant-animal dichotomy mentioned above is so pervasive that neither plants nor animals have been deemed by the editors of this encyclopedia to merit their own separate entries. This in part reflects our bias as animals studying life zoologically from the inside: not only are we more apt to distinguish among those of our own largely mobile and animate kingdom, but we tend to confine the rest to our living antithesis, the slow-moving green world of plants. As our understanding of life and its diversity continues to grow, and life continues to evolve, our taxonomies are bound to change.

—Lynn Margulis and Dorion Sagan

See also: Archaebacteria; Bacteria; Botany; Coevolution; Coloniality; Ecology; Embryology; Evolution; Evolutionary Genetics; Fungi; Lichens; Museums and Biodiversity; Protoctists; Zoology

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Flabellidium Spinosum

Flabellidium spinosum, a bryophyte (moss), was never honored with a common name. This species is known only from the original specimen collected in the Tres Cruces Cordillera near Santa Cruz, Bolivia, in 1911. It is a representative of all the species that slip, unnoticed, into oblivion when an ecosystem is destroyed.

F. spinosum was a fragile moss with fronded, yellow-green branches growing to only about 1 cm in height. From study of the type material, it is believed that *F. spinosum* was the sole representative of its genus (Enroth, 1995).

Bryophytes are dependent on water for acquisition of nutrients and for completion of their reproductive cycle. In turn, bryophytes play a major role in maintaining an ecosystem’s humidity level by their ability to absorb and retain water. Bryophytes are used as indicators of ecosystem health, because any change in water, soil, or air quality caused by pollution or other factors, will have an impact on their growth. The area in which *F. spinosum* was collected has been cleared of its forest to make way for agriculture, and along with the forest have gone the many organisms that formed the fragile web of life.

The International Union for the Conservation of Nature monitors the status of species at risk of extinction. This organization has given its most dire assessment of the status of *F. spinosum:* "We consider that there is no reasonable doubt that the last locality for this species has been destroyed and that the last individual has died" (Hilton-Taylor, 2000).

—*Julie Pomerantz*

See also: Bryophytes; Extinction, Direct Causes of

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Flagellates

See Protoctists

Flies

See Arthropods, Terrestrial

Flycatchers

See Arthropods, Terrestrial

Food Webs and Food Pyramids

Food webs and pyramids are the most popular ways of representing the trophic structure (that is, the feeding relationships and related functional groupings) of ecosystems. Food webs show the connections between population systems at different trophic levels and within the same level of organization; food pyramids illustrate the proportions of the different feeding groups. Both are representations of the functional aspects of ecosystems involving transfers of energy and materials between the component populations—the connections that support life in species assemblages. Webs and pyramids can be used to characterize local systems, subdivisions of local systems isolated for emphasis, or larger, more inclusive ecologic systems at the regional scale. Along with composition and diversity, trophic structure is one of the fundamental properties of ecologic systems of all kinds.

Food chains are linkages embedded within more extensive webs, teased out to emphasize relationships of particular interest or to highlight especially important organisms. An example is an intertidal marine food chain, which could consist of a bottom-dwelling green alga that imports the energy for this part of the overall food web by converting sunlight into chemical energy through photosynthesis. A grazing gastropod harvests this resource (representing the next position in the chain). A dominant species of crabs patrolling the intertidal zone preys on the gastropod (a third level), and occasionally a seagull preys on the crab and exports the energy away from this limited system. The algae-gastropod-crab-bird food chain is but one component or pathway in a much more complex web or network of trophic interactions within the same ecosystem. Such relationships may be stable over long periods of time, vary seasonally, or take place only during a certain stage in what is called ecologic succession; and the chain may be repeated regionally in numerous local ecosystems, or could be unique to one place.

It must be remembered that the flow of energy and movement of chemicals through ecosystems are closely coupled. Organisms that convert sunlight into available energy for an entire system rely on the presence of critical nutrients, especially nitrogen and phosphorous—the universal fertilizers of ecologic systems that depend on photoautotrophy. Although chemical movements vary greatly among systems, in terms of available pools versus storage sinks, cycles versus unidirectional transfers, and the specifics of chemical utilization by component organisms, in general terms chemicals can be recycled (mass balance considerations apply), whereas energy is dissipated (the laws of thermodynamics are at work) as the transformed chemical energy passes through food webs.

Primary Production

Everything that happens in an ecosystem depends on the initial importing of energy and nutrients by primary producers. Most systems are supported by photoautotrophs, which convert the radiant energy of the sun into chemical-bond energy. The ability to photosynthesize stable carbohydrate compounds is found today primarily in three important groups of organisms: blue-green bacteria (also called cyanobacteria) in aquatic environments; algal protists (many different groups), also in aquatic settings; and multicellular plants, chiefly in terrestrial environments but with some representatives in aquatic systems. At thermal vents and chemical seeps in the deep ocean, chemoautotrophic bacteria are the primary producers. Ecosystems that depend on these inputs are said to be autotrophic. Other systems, however, depend on input of organic material from adjacent autotrophic systems. These include rivers that import detritus from upstream locations, lakes that depend on the organic material delivered by runoff and inflow, and especially vast areas of the deep-sea floor that need detritus falling from the upper water column to support life well below the photic zone. These systems are referred to as heterotrophic.

All ecosystems are open, in the sense that energy in one form or another has to be imported from the outside; and all systems maintain organization and support their own development through time with inputs of energy and chemicals. Most of this activity can be summarized in two equations. Energy transfer is represented by: $P_g = P_n + R$, where P_g is gross productivity, P_n is net productivity, and R is respiration (an expression of the first law of thermodynamics as it applies in an ecosystem, either in terms of initially importing and transforming energy or in terms of passing the energy to higher levels in the system). The available energy present at any position in a food web at any given time is: $\Delta B = P_g - R - H - D$, where B is biomass, P_g is gross production, R is respiration, H is the rate of harvest, and D is the mortality rate. Because of losses inherent in transforming radiant energy into chemical compounds and in transferring this material through processors at different organizational levels, energy flow is not very efficient, and only a limited number of tiers in a food pyramid or steps in a food chain are allowed to develop (usually < 5), although an enormous amount of variation in trophic structure has been observed.

Consumers

The organisms that eat primary producers are the primary consumers. Other organisms that process imported detritus or recuperate energy/chemicals within systems are called decomposers. These organisms in turn are preyed upon by larger, less numerous species, and so on until the “top consumer” is reached in the food pyramid. The number of levels is controlled in general by biomass accumulation that can be utilized efficiently at the next higher position in a food chain. By the time the fourth or fifth step is reached, available energy is in short supply, and top predators might have to visit adjacent local ecosystems to supplement their diets. To make the array of consumers more complex, either primary production must increase or more efficient transfer of energy across levels (sending more energy through consumers and less through the decomposers, or appearance of an evolutionary innovation resulting in more efficient use of net production) needs to take place. Interactions between components of food webs can be extremely complicated, or they can consist of relatively few connections, involve what are referred to as trophic specialists (obligate interactions) or generalists, and be able to withstand disturbances or be prone to collapse during the mildest disruption in population structure, energy/nutrient availability, or geometry of the connections. An interesting complication is that consumers may feed at different positions in the food web at different stages of their life cycles.

Variations

Not only are food webs in different environments composed of different organisms with differing levels of connectivity, but such networks also change over time. Early stages of succession are dominated by organisms with high resource utilization rates, fast growth, and high rates of propagule production. Productivity is high at first, but as later colonists arrive and establish themselves, systems settle down to a more efficient functional regime, consisting of more trophic specialists that grow more slowly and have lower fecundity. Biomass builds up during the later stages, and the important chemicals can be recycled. Thus one of the important ways of identifying recently disturbed ecosystems is to document the properties of local trophic structure.

A recent breakthrough in food web theory involves the realization that adjacent local ecosystems actually interact with each other, comparable to the population systems making up their internal working parts. It is well known that adjacent systems share migratory species or predators with large hunting ranges, but it has been demonstrated only recently that significant amounts of chemicals and energy can be imported from neighboring systems, and that this may be more widespread than was once suspected. Food webs that extend over regional scales could be used in these cases to map the transfer of energy and materials, revealing the functional identity of regional ecosystems.

A final word is in order about the effects of humans on food webs, which have been pervasive. Human activity and by-products degrade and destroy trophic organization in many ways. Elimination of habitats of the dominant species, overharvesting of producers and consumers (especially top predators), and the intended or unintended introduction of exotic plants and animals all do great damage to food webs. If ecosystems survive at all, they may be less diverse, less complex in terms of trophic connections, and consist of monotonous copies of other systems similarly despoiled and invaded. Species at all levels of food pyramids have been affected, and few natural systems are likely to remain truly pristine as the biodiversity crisis continues to unfold.

—*William Miller III*

See also: Bacteria; Carbon Cycle; Carnivora; Coevolution; Communities; Ecological Niches; Ecosystems; Positive Interactions; Protoctists; Succession and Successionlike Processes

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Foraminifera

See Protoctists

Freshwater

Freshwater occurs in minor amounts on the earth, but it is found virtually everywhere: in the atmosphere, streams, lakes, permafrost, glaciers, ice caps, icebergs, and below the ground. Although the salty oceans contain 97 percent (1,322,000,000 cubic kilometers) of the earth's water, glaciers contain about 2 percent (29,200,000 cubic kilometers); freshwater on land and in the atmosphere accounts for only 0.635 percent (8,630,000 cubic kilometers) of the total. It is estimated that groundwater (8,400,000 cubic kilometers) contains the significant portion of the total on the land; freshwater lakes (125,000 cubic kilometers), saline lakes and inland seas (104,000 cubic kilometers), soil moisture (67,000 cubic kilometers), atmosphere (13,000 cubic kilometers), and stream channels (1,250 cubic kilometers) make up the rest.

Many studies predicting the state of water resources of the United States in the future are pessimistic, because of not enough surface water, removal of too much groundwater, pollution of surface and groundwater, deterioration of drinking water quality, and flooding and destruction of wetlands. It has been estimated that the water table in the United States has been dropping 2 to 3 feet per year over large areas. Urban development, agriculture, deforestation, and desertification increase runoff and decrease infiltration to the water table.

Removing too much surface water for use in one place deprives other places of adequate water. Water taken for Los Angeles and irrigation removes so much from the Colorado River that the river is often dry where it flows into the Gulf of California. River diversions cause wetlands along rivers to dry up, causing waterfowl and other wildlife dependent on them to disappear. In the southern part of Florida, the Everglades has been drying up, because its original supply of water came from Lake Okeechobee. To aid farming, canals were cut from the lake, bypassing the Everglades and leaving the wetlands to subsist on local rainfall. In addition, a thousand-square-mile area of the Everglades was diked and ditched and equipped with large pumps, to provide land for sugar cane production. Recently Congress has passed legislation to remedy some of these problems.

Water on earth occurs in three forms: as a solid (ice), a liquid (water), and as a gas (water vapor). In liquid water, the molecules are not as tightly packed as they are in ice. Although water is densest at 4 degrees centigrade, ice is less dense, and it floats. As a result the water at the bottom of deeper lakes will not freeze.

The water table marks the division between the zone of aeration and the zone of saturation, with most of the water lying within 3,800 m of the surface and available with current technology. Rocks that contain water within the zone of saturation are called an aquifer, and the amount of water in an aquifer is determined by porosity—the amount of space and permeability, and how connected the pores are. Rocks with high porosity and low permeability will not transmit water easily. In rocks like granite, which contains a negligible number of pores, the water is located in cracks, while in some sandstone, it is in the spaces between the grains. Sandstone aquifers usually contain much more water than do granite aquifers. Some rocks, such as shale, are nearly impervious. As the water table drops, spring flow diminishes, wells become less productive or dry up, and surface flow in streams is also reduced. In addition, as the space the water occupied empties, the land above may subside, some-

A Native American woman collects water from a stream in the Southwestern United States, c. 1915 (Library of Congress)

times by as much as 30 feet: building foundations may crack, as may roads, sewers, and water lines. Along the coast, saltwater often intrudes into the aquifer, and sinkholes develop where the supporting limestone is reduced as the groundwater drains away. Nearly half of the people in the United States use groundwater for drinking.

Under normal circumstance most plants get their water from soil moisture. However in dry environments, some plants, called phreatophytes, can retrieve water from deep aquifers. They consume huge quantities of water and flourish along canals and reservoir where notable amounts of water are removed and returned to the air through leaves. Stream flow is very variable, depending on geology and climatic conditions. In the United States a network of gauging stations measures the amount of water passing by particular places along rivers, providing a good record of the amount of surface water. In general, a north-south line just east of the Oklahoma and Kansas boundary, for example, divides the country into two parts: a western part where evaporation exceeds precipitation and an eastern part, where precipitation exceeds evaporation. To ensure sufficient water supplies for homes, industries, and irrigation, dams are built to store water in times of excess flow.

It has been estimated that perhaps as many as 2 billion people worldwide do not have access to safe freshwater today. The amount of water we have on earth will remain essentially the same. Increases in personal per capita use, population increase, and the resulting increase in industrialization are going to stress both the quality and quantity of this resource.

—*Sidney Horenstein*

See also: Dams; Interior Wetlands; Lakes; Rivers and Streams

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Frogs

See Amphibians

Fungi

Familiar as visible reproductive forms such as mushrooms, morels, and puffballs, but more often single-celled yeasts and other microscopic forms invisible to the naked eye, fungi can be defined as nonplant, nonanimal eukaryotes that develop from fungal spores. The largest include the shelf fungi that grow on the base of trees.

Although sometimes similar to, and confused with, members of the protoctist kingdom ("protozoans"), fungi never display the cell appendages known as undulipodia at any time in their life cycle. Undulipodia, sometimes called flagella, are in fact distinct from bacterial flagella made of flagellin proteins. Undulipodia—the generic term—have many familiar examples: cilia, sperm tails, and eukaryotic (but not prokaryotic) flagella. Cross-sections of these structures reveal an internal symmetry of nine pairs of microtubules. Thus true undulipodia, common to other kingdoms made of eukaryotic cells, were either never present or, more probably, lost in the ancestors of fungi during the course of evolution. This makes sense, because fungi, which disperse by airborne (or animal-attached) spores, excel at settling land and soil. Swimming by undulation is impossible outside water.

Although fungi sometimes mate, their sexual activities are radically different from those of plants or animals. A single species, for example, may display thousands of distinct mating types; all except those of the exact same mating type cannot mate with each other. Fungi also differ from plants and animals in that they do not typically form cells with two sets of chromosomes; the result of mating fungal threads (hyphae) or spherical cells are new structures with only one set of chromosomes, or cells with two nuclei that do not merge (or merge only directly before spore formation; see below), as occurs with plants and animals.

Fungal Nutrition and Cell Reproduction

Like virtually all animals, fungi are heterotrophs (Greek: *hetero* = "other"; *trophos* = "feeding"); that is, they eat other organisms or leakage of organic materials from other organisms to survive, rather than making their own food. That is why we are accustomed to seeing them on, or associating them with, dead, dying, or sickly tissue.

Unlike animals, however, fungi do not eat but break down food on the outside of their bodies, by producing powerful enzymes and then absorbing the other organisms into their cells. They thrive, for example, on keratin, an animal protein found in hair and nails, and can decompose cellulose, a hard-to-digest compound that helps lend rigidity to the wood of trees. Their own cells are surrounded by walls of chitin, also found as the exterior hard coating of arthropods such as insects. Chitin is a nitrogen-rich long-chain polysaccharide compound that makes fungi physically tough and helps them to resist extremes of wet and dry, hot and cold. Inhabiting diverse ecosystems from the Arctic tundra to human feet, mouth, and intestines (*Candida* species are a normal partner on the human body, causing problems only when they overgrow), fungi are among the most tenacious organisms on earth.

Fungi grow by spores that germinate into thin growing tubes known as hyphae. These microscopic, translucent, rootlike structures are incompletely divided by walls called septa, although not in all species. The septa are somewhat like partial walls in a modern apartment, orchestrating but not completely containing the flow of intracellular structures such as mitochondria and, in sex, nuclei. Thus, unlike most cells of multicellular organisms, in fungi the cytoplasm, or area around the nucleus, can flow more or less freely from cell to cell. When the hyphae aggregate in sufficient numbers they become visible as a fungal mass, the body of the fungus, called mycelia. Mycelia, often seen as thready, whitish masses—fuzz—may be subterranean; attached to tree roots, many fungi develop more familiar reproductive parts such as mushrooms and the shelf fungi at the bottom of trees, the parts of their bodies that extend above ground.

Kinds of Fungi

The fungi fall into four great groups, or phyla, below the level of kingdom: the zygomycotes, the ascomycotes, the basidiomycotes, and the deuteromycotes.

Zygomycotes

The zygomycotes are mating molds. Hyphae of complementary mating types fuse sexually to become zygosporangia. Mating molds also make stalks called sporangiophores, although these are produced without hyphal fusion, on which appear sporangia. (The *zygo* in zygosporangia, as in the fertilized egg or zygote, refers to the act of fusion.) You can see the sporangia as fuzz on bread or fruits. The zygomycotes are extremely important for their role in forming endomycorrhizae within the roots of plants, where they are crucial at accessing nitrogen, which helps in plant growth.

Ascomycotes

The ascomycotes make spores, known as ascospores, which are surrounded by the ascus, the baglike structure for which the phylum is named; all members from the highly edible morels to single-celled yeasts contain these structures. Asexually produced reproductive structures known as conidia are the most common means of reproduction. There are about 30,000 species of ascomycotes.

Basidiomycotes

Basidiomycotes produce basidia, clublike bodies within their gills or pores. These are best known to us because their clumped sexual reproductive organs pop up as edible, poisonous, and psychedelic mushrooms. The basidiospores result from a complex sexual life cycle that includes fusing hyphae and the merging of genetically different nuclei. There are two classes, the Heterobasidiomycetae and the Homobasidiomycetae; in the former are found the rusts and smuts, such as corn smut, "huitlacoche" or "cuitlacoche," a Mexican delicacy, while to the second group belong

Fungus growing on a tree, Minnesota (Richard Hamilton Smith/Corbis)

most mushrooms. Ectomycorrhizae, symbioses bringing phosphorus and other nutrients to trees and shrubs, are engaged in by thousands of basidiomycote species.

Deuteromycotes

Deuteromycotes were originally known as the Fungi Imperfecti because, unlike other fugi phyla, they never form structures from sexual reproduction; this makes them seem "incomplete." Evolutionarily, this group is thought to be derived from sexual ancestors that perhaps took more time and energy to reproduce. The single-parent spores, also known as conidia, lead to colonization of many environments. Penicillin, a compound that destroys bacterial cell walls, is produced by the deuteromycote *Penicillium*. Other species of this group are used in making soy sauce. Some, such as *Candida* or *Tinia*, cause human skin infections such as vaginitis, athlete's foot, and diaper rash.

Fear of Fungi

Radically different attitudes exist culturally, especially between the East and the West, in regard to fungi. In English-speaking countries, which have been called "mycophobic" (fungi avoiding), mushrooms and molds have traditionally been considered inedible, poisonous, or evil. (Consider the term *toadstool,* with its dim connotations of evil and witchcraft.) The natural diversity of fungi has been much better appreciated, in general, by some non-English-speaking cultures. Although fungi can produce mycotoxins and disease, and while it can be fatal to eat misidentified fungi—no doubt the original scientific impetus behind cultural prohibitions and superstitions—fungi are also of great commercial and aesthetic benefit. They ferment the alcohol in wine, beer, and champagne; make flour rise in bread, giving it its texture; ripen thenay, vendome, camembert, brie, and many other cheeses; and scavenge nutrients that they then deliver through the roots to plants. Even this paper, a wood product, is made possible by fungi associated in the roots of trees. Indeed, without fungi, neither forests nor life on land as we know it could have evolved.

Fungi and Others

Although we consider them dumb growths, fungi, like plants, have entered into complex relationships with vastly different organisms. For example, consider the leaf-cutting ants, a division of the attine ants that harvest lepiotaceae fungi in specific areas within their nests where they feed on the ends of hyphae. Unable to digest cellulose of leaves, the leaf cutters avail themselves of the fungus's ability to convert cellulose into carbohydrates somewhat as we do in using yeast to make beer. The ants (*Atta cephalotes*) organize their societies around fungal farming, with medium-size ants transporting leaves to the nest and smaller ants inoculating fungi into it with their feces, as well as eliminating other fungi by ingesting them and by means of chemical secretions. The ants have also modified the architecture of their nests to accommodate their fungus gardens. As with our cultivation of corn, which now grows so thickly in its leaves that it cannot reproduce without being stripped by hand or machine, the fungus never undergoes reproduction sexually by producing mushrooms, but instead depends solely upon the ants for their continued existence.

The queen carries spores to begin fungal cultivation of the same asexually propagated basidiomycote fungi; comparative morphology studies suggest that the same species of fungus has been involved with these ants for 23 million years—a length of time that dwarfs human agriculture, thought to have begun a mere 10,000 years ago. Many other fungal symbioses exists, although this one is striking. The fungi are notable in that they are both strongly attractive and repulsive to other forms of life, helping to convert members of their fellow kingdoms back into assimilable nutrients upon their death, but also tempting them to ingest and carry (but not devour) their spores. Like plants, the fungi walk a fine line between being eaten and destroyed by animals, and being ignored and thus insufficiently propagated by them. Psilocybin, which causes hallucinations in humans, grows in cow feces. *Pilobilus*, a fungus that moves through the intestinal tract of horses, is eliminated by them during defecation. It then jumps several feet to fresh grass. Later, it is eaten by the animals and the cycle continues. As with other organisms, the "environment" of fungi often consists largely of other organisms.

The Role of Fungi in the Evolution of Land Life

Although fungi are often associated with disease and madness (LSD is a derivative of ergot, a fungus infecting rye grass), they played a major role in the evolution of life. They were one of the first lineages of eukaryotic cells (cells with nuclei) to evolve multicellularity after diverging from the protoctists; plants and animals were the others. The best guess is that they either were the first colonizers of more or less dry land, or partners with photosynthetic settlers of the land—algae on the way to becoming plants. One strong clue is that the earliest known plant fossils, from the Rhynie chert of the Devonian Period, more than 350 million years ago, bear fossils of fungi along with plants. The terrestrial preference of members of this kingdom is attested to by the existence of only a very few marine forms of fungi. Without the cell whips known as undulipodia, fungal cells are poorly adapted to an aqueous environment: the very few marine forms (such as underwater mushrooms) probably evolved secondarily to a water habitat, just as marine mammals such as seals and walruses (whose ancestors had already moved onto the land) evolved blubber and other adaptations to go back to the water. The mycelial and hyphal networks of fungi help create soil and digest the hard parts of organisms requiring rigidity to move to land. Skin, cotton, feathers, wood, hair, caulking, refrigerator liner, camera lens mounting compound, and other refractory materials are digested by these tenacious life forms. Their injection of enzymes into the environment and subsequent absorption could have played a role in paving the way for the arrival of animals, who came to land after (not before, as is commonly thought) plants and fungi.

The fact that lichens (fungi-algae and fungi-photosynthetic bacteria alliances) are among the first to break down solid rock suggests the soil-making powers of these beings. Another indicator of the role of fungi in making land inhabitable by the rest of life is the existence of mycorhizae root symbioses in many important plants. Of course, although their cells do not swim, as we all know from personal experience, fungi tend to like moist and damp environments. Thus, from a perspective of global evolution, one can argue that watery life moved to land by extending the domain of the original wet, cycling processes of marine life to land. This process, which we traditionally picture as the conquering of the land, can also be regarded as the extension of the original marine ecosystem to include land in its wet fold; life did not come to land so much as re-form it according to the original template of a marine ecosystem. In either perspective, fungi were crucial.

—Lynn Margulis and Dorion Sagan

See also: Adaptation; Arthropods, Terrestrial; Evolution; Five Kingdoms of Nature; Lichens; Microbiology; Protoctists; Soil; Topsoil Formation

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Galapagos Islands and Darwin's Finches

These two names, Galapagos Islands and Darwin's finches, are intimately connected in our minds, and rightly so. The famous naturalist Charles Darwin visited the Galapagos Islands from September 15 to October 20, 1835, during the cruise of HMS *Beagle* around the world. In the narrative of his travels Darwin (1845, 456) wrote that the finches "form a most singular group of [birds], related to each other in the structure of their beaks, short tails, form of body, and plumage." He added, "There are thirteen species, which Mr. Gould has divided into four sub-groups." The English ornithologist John Gould (1804–1881) studied the birds collected by Darwin in the Galapagos and described nine of the fourteen species of finches recognized today. These drab-colored birds, for many years called Galapagos finches, were named after Darwin in a 1936 paper by Percy R. Lowe, another English ornithologist. And Darwin's finches they have remained ever since. In a classic 1947 monograph that influenced all subsequent thinking about these birds, the distinguished British ecologist David Lack speculated about the evolution of Darwin's finches. The technical name Geospizidae was proposed for Darwin's finches by the American ornithologist Harry S. Swarth, after *Geospiza,* the first genus described by Gould in 1837. All fourteen species of Darwin's finches are now included in the subfamily Geospizinae of the finch family Fringillidae. Thirteen of them are endemic to the Galapagos Islands—in other words are found nowhere else. The exception is the Cocos finch (*Pinaroloxias inornata*). It lives on Cocos Island, an 18-square-mile volcanic island isolated in the Pacific Ocean about 300 miles southwest of Costa Rica (to which it belongs) and 400 miles northeast of the Galapagos.

Discovered by the bishop of Panama, Tomás de Berlanga, in 1535, the Galapagos were called Islas Encantadas (the Enchanted Isles) in remote times, then Archipiélago de Colón by Ecuador in 1892. Their current name is an old Spanish vernacular for their giant tortoises. Since 1832 the Galapagos Islands have constituted a province of the Republic of Ecuador. Straddling the equator in the Pacific Ocean about 600 miles west of mainland Ecuador, the fourteen large islands and many small ones cover a land area of 3,075 square miles, more than half of which is accounted for by the largest island, Isabela (or Albemarle; 1,650 square miles).

At first uninhabited, these islands were visited in past centuries by buccaneers like William Dampier, then by whalers. They all stopped there to resupply. Their crews consumed large numbers of the now endangered giant tortoises and released domestic animals to serve as food for later trips. Today the Galapagos have a permanent population of more than 12,000 people, many of whom live in Puerto Ayora on Santa Cruz Island (Barrington), the town in which the famous Charles Darwin Research Station is located. Over the years the Galapagos Islands have received both English and Spanish names, a rather confusing state of affairs. Listing the islands in alphabetical order, with the Spanish names first (these are in use today; see Wiggins and Porter, 1971, pp. 2–3), should be useful: Baltra (South Seymour), Cowley (Cowley), Darwin (Culpepper), Española (Hood), Fernandina (Narborough), Floreana (also Santa María; Charles), Gardner (Gardner), Genovesa (Tower), Isabela (Albemarle), Marchena (Bindloe), Pinta (Abingdon), Pinzón (Duncan), Rábida (Jervis), San Cristóbal (Chatham), San Salvador (James), Santa Cruz (also Chávez; Indefatigable), Santa Fé (Barrington), Seymour (North Seymour), and Wolf (Wenman). Although the Galapagos are located on the equator, their climate is not uniformly torrid. Bathed by cold waters sweeping in a great westerly arc from South America, their seasons alternate between dry and wet. The duration and severity of drought or rainfall vary. The chief agent responsible for this irregularity is a reversal of oceanic currents. When the warm Equatorial Current reaches the Galapagos, a condition known as El Niño (the "child," or baby Jesus in Spanish, because it often occurs near Christmas), torrential rains fall on the islands.

Although best known because of Darwin's visit and for the finches he discovered, there are many more aspects of the Galapagos Islands that deserve our attention. One is their volcanic nature. Several Galapagos volcanoes are active and have had dramatic recent eruptions—for example, Volcan Alcedo on Isabela in 1954 and Fernandina's caldera in 1968. A striking feature of Galapagos landscapes is the huge and desolate fields of rugged black lava that here and there bisect areas where the scrubby vegetation has been spared by recent flows. Another peculiarity of the Galapagos is their geographic isolation. Inasmuch as they were never connected to the South American continent, their flora and fauna are derived from just a few colonists that floated in the air or drifted in sea currents across the 600 miles of isolating ocean during the 3 to 5 million years that passed after the Galapagos first emerged from the sea. Their dry and uninspiring vegetation is itself fascinating. The Galapagos are home to a group of plants placed in the genus *Scalesia,* a member of the Family Compositae or Asteraceae, which includes dandelions and sunflowers. Unlike our weedy dandelions, however, these Galapagos plants are trees. They, like their avian colleagues the Darwin's finches, show what evolutionary biologists call adaptive radiation—in other words, the spectacular evolution of new forms of life, or species, from a common ancestor.

The Galapagos Islands are a paradise for biologists who study the process and pace of evolution. In addition to the finches and the *Scalesia* trees, other evolutionary marvels in the Galapagos include, of course, the giant tortoises (*Geochelone*), the extraordinarily tame Galapagos hawk (*Buteo galapagoensis,* a relative of our red-tailed hawk), the land and marine iguanas (*Conolophus* and *Amblyrhynchus*), the mockingbirds (*Nesomimus,* which, in fact, attracted Darwin's attention even before he took a good look at the finches), the flightless cormorant (*Nannopterum harrisi*), the penguin (*Spheniscus mendiculus:* on the equator, but in

Bartholomew Island (Galen Rowell/Corbis)

cold waters), and many other species of animals and plants.

Ecuador recognized the value of the Galapagos as the site of a natural experiment in evolution and as a great natural monument by establishing the Galapagos National Park in 1959. Twenty years later the Galapagos became a World Heritage Site. This double status grants protection to virtually all land area within the archipelago. Unfortunately the adjoining seas do not yet enjoy such status, and overfishing has become a serious problem. The northwestern curl of the cold Humboldt Current, sweeping from the depths and northward along the arid coast of Chile and Peru, bathes the Galapagos waters. The nutrients carried by this current support a rich marine ecosystem of invertebrates, fish, and birds. The wonderful marine life of the Galapagos urgently needs protection.

In spite of being a National Park, the Galapagos receive ever more immigrants from the overcrowded Ecuadorian mainland. Because these people need land and food, the habitats of several islands are under heavy pressure. Even well-meaning ecotourism has its downside. Thousands of people from all over the world visit the Galapagos each year. This heavy traffic provides income that is welcomed by Ecuadorian authorities, but relaxation of the once extremely stringent rules for tourist behavior threaten the birds and habitats of the Enchanted Isles. But dangers to these natives' survival are not new. The buccaneers of old, not content to gorge on the meat of the giant tortoises, also released such domestic animals as goats, and the filthy holds of their ships contained rats that promptly found the shore a better place to live. Such commensals, which also include mice, dogs, burros, cattle, and cats, multiplied unchecked, and conservation authorities have expended considerable effort and money—and ingenuity—to try to curb, if not eliminate, these pests, which kill native animals and destroy native vegetation. That vegetation itself loses in the competition with introduced plants. These invaders are so prolific that some Galapagos areas have few if any native plants left.

Most evolutionists believe that organisms like Darwin's finches stemmed from just a few colonizing individuals (called a propagule) from an ancestral species on South America's mainland. What groups did these original colonists come from, and from where in South America? How long ago did colonization take place? How did the new species evolve after an ancestor arrived in the Galapagos? Ever since Darwin, sharp ornithological minds have pondered these questions, measured the specimens (called study skins) of Darwin's finches collected during various expeditions and now deposited in museums (San Francisco's Academy of Sciences, New York's American Museum of Natural History, Washington's Smithsonian Institution, and Tring's British Museum of Natural History), and then speculated.

In addition to morphological evidence provided by specimens, ornithologists have also studied the behavior of Darwin's finches, especially their displays, vocalizations, food, and feeding habits. The most recent development in this ongoing search is the analysis of sequences of amino acids in the DNA molecule. Besides Charles Darwin, John Gould, Harry Swarth, and David Lack, cited above, other players in the study of Darwin's finches are Robert Ridgway, Robert Bowman, David Steadman, Joseph and Maria Vagvolgyi, and Luis Baptista. But the researchers who have worked most persistently on Darwin's finches are a Princeton University team: Peter and Rosemary Grant, their children, and their students. They have studied these birds since 1973 and have published many papers in technical journals. Peter Grant's 1986 book explains much of the work through the mid-1980s, and Jonathan Weiner's presentation of the Grants' work, published in 1994, is a great read for anyone interested in the finches, the Galapagos, and evolution.

Since John Gould's descriptions, ornithologists have classified (grouped) Darwin's finches into four genera: *Geospiza* (ground finches, six species), *Camarhynchus* (tree finches, six species), *Certhidea* (warbler finch, one species), and *Pinaroloxias* (Cocos finch, the only species found outside the Galapagos). The most recent workers divide tree finches more finely and include three species in *Camarhynchus* (tree finches sensu stricto), one in *Platyspiza* (vegetarian finch), and two in *Cactospiza* (woodpecker finch and mangrove finch). Ground finches are seedeaters with finchlike, conical beaks; males are black and females brownish and streaked. Tree finches eat mostly insects and have variable bills; males are partly black or lack black. The woodpecker and warbler finches, both insectivorous, are grayish with a thin, pointed bill. And the largely insectivorous Cocos finch is black (males) or brownish (females) with a thin and decurved beak. These differences may seem straightforward to the armchair traveler, but their field identification is difficult.

Several islands have more than one species of *Geospiza* and *Camarhynchus*, which are found in the same habitat and closely resemble each other. Also, species vary geographically within the Galapagos. For example, *Geospiza fuliginosa* (small ground finch) varies

Darwin's finch at nest (Galen Rowell/Corbis)

in color and beak shape: the population on Genovesa (Tower) has been placed by some authorities in the species *Geospiza difficilis*. To complicate matters, there is individual variation in populations of some species. The remarkable thing is that ornithologists like Lack, Bowman, the Grants, and their students have sorted out this puzzle.

Some authors stated that an original and ancestral colonist was similar to the now endangered St. Lucia black finch (*Melanospiza richardsoni*), endemic to that Lesser Antillean island. Others suggested that a bird like the widespread western South American dull-colored grassquit (*Tiaris obscura*) reached the Galapagos 3 to 5 million years ago. Whichever the ancestor was, once there it multiplied and diverged morphologically and behaviorally. A complex sequence of dispersals to other islands within the archipelago followed the initial colonization event, with subsequent periods of divergence, followed in turn by more colonization and divergence: the process called adaptive radiation. How many of these cycles there were, and how long each lasted, are questions that researchers using DNA sequencing now attempt to answer.

In the meantime, visitors to the Galapagos watch ground finches with enormous bills and others with much thinner bills. They marvel at the woodpecker finch, a food specialist. It picks up a cactus spine, pushes this tool into holes, thereby flushing out the grub living inside, and then promptly eats it. In addition, some finch species eat blood, whereas others pick ticks off marine iguanas, and still others turn over stones to look for food underneath. Other species show habitat specialization.

Thus, as its name indicates, the mangrove finch (*Cactospiza heliobates*) lives only in mangroves. A declining species, it is now found only locally along Isabela's west coast. It used to occur on Fernandina but has not been found there recently. Populations of six of the thirteen Galapagos species have become extinct since their description by John Gould. Such local disappearance of populations of Darwin's finches is worrisome.

We risk losing, not just a few drab-looking finches on remote islands in the Pacific, but a living laboratory of evolution. Over more than two decades of painstaking fieldwork, Peter and Rosemary Grant and their students have documented that natural selection—the process that Darwin identified as the motor of evolutionary change—is at work in Darwin's finches right now. Periods of rainfall result in abundant food (seeds, insects). Subsequent droughts result in famine. Heavy mortality during times of food scarcity, linked with severe competition for these limiting resources, induces selection that results in slight modifications in the birds' bill size and shape in just a few generations—a few years. As these beak features are under genetic control, evolutionary change in some Darwin's finches takes place within a single researcher's lifetime!

To preserve for posterity such an open book of evolution, the Galapagos Islands and their Darwin's finches need our complete protection. We hope to avoid the mistakes made in the Hawaiian Islands, where similar adaptive radiations in their birds have been so decimated by human activities that the remaining avifauna is but a faint ghost of a glorious past.

—*François Vuilleumier*

See also: Adaptive Radiation; Alien Species, Birds; Darwin, Charles; Evolution; Speciation

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Geological Time Scale

The geological time scale is a system of division of geological time, generally presented in chart form (see Table 1). The time scale is a scientific statement, and as such is constantly subject to refinement and correction, as new dates are obtained for division boundaries, finer subdivisions are recognized, and rock layers in different regions of the earth are matched up more accurately.

The idea that the earth has had a long history, and that the sequence of events that have led to the present state of the earth can be studied scientifically, is only a few centuries old. The Danish physician Niels Stensen (known as "Steno"; 1638–1686) formulated two laws pertaining to the understanding of sedimentary rocks and their relative ages. Steno saw that sedimentary rocks are formed by the cementing together of particles of sand, clay, or lime, and thus they are formed from the

Table 1
Geological Time Scale

Eras	Periods	Epochs	Duration*
Cenozoic	Quaternary	Recent	Present–0.01
		Pleistocene	0.01–1.6
	Tertiary	Pliocene	1.6–5.3
		Miocene	5.3–23.7
		Oligocene	23.7–36.6
		Eocene	36.6–57.8
		Paleocene	57.8–66.4
Mesozoic	Cretaceous		66.4–144
	Jurassic		144–208
	Triassic		208–245
Paleozoic	Permian		245–286
	Pennsylvanian	Carboniferous	286–325
	Mississippian		325–360
	Devonian		360–408
	Silurian		408–438
	Ordovician		438–505
	Cambrian		505–570
Precambrian			570–4500

*Approximate time in millions of years before present

Source: Eldredge, Niles. 1999. *The Pattern of Evolution.* New York: W. H. Freeman and Company.

Note: A simplified chart of geological time for the most recent million years, emphasizing the nested, hierarchical structure of the divisions of geological time: epochs are parts of periods, which are divisions of geological eras.

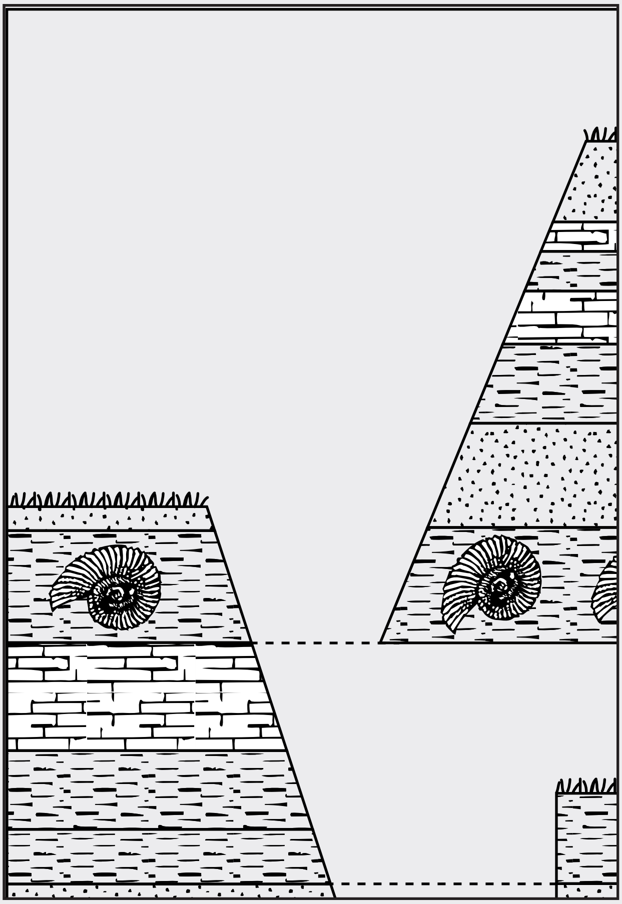
same kinds of sediments that are accumulating today in lakes, oceans, and sand dunes. He deduced that (1) the layers of sedimentary rocks were initially formed in horizontal beds (so that layers that are no longer horizontal must have been secondarily tilted by forces within the earth—the "Law of Original Horizontality"), and (2) in a sequence of layered rocks, those on the bottom of the pile must have been deposited first (the "Law of Superposition"). It was especially the Law of Superposition that allowed geologists to see a connection between a deposit of sedimentary rocks and the passage of geological time.

Even well into the first half of the nineteenth century, it was still generally supposed that the earth was no older than the approximate date of 10,000 years—a date based on an analysis of the ages of the ancient men (such as Methuselah) as recounted in Genesis, the first book of the Bible. But early geologists of the late eighteenth and early nineteenth centuries (all of whom were amateurs, including some clergymen, as the science of geology was just being developed by these early practitioners) were already hard at work deciphering the layers of rock and noting in particular the fossils contained in them. Baron Georges Cuvier and his collaborator Alexandre Brongniart produced a map of the Paris region (the so-called Paris Basin); across the English Channel, William Smith produced England's first geological map in 1815.

Smith was a surveyor, and he was mapping the countryside in connection with the building of canals in the early days of Britain's Industrial Revolution. As he climbed the hills to set up his surveying equipment, Smith noticed that the fossils exposed along the way always occurred in the same order. He reasoned that the same fossils collected on two separate hillsides must have been living in the same seaway at the same time (Smith's fossils were ammonoids and other marine mollusks—see Paleontology). Further up the hill, he would observe a somewhat different group of fossils—also found elsewhere. On hillsides further away, he would perhaps not find the lower assortment of fossils, but would find the higher one—plus yet another different assortment of fossils above that one (see Figure 1). Thus Smith saw that (1) not all layers of the earth are exposed at one place (not even in the Grand Canyon!), but that (2) by careful comparison of the layers—and especially their fossil content—from place to place, geologists could work out the overall sequence of rock layers of an entire region.

With these principles in mind, geologists rapidly began to map all the rocks exposed in streams, road cuts, and hillsides around them. Most famous were the joint expeditions of

Figure 1
Using Fossils to Correlate Rocks



Source: Based on Eldredge, Niles. 1999. *The Pattern of Evolution*. New York: W. H. Freeman and Company.

Note: Geologists use patterns of fossil occurrence to determine age equivalency in isolated bodies of rock. This figure shows three outcrops: two that contain a Devonian trilobite species, and two that contain a Mesozoic ammonite species. In general, many species are used to establish correlations between rock strata.

Roderick Impy Murchison (who later discovered Murchison Falls in Africa) and Adam Sedgwick, rector of the cathedral in Cambridge and, coincidentally, the closest thing to a scientific mentor that Charles Darwin had before he embarked on his fateful voyage on the HMS *Beagle* in 1831.

Friends at first, Sedgwick and Murchison set out during the summer months over successive years in the 1820s to examine the sequence of rocks of western England and Wales. Dividing up the territory, Sedgwick worked in Wales while Murchison worked in England. Sedgwick called his rocks "Cambrian" (the old Roman name for Wales was "Cambria"), while Murchison was working in a sequence he called the "Silurian" (the Silures were a primordial tribe of native Britons). Sedgwick was working up the sequence—realizing that his rocks were the oldest in the region to have fossils; Murchison was working downward—and soon they discovered that the rocks near the top of Sedgwick's Cambrian sequence were the same as those mapped by Murchison as his lower Silurian sequence. Their friendship was ruined over this early geological squabble over how to name rocks; later, another geologist (Charles Lapworth) solved the problem by naming the rocks in dispute the Ordovician System (the Ordovices were still another ancient tribe of the region).

Other geologists soon followed suit. The Devonian was named from rocks mapped in Devonshire—though even better exposures in New York state almost caused their name to be the "New Yorkian." The Permian Period was named after the Perm district in Russia, while the Carboniferous was named for the famous "coal measures" that were being mined so extensively in Britain during the Industrial Revolution.

The Triassic derives its name from a threefold division of rocks recognized in Germany; Jurassic is named for the Jura Mountains of France, where these rocks are extensively exposed. The Cretaceous comes from the Greek word *kreta,* meaning "chalk"—many chalk deposits, including the white cliffs of Dover, are of this age. The Tertiary and Quarternary were divided into epochs by Charles Lyell, who produced the forerunner to the modern classification of Paleocene, Eocene, Oligocene, Miocene, Pliocene, Pleistocene, and Holocene. *Cene* means "recent," and the divisions are intermediates between "ancient recent" (Paleocene) and "completely recent" (Holocene).

The sequence of these basic divisions of geological time (the so-called geological periods) had been established by Steno's laws and the use of fossils to correlate rocks (meaning the principle that the same or closely similar fossils in two different bodies of rock imply that the rocks are very similar in age). By the 1840s, it had also been recognized that the fossils in rocks from Cambrian through Permian age, though they may look quite different up through the sequence of rocks, have an overall similarity; trilobites, for example, are found in all these rocks from the Cambrian through the Permian periods. They are not found in younger rocks. Similarly, certain kinds of corals are found only in rocks of Cambrian through Permian age; and in all these rocks, brachiopods usually predominate over all other forms of shelled invertebrate life. Thus geologists readily accepted the suggestion that these rocks might be classified together as the Paleozoic Era (meaning the era of ancient life; sometimes this division of geological time is called the "Age of Invertebrates").

Similarly, fossils of a certain type—especially the dinosaurs, but including many groups of marine animals, such as ceratite and ammonite ammonoids (see Paleontology)—are characteristic of Triassic, Jurassic, and Cretaceous rocks and are not found in the younger rocks of the Tertiary. So these three periods were lumped, logically enough, into the Mesozoic Era (for "middle life"—also known informally as "The Age of Dinosaurs"). The final division, consisting mostly of rocks of Tertiary age, was called the Cenozoic Era (meaning "recent life"), and it is sometimes informally called the "Age of Mammals."

When radioactivity was discovered at the end of the nineteenth century, geologists were quick to realize that radioactive elements occur naturally in minerals in the earth's crust. The idea is that, if we know the rate at which an element decays from its initial state to its final state (sometimes called the "parent" and "daughter" states), we can estimate the age of a sample of rock by measuring the ratio of parent and daughter elements; for example, various forms ("isotopes") of uranium decay into different isotopes of lead at known rates. It is important for these calculations that we can be sure that the initial formation of the rock had 100 percent of the "parent" isotope. Sedimentary rocks, composed of grains weathered from other rocks, are therefore poor candidates for this so-called radiometric dating. But igneous rocks (formed from a hot melt, such as the lavas of volcanoes), and even metamorphic rocks (which are formed from other rocks through heat and pressure), do lend themselves to radiometric dating.

Thus to add numbers to the geological time scale—and to date parts of the earth's crust before there were fossils both abundant and well-preserved enough (see Evolution and Paleontology)—geologists rely on igneous and metamorphic rocks. Fossils do not generally occur in these rocks, but igneous rocks in particular, whether ancient lava flows or layers of granite injected into a sequence of sedimentary rock, can be radiometrically dated. The way geologists have been able to match up the sedimentary sequences, recognized and named by their relative position and fossil content (for example, Middle Devonian), with the actual age in years since they were formed (the so-called absolute ages of the rocks), is by finding, for example, rocks classified as Middle Devonian based on their fossils and measuring the age of the volcanic rocks sometimes found intruding the sediments. The ages measured radiometrically are always in the same order as the sedimentary sequence—meaning, for example, that the rocks dated as Middle Devonian based on their fossils always are dated somewhere around 380 million years old, no matter what the technique used, and no matter where in the world the samples come from; uppermost Cretaceous rock always dates to between 70 and 65 million years (the last great mass extinction occurred 65 million years ago); and rocks considered uppermost Permian in age—the very end of the Paleozoic Era and the time of the greatest mass extinction to have struck the earth so far—always come out to be 248 million years old.

The great depth of time of the Precambrian—just over 4 billion years of the earth's 4.65-billion-year history—has been analyzed mostly by radiometric dating, supplemented by studies of fossil bacteria and other forms of microbial life. The oldest rocks so far discovered and dated are just over 4 billion years old. We calculate the age of the earth as 4.65 billion years based on the ages of meteorites and the oldest moon rocks—and the certain knowledge that the restive crust of the earth has long since obliterated all traces of the original rocks, through the ravages of erosion and the swallowing of crustal plates back into the earth in the processes of plate tectonics.

—Niles Eldredge

See also: Evolution; Hutton, James; Lyell, Charles; Paleontology; Plate Tectonics

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Geology, Geomorphology, and Geography

Geology, geomorphology, and geography are all scientific disciplines that study the earth. At first glance these three disciplines may seem separate and easily distinguishable from one another. As you read on, however, you will find that the overlap is considerable, and in many instances one cannot be exactly sure of which discipline a particular subject pertains to.

Geology is the study of many aspects of the earth, but it does not include meteorology, climatology, oceanography, geochemistry, or geophysics—although elements of geology are part of them, and they are part of geology. All of these disciplines and others are included in the more general study, the "earth sciences." Geology can also be thought of as the study of the solid earth and its complex interaction between air (atmosphere), water (hydrosphere), and life (biosphere).

Geology can be best described as a science that explains how the earth works, the changes that take place on the earth, and the reasons for the changes. Plate tectonics is the theory that ties many geologic phenomena together and explains how the earth operates. Basic to the science of geology is the principle of uniformitarianism—the assumption that the so-called laws of nature have not changed over time. Geologists apply the principle to rocks of any age. By examining processes going on

Geologists at work. Geology can be described as a science that explains how the earth works, the changes that take place on the earth, and the reasons for the changes. (USGS/CVO)

today and their results—the structure of sand dunes, for example—a geologist who sees the same structure in ancient rocks assumes that they are also sand dunes. Examining rocks erupted from volcanoes can indicate that ancient rocks were volcanic, even though traces of the volcano itself have been eroded away. Geologists like to use the phrase “the present is the key to the past” to describe these procedures concisely. In actuality, this is true for the most part, but there are events that have occurred in the past that have not yet occurred during historical times. For example, the large impact of a meteorite may have caused dinosaurs to become extinct. For historical reasons, because it was part of the early development of modern geology, geologists like to keep using the term *uniformitarianism*, but in reality it is just another name for the scientific method. The study of geology leads to a greater appreciation of science in general and the origin of materials we need for our survival, comfort, and pleasure; it also helps us to understand how demands for these materials affect the environment and the balance of nature, and ultimately people on earth.

Geology is divided into a number of specific branches that study the composition of the earth (mineralogy, petrology, petrography); the structure of deformed rocks (tectonics, structural geology); the history of the earth and its life (historical geology); the physical properties of the earth, earthquakes, and their effects (seismology); volcanism (volcanology); landforms and the processes that produce them (geomorphology); fossils and ancient life (paleontology); and sediments and sedimentary rocks, their origin and age (petrology, stratigraphy). Geology also draws on many other disciples, including chemistry, physics, mathematics, and biology.

Many geological changes occur at a very slow rate, some not even observable on a human time scale, making it very difficult to demonstrate how certain materials or features were formed. At the other end of the scale, some features are too large to duplicate in a lab—thus geologists compromise by creating scale models.

Geology also has a practical side. Everything we have and use on earth (excepting meteorites) comes from rocks, plants, or animals. Geologists explore the earth for economically important substances such as metallic ores, sand and gravel deposits, coal, oil, and gas. Equally important is the search to find a way to predict volcanic eruptions and earthquakes.

Geomorphology is the discipline concerned with the shape of the landscape and the processes that create it, their description and classification; it is usually considered a part of the geological sciences. It also includes the study of submarine features, and some scientists extend it to the study of planetary landscapes. Landforms are discrete or individual features, like a volcano or a valley. Landscapes are an assemblage of landforms that are created by complex, climate-controlled processes. Geomorphologists study the relationships between landforms and the processes currently acting upon them. Geomorphology is also a historical science, because it is necessary to consider past events that help shape the landscape. As is the case in many other sciences, geomorphology is interwoven with other sciences, inasmuch as it involves the atmosphere, hydrosphere, and biosphere, physics and chemistry. The erosional response of the surface to uplift falls in the realm of geophysics, which is concerned with the mechanics and rates of uplift. How much sediment a stream carries is included in hydrology, which measures the frequency and intensity of flooding. Pedology, the science of soils, involves the effects of soil properties on slope stability, which, applied to geomorphology, makes a contribution to topography and soil-forming processes. On a smaller scale, geomorphology is concerned with how topography controls plant growth (biology) on the microenvironmental level, and the role that vegetation cover plays in affecting slope stability.

Geography is defined as the study of the earth's surface. Although it is usually associated with maps and map-making, it is a much broader discipline; although maps are an important tool used by geographers (as well as geologists), they are a small part of the subject. Geography describes and analyzes the spatial variations in physical, biological, and human phenomena that occur together on the surface of the earth, and it deals with their interrelationships and their local and regional patterns. It is especially concerned with human utilization of natural resources and with the impact of human activities on the environment. Included in human geography is the study of the distribution of population and the religions of people, and the varieties of designs of cities, road systems, and dams. Physical geography is the observing, measuring, and describing of the earth's surface, and some geographers include geomorphology, climatology, biogeography, and soil distribution as branches of this subdivision of geography. Therefore, geography is a broad-ranging discipline that involves the discerning of patterns of anything on the surface of the earth that involves both natural and human features, including economic and political activities. Geographers therefore are knowledgeable about the earth sciences, biology, and sociology, making their subject interdisciplinary.

—*Sidney Horenstein*

See also: Climatology; Geological Time Scale; Hutton, James; Meteorology; Plate Tectonics

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Giant, Flightless Island Birds

In the course of evolution, islands have often served as nature's laboratories where isolated populations are permitted or forced to follow unusual evolutionary paths. One path followed in several locations was the tendency of birds to evolve to unusual size and to lose the capacity for flight when shielded from predators. The dodo (*Raphus cucullatus*) of Mauritius and the lesser known solitaire (*Pezophaps solitaria*) of Rodriguez are probably the best known and most recent examples of extinct giant, flightless island birds. In other birds, such as the moas of New Zealand and the elephant birds (*Aepyornis maximus* and *Mullerornisbetsilei*) of Madagascar, the sizes reached were even more extreme. These giant, flightless birds share two characteristics: their vulnerability to introduced predators—the greatest of them all being man—and the fact that with very few exceptions they are now extinct.

When Europeans first landed on Mauritius, they were dismayed to find a lack of desirable game. The only large animals to be found were the ungainly dodos. These pigeon relatives were 15 to 20 kg in weight, with males larger than females. Some accounts also suggested that the birds were sexually dimorphic in plumage and coloration. Both the dodo and the solitaire are thought to have been primarily frugivorous, and it has even been hypothesized that the dodo's digestive system played a critical role in the germination of the seeds of a now endangered tree (*Sideroxylon grandiflorum*) (Temple, 1977). Invertebrates might also have been consumed as a component of the birds' diet (Livezey, 1993). The sailors remarked about the birds' seasonal accumulation of body fat. This ability to put on great amounts of fat in times of plenty may have been important in sustaining them through the leaner months. These observers also noted that dodos were territorial, and that parent birds were vigilant guards of their nests and young. Significant parental investment was justified, since each nest contained a single egg. This reproductive strategy was suitable in the absence of predators, but it did not allow for compensation when the equilibrium of the population was disrupted. The early naturalists were harsh critics of the quality of dodo meat; nevertheless they continued hunting them until the last had been consumed in the early eighteenth century. The extinction of the dodo (and solitaire) was particularly significant, because it was the first case during historical times in which humans recognized the tragic results of their overharvesting.

In addition to human predation, habitat destruction has also been identified as a major factor in the extinction of several giant birds. The moas (families Dinornithidae and Anomalopterygidae) of New Zealand, elephant birds of Madagascar (*Aepyornis maximus* and *Mullerornisbetsilei*), and mihirung (*Genyornis newtoni*) of Australia shared this fate.

Prior to the arrival of humans approximately 1,000 years ago, several species of moa inhabited the heavily forested islands of New Zealand. Among the two families of moas were species ranging in weight from 20 to more than 200 kg. These enormous birds were herbivores, and they occupied the niches filled in other places by mammals such as the ungulates. Although the moas were previously thought to have been grazers, analyses of well-preserved specimens indicate that they were in fact browsers. Twigs, leaves, fruits, and seeds of woody plants have been found in the gizzards of some specimens. Large quantities of stones that aided the digestion of tough plant material were also found among the gizzard contents. Differences in beak morphology and body size suggest that the various species were adapted to particular feeding niches, and defense mechanisms of certain plants hint at coevolutionary relationships between moas and some plant species (Cooper et al., 1993).

Little is known about the habits and life histories of the moas, except what can be inferred from their anatomy and the contexts in which remains have been found. Maori folklore greatly romanticized the moas but contributed little factual information. Prior to the arrival of humans, the islands of New Zealand were heavily forested, and moas are thought to have been primarily forest-dwelling birds. Analysis of moa remains indicates that certain species occupied distinctive habitats ranging from the coastal lowlands to montane forests more than 1,000 m above sea level (ibid.). Some moa nests, each containing a single egg, have been found in caves, and others have been found in open areas. Like the dodo, moas were probably long-lived, slow-growing birds with a low total lifetime reproductive potential (Anderson, 1989).

Moa species endured significant climatic and habitat changes caused by volcanic eruptions and periods of glaciation that undoubtedly had significant impact upon their populations. Nevertheless, significant numbers of the birds persisted, as demonstrated by the vast quantities of moa bones found in the refuse middens of the first human inhabitants. It appears that the new human inhabitants found the moas to be fairly easy prey, and, as the only large game, moas were aggressively hunted for food. Moa skins and bones were used to craft tools, ornaments, and garments. Nests were robbed, and the eggs became a source of both food and storage containers.

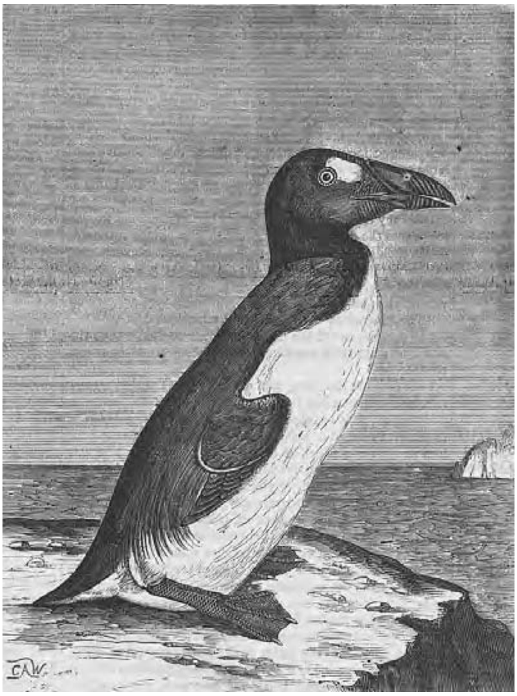
In addition to direct predation, humans also affected moa populations through deforestation and the introduction of other invasive species. Forest fires destroyed both the habitat and food supply of the moas. Introduced plants interfered with the regeneration of native plant communities and may not have been suitable as food for the moas. Rats (*Rattus exulans*) and dogs had a significant impact on the smaller terrestrial avifauna and may also have affected the moas, although probably to a lesser extent.

It is generally accepted that the extinction of the moas was a direct result of human impact. However, there is some controversy regarding the rate at which the extinctions occurred. Trotter's and McCulloch's (1984) assessment of the fossil and archaeological evidence indicates that peak periods of moa hunting occurred 800 years ago in the northern areas and 500 years ago in the southern areas, possibly in association with southward human population expansion. Another more recent analysis by Holdaway and Jacomb (2000) suggests that all species of moas were driven to extinction within 100 years of human arrival, because rates of predation overwhelmed the populations' regenerative capacity. All of the moa species were extinct by the time of the first European arrival in the late eighteenth century. Other flightless birds—such as a flightless goose (*Cnemiornis calcitrans*) and the giant rail (*Aptornis otidiformis*)—also fell victim to predation, and the giant eagle (*Harpagornis moorei*), a carrion eater, was probably a secondary victim of moa extinction (Trotter and McCulloch, 1984).

The dodo, solitaire, moa, and other giant birds shared similar evolutionary histories, including their common fate of extinction. Isolated populations of birds, in the absence of predators, were freed from the need to be light and swift. Evolution of large body size is often associated with a decreased metabolic rate, which in turn is associated with a greater ability to withstand extremes of temperature, the capacity to endure periods of fasting, and increased longevity (Livezey, 1993). In this situation, the capacity for flight became an unnecessary and metabolically costly extravagance, and so it was gradually abandoned. The absence of predators also allowed these slow-growing, long-lived birds to adopt a strategy of low total-lifetime reproductive output, in which a high degree of parental investment was devoted to small numbers of offspring (ibid.). In some cases, the birds were the only large terrestrial vertebrates, and so they followed a course of adaptive radiation to fill the otherwise unoccupied niches.

In the security of their island sanctuaries, giant birds flourished. On the island of Madagascar, eggs of the elephant birds (*Aepyornis maximus*, *Mullerornisbetsilei*) were deposited in such vast numbers that they can still be found quite readily despite the fact that the birds became extinct in the seventeenth century (Dewar, 1984). The mihirung (*Genyornis newtoni*) of Australia was represented in the fossil record for at least 50,000 years before its sudden extinction, coinciding with the arrival of humans (Miller et al., 1999). The success of this pattern of evolution is demonstrated by the many other extinct species of large, flightless island birds that are known, and others that are still being discovered by paleontologists.

Sadly, just as the pattern of evolution has been repeated, so too has the course of human impact on naive environments. The characteristics of the giant, flightless island birds that made them well adapted for their isolated life also made them extremely vulnerable to humans. When attacked, the birds were essentially defenseless. Long-legged birds such as some of the moas may have been able to kick, but that would have been little defense against men armed with spears. Some of the birds may have been adapted for running, but most of them were probably slow and burdened by their ponderous weight. For birds such as the short-legged dodo, kicking and running were beyond their ability. Indeed, accounts of dodo hunts suggest that they offered no struggle at all, perhaps because they lacked the instinct of fear. Young birds, with their prolonged incubation and altricial periods, were particularly vulnerable both to humans and to other predators. With few offspring produced, individual losses



Engraving of the extinct Auk (Bettmann/Corbis)

significantly affected the population (Livezey, 1993). The fact that other large birds such as ostriches and emus have survived may be in part because of their reproductive strategy of laying eggs in clutches and thereby decreasing the importance of a single offspring. Environmental changes caused by deforestation may have eliminated the food supplies of these specialized herbivores. Adaptive changes designed for life in a system at equilibrium had become the burden of species in the face of change.

—Julie Pomerantz

See also: Alien Species, Birds; Coevolution; Extinction, Direct Causes of; Mass Extinction

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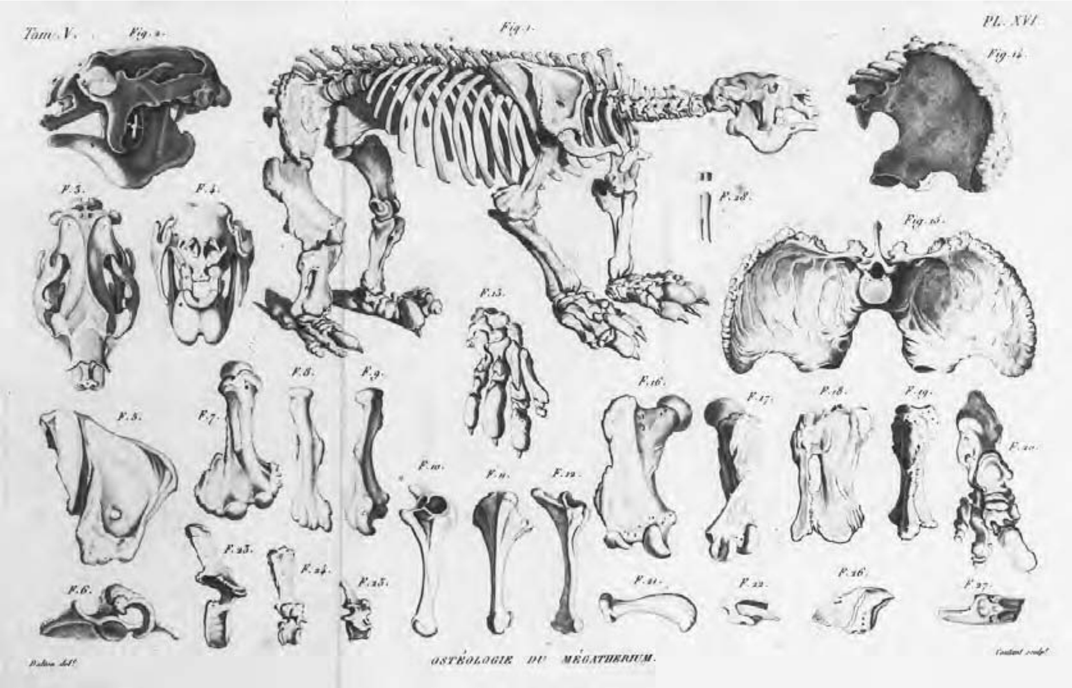
Giant Ground Sloth

Giant ground sloths (*Megatherium* and *Eremotherium* spp.) roamed the Americas at the end of the last ice age. Shortly after humans entered the scene, the giant sloths disappeared from the New World's cast of characters, as did mammoths (*Mammuthus* spp.), the bighorned *Bison antiquus*, and many other large mammals. The exact cause of the Late Pleistocene megaherbivore extinctions remains a matter of debate, but the timing of these extinctions, following so quickly upon the heels of man's arrival, suggests more than mere coincidence.

Several species of the genus *Megatherium* inhabited North and South America. These creatures, weighing several tons, were some of the largest mammals ever to walk the earth. Next to a giant ground sloth, a 500-pound grizzly bear would seem puny in comparison. Unlike their much smaller arboreal relatives, the modern two- and three-toed sloths (*Choloepus* and *Bradypus* spp.), the giant ground sloths were terrestrial, and skeletal evidence indicates that despite their massive size they were able to stand up on their hind legs using their stout tails for balance (Casinos, 1996). The smaller forelimbs armed with huge claws were most likely used to strip leaves and bark from trees. One author (Farina, 1996) has recently theorized that some of the giant sloths may in fact have been carnivores, using their dexterous forelimbs and sharp claws for hunting, but the small, blunt teeth would appear to have been better adapted for a herbivorous diet.

A few early paleontologists were tantalized by the discovery of bits of sloth skin, which seemed so fresh that they believed the animals had been recently alive. However, further examination of these specimens using radiocarbon dating has revealed that they are in fact much older and simply very well preserved because of environmental factors. It is generally agreed that all of the giant ground sloths became extinct about 10,000



Print of the fossil skeleton of a sloth discovered in South America, from an 1825 book by Georges Cuvier (Library of Congress)

years ago—shortly after the arrival of humans in the New World.

Scientists who theorize about the cause of the great wave of extinctions that swept through the large and medium-size herbivores in the Late Pleistocene are generally divided into two camps. Some believe that climate change and the retreat of the glaciers led to changes in vegetation, which caused the herbivores' demise. Others believe that the primary force was predation by human hunters. Large herbivores have relatively low reproductive rates, and their populations decline rapidly if predation surpasses the low population growth threshold (Owen-Smith, 1989). Most scientists believe that a combination of factors was involved.

The "keystone herbivore" hypothesis proposed by Norman Owen-Smith suggests that the megaherbivores were not only among the victims of the great wave of extinctions that occurred in the Late Pleistocene, but they may also have played a key role in the genesis of this extinction event. According to the hypothesis, large herbivores are instrumental in modifying the landscape by clearing old growth and making way for savanna and forest regeneration. These changes may make the landscape more favorable for smaller, more selective herbivores. A modern example of this has been observed in areas where elephant populations have been eliminated. In the absence of the megaherbivores, thickets and woody vegetation overgrow the savannas, making them less hospitable to other grazing herbivores. Elimination of the Pleistocene megaherbivores by human predation or climate change would have also resulted in secondary changes in vegetation that might have had a cascade effect, resulting in the loss of other species dependent upon the megaherbivore-modified landscape (ibid.).

—Julie Pomerantz

See also: Ecosystems; Extinction, Direct Causes of; Herbivory; Mass Extinction; Order Uranotheria; Paleontology; Pleistocene Epoch

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Glaciation

Glaciation refers to the work glaciers do: eroding the surface and transporting and depositing rock debris. As glaciers move they drag rock debris incorporated within the ice across the bedrock, grinding and scratching the surface. They also pluck rock material from the bedrock as water freezes and expands, loosening blocks that then freeze to the bottom of the glacier, which pulls out the blocks as it moves. Some of the rock is ground up, producing very fine particles called rock flour, which turns the meltwater from glaciers a milky white. Glaciers move enormous quantities of rock as they gouge, plow, and carry the rock on their way across the terrain.

Valleys carved by glaciers have a U-shaped profile, which distinguishes them from the V-shaped valleys eroded by rivers. A glaciated valley tends to be linear, the result of the glaciers' being somewhat inflexible as they wear away and truncate ridges that jut into the valley. Thicker glaciers apply more weight on the valley floor, thus grinding away more rock than their tributaries, which are smaller. Larger main glaciers therefore are deeper than the smaller tributaries. After the glaciers melt away, the tributaries are left as a hanging valley high above the main valley, sometimes with scenic waterfalls.

Cirques are steep-sided, rounded hollows carved into the head of a valley. They usually originate at the upper part of a valley where snow and ice accumulate. Through the processes of weathering and erosion of the valley sides by ice (including ice wedging, plucking, and rock falls), the cirque grows. The large amounts of snow that accumulate are converted to ice, which with the rock that falls on it grinds away at the cirque floor, creating the bowl-shaped depression. Two cirques back to back with a sharp ridge separating them form what is called an arête. When several cirques are distributed around a mountain, the enlarging cirques may intersect, creating a central peak called a horn.

Continental glaciers, like valley glaciers, grind the surface of the bedrock, producing grooved, striated, and polished rock. Ice sheets are often thick enough to cover mountain ranges, and as they move over them the ridges are rounded, smoothed, and molded in the direction of the ice movement.

When ice sheets melt they leave behind the rock fragments they have picked up on their trip. The rounded and unlayered debris that is left behind when the glaciers melt is called till. Because some of the rock that valley glaciers carry fell from the valley walls onto the surface of the glacier, the till is composed of both rounded and angular rock fragments.

Glacial erratics are large rocks that have been left behind by the melting glacier and

The Saskatchewan Glacier, Alberta Canada, 1954 (USGS/McGimsey)

have been transported from a distant place, so that their composition is unlike that of the bedrock they sit on. Once the source of the erratic has been determined, it then can be used to indicate the direction and movement of the glacier that transported it.

Moraines are deposits of till left behind after the glacier has receded. In valley glaciers, rock debris that has fallen onto the sides of the glacier from the valley wall creates what are called lateral moraines; they are marked as distinctive ridgelike piles of till along the side of the glacier. Where tributary glaciers come together, the adjacent lateral moraines join, forming a long ridge known as a medial moraine. Large glaciers can have several medial moraines built by numerous tributaries that join the main glacier.

When a glacier appears to be stationary because the forward motion and melting are equal, an end moraine is built up in front of the glacier. A terminal moraine is an end moraine built during the farthest advance of a glacier. Recessional moraines are end moraines that are created when a retreating glacier stops temporarily. When glaciers begin to move again, they override and destroy previous moraines, causing signs of the older movements to be lost.

Under some circumstances advancing ice sheets may shape previously deposited till into streamlined, elongate hills called drumlins. The long axis of the drumlin is parallel to the direction of ice movement.

As glaciers melt, large numbers of meltwater streams leave the ice mass, carrying substantial amounts of sediment that had been incorporated within the glaciers. The sediments deposited by these streams are spread over the landscape in front of the glacier, filling in irregularities on the surface and forming an outwash plain. They are easily recognized because they are well sorted and layered, while till is unlayered and unsorted.

An esker is a long, sinuous ridge that forms beneath a large glacier in a tunnel under the ice. After the glacier melts away they are prominent, standing up above the glaciated surface; often roads are built on their surfaces. Eskers can be as high as 30 m, and their sorted, layered, and cross-bedded sediments are mined for sand and gravel.

As the glacier retreats, large blocks of stagnant ice may be covered with sediment; the ice eventually melts, forming depressions called kettles. These kettles fill with water forming small lakes, and they are often numerous, as in the upper Midwest. Glaciers are responsible for a variety of lakes, such as tarns, which form in cirque bowls after the glacier has melted away. Other lakes form in gouged-out depressions on bedrock. As a glacier recedes meltwater can be trapped between the ice front and a moraine, filling up the space between them and forming a lake. This occurs because the weight of the glacier causes the land to slope toward it, forming a lowland that traps the water. Distinctive deposits named varves or rhythmites are formed on the lake bed. In the summer, when melting occurs, coarser sediment is carried into the lake, but in the winter, when melting has diminished and the lake freezes over, only very fine sediment suspended in the water settles out. As a result, a thicker, lighter summer layer and a darker, thinner winter layer of sediment are formed. Each pair represents one year of deposition, and by counting the pairs researchers can determine how long the lake was in existence. By determining the age of the organic material by means of radiocarbon dating and by looking at the entrapped spores and pollen, a good idea can be gained of when and how the climate and vegetation changed.

Some of the sediments found on the outwash plain are rock flour that settled out of the streams on mudflats and shallow lakes. Later, during dry seasons, the rock flour is easily picked up by the wind, carried away, and deposited as loess. Some of the best agricultural soil in the United States is found on these deposits.

An direct effect of glaciation is the worldwide lowering of sea level by 130 m as water from the oceans became the snow and ice that resided on the land. Rivers flowing across the exposed shelf, some supplemented by glacial water, carved great valleys that are now covered by the risen sea. On the exposed shelf animals lived and died, and today their bones and teeth are dredged up, showing that what is now covered with water was once land. Large areas of the continental shelf were exposed, connecting landmasses and allowing animals to migrate to new places.

The weight of the thick glaciers pushed down the land in a way similar to what happens when you sit on a cushion. When you rise the cushion rebounds, which is similar to what happens to the surface of the earth that had been covered by glacial ice. In the Canadian Arctic, for example, uplift of the land, which is still going on today, is easily seen by the numerous raised beaches that form a flight of stairs up the barren slopes.

Glaciation has had profound effects on the surface of the earth, reshaping it by both erosion and deposition and by interrupting or modifying many normal geologic processes. Glaciers created many thousands of lakes, altered or obliterated old drainage systems while they created new ones, and deposited sediments that became fertile soil in many parts of the world. The effects of glaciation have reached far beyond the margins of the ice and influenced many aspects of the physical and biological world.

—*Sidney Horenstein*

See also: Climatology; Global Climate Change; Pleistocene Epoch

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Global Climate Change

The global climate has changed throughout geologic time on timescales that vary from a few years to millions of years. Some short-term global changes occur during volcanic eruptions. In 1991 Mount Pinatubo in the Philippines erupted, producing huge quantities of gas and ash reaching the stratosphere, where it blocked some of the solar radiation from reaching the earth's surface, resulting in a worldwide cooling. It is estimated that 20,000,000 tons of SO_2 gas erupted into the stratosphere, and the resulting H_2SO_4 (sulfuric acid) reflected 2 to 4 percent of the incoming solar radiation back into the space, reducing the mean global temperature at the surface about 0.5°C. In some parts of the Northern Hemisphere the drop in temperature was as much as 1°C. Some older eruptions (for example, the famous Krakatoa, Indonesia, eruption of 1883) reduced worldwide temperatures about 0.5°C, about the same as the change with Mount Pinatubo, cooling the earth for almost ten years. In 1815 Tambora (Indonesia) produced an even larger eruption, causing the Northern Hemisphere to experience the "year without a summer" in 1816. In northern New England snow fell June 5 and 6, and western Europe experienced many crop failures.

That volcanic eruptions cause climatic change was recognized by Benjamin Franklin, who in 1784 suggested that the cold weather in Europe during 1783 and 1784 was due to massive lava eruptions in Iceland. Single eruptions like these appear to have short-term effects on global climate with no long-term consequences. However, scientists have wondered what would happen if a number of volcanoes erupted continuously over a long period of time. Would the earth's climate cool to such a drastic degree that many animals and plants would become extinct because of the loss of habitat? One of the proposals that explains the extinction of the dinosaurs involves such a scenario, that is, when huge volumes of basalt erupted in India over a 500,000-year interval. The effect of eruptions such as Mount Pinatubo are one of the reasons that people became concerned about one possible outcome of nuclear war—a nuclear winter. Megaton exploding weapons would create huge volumes of dust that would be thrown up into the atmosphere like the dust of volcanic eruptions. Combined with the ash of the resulting fires, the dust would cause a dramatic cooling of the earth, a "winter" that could cause famine and other forms of deprivation that would kill most of the world's population. This explanation may be part of the most commonly accepted scenario of the dinosaur demise that occurred at the end of the Cretaceous period. It is believed that a meteorite struck the earth in the Yucatan Peninsula area of Mexico, causing a voluminous amount of debris to be ejected from the surface into the atmosphere. The debris resulted in a meteoritic winter that killed the dinosaurs and many other animals.

Another type of short-term climate change is the so-called El Niño effect, which occurs every 2 to 7 years around Christmastime, when the typical weather pattern in the Pacific Ocean breaks down. The trade winds weaken, and low pressure establishes itself in the central Pacific, causing winds to blow into the Pacific Basin from the west. This change causes warm surface water to move toward South and Central America, reversing the directions of some currents and placing warm water along the coasts. The warm water produces heavy rain over the coastal deserts, subjecting them to disastrous flooding and erosion. The western United States also experiences major flooding events as a result of El Niño. This temporary influx of rain on arid and semiarid regions creates the conditions for disastrous downslope movements in the form of mud slides, destroying entire villages and taking its toll of human life. Shifts in warm water in the southern Pacific and Indian Oceans cause cooler water to move along the coast of Australia, resulting in decreased rainfall.

One result of this temporary climate change is the occurrence of major brush fires, which destroy not only vegetation but also wild and domestic animals. The warm water El Niño brings to the coasts of North and South America substantially reduces the upwelling of cold, deep water, adversely affecting the cold water fisheries off the coast of Peru and Ecuador and creating economic hardships.

The most dramatic recent global climate change occurred during the Pleistocene epoch when the earth cooled sufficiently to allow glaciers to form, enlarge, and ultimately cover about 30 percent of the land surface (see Glaciation and Ice Caps and Glaciers). The glacial periods alternated many times with warm intervals called interglacials. Presently, we are in a warm period, and if all of the factors are still in place that caused the previous cooling, the earth should experience another glacial episode about 10,000 years from now. Glaciation causes changes in ocean circulation and weather patterns and a drop in sea level; all of these changes combined with other factors produce shifts in the climatic belts and cause the redistribution of plants and animals. The earth began to cool about 40 million years ago, eventually bringing about a dramatic cooling. Although it is still not entirely clear why glaciation occurs, it involves changing positions and configurations of the ocean basins and continents, uplifts of mountains, and changes in the amount of solar radiation striking the earth, as described by the Milankovitch cycles. Once ice and snow accumulate, there is a feedback process that enhances solar radiation loss as the white surface reflects solar radiation back into space. The glaciers underwent a series of advances and retreats with corresponding shifts in climate.

About 60 million years ago the climatic parameters were very different than they are today. The polar latitudes were warmer, and the ocean surface temperatures near Antarctica were 10° to 15° warmer than today. The data suggesting these temperature differences are derived from analysis of the composition of the shells of one-celled animals, which are used as geologic thermometers. At this time there was less of a temperature difference between the tropics and the poles than there is today. Ocean circulation may have been slower because there were no large volumes of cold polar water to sink and cause vertical circulation, and the vertical changes in temperature in the oceans were thus not as pronounced. Most of the United States was located in tropical and subtropical climates. In the arctic, nicely preserved fossils, including crocodiles and palm trees, have been discovered. The area of tundra and deserts were greatly reduced as compared to today.

Why were climates so different at that time? Perhaps it is the result of the continents being low and partly covered by oceans. Europe, North America, and Greenland were beginning to separate, and as the North Atlantic began forming, large amounts of greenhouse gases were released from volcanic eruptions, causing global warming.

A major ice age that lasted tens of millions of years occurred during the Carboniferous period. For this length of time the conditions that created glaciation had to persist and were probably related to changes in size, shape, and orientation of the continents and oceans. For one thing, continents had to have been located at the poles (as glaciers cannot be built on the ocean surface), and indeed, part of the super continent Pangaea was located in the southern polar area. Pangaea also blocked oceanic circulation. Many scientists believe that the possibility of glaciation increases when there is more north-south oceanic circulation than east-west flow. The north-south movement of warm water evaporates more cold water and provides the moisture for snow accumulation. Glaciation ended because Pangaea broke up, changing oceanic circulation and moving away from the poles.

In the central United States there are thick deposits of sediments that contain many layers of coal formed during the Carboniferous period. In general, the layer sequence includes coal, clay, sand, clay, and coal and is repeated many times. The coal derived from plants that lived in swamps shows that the climate was warm at the time. The sequence of layers is interpreted to be the result of flooding, the gradual lowering of sea level, and the rising of sea level and flooding again, repeated over and over. The best explanation for this oscillating sequence is the rise and fall of the oceans during glaciation.

Fossil coral reefs, ancient soils like laterite, the formation of the aluminum ore bauxite, and others features are the tools geologists use to determine the climates of the past. With such evidence and techniques like paleomagnetic data, the latitudinal position of continents can be determined, giving us a picture of the global climatic changes that the earth has undergone through geologic time. In the references cited at the end of this entry, in the books on historical geology, the reader will find numerous examples of the past climates of the earth and graphs showing, for example, qualitative mean global temperature and precipitation through geologic time reconstructed from the data derived from rocks.

Today, as in the past, gases in the atmosphere play a key role in global climate. Gases in the atmosphere allow solar radiation to pass through to the surface where it is converted to heat when it strikes the surface. It is the same process that causes automobile interiors to get very hot. Shortwave radiation (ultraviolet) passes through the glass (the atmosphere) and is converted to infrared radiation when it strikes the surfaces within the car (the earth's surface). The glass prevents the heat from escaping, and the interior builds to surprisingly high temperatures. This retention of the heat is known as the greenhouse effect. In addition to the natural greenhouse phenomena, people are adding industrially produced gases to the atmosphere and changing the parameters, which many scientists say is causing the earth to warm up. With the production of CO_2, the primary greenhouse gas, from burning trees, coal, oil, and natural gas, estimates of the amount of future CO_2 production and the future increase in industrialization indicate that temperatures could rise by 2° to 10° degrees by 2100. Keep in mind that there are many other estimates based on different parameters that give more weight to one factor than another. But the results are the same: temperatures will rise, the polar caps will continue to melt causing sea level to rise, and overall global climate will change. Using the estimate of 5°C for the total global warming in the past 11,000 years, this increase indicates that a substantial further change in climate will take place. Intuition and computer modeling suggest that many changes will occur in respect to temperature ranges, locations of increased and decreased precipitation, cloud cover changes, and increases in the severity of adverse weather. One model suggests that the interior of the United States will experience severe summer drought in the grain-producing farmlands, and that wet and cool climates will be replaced by hot and dry climates and vice versa.

In addition to melting of glaciers, other effects have been recognized as resulting from increased heating of the earth. High mountain zones where the temperature is always below freezing have risen 500 feet since 1970. Butterflies, mosquitoes, and plants are now found at higher elevations. The spread of infectious disease is occurring; for example malaria, which has returned to the Korean Peninsula, was also reported during a hot spell in Toronto, Canada. One future result of global warming will be increased health hazards related to the increase of heat waves and the spread of infectious diseases. Many pathogens mature more quickly as temperatures increase, and mosquitoes that carry malaria can survive hot weather in pools of water that are hidden from the scorching sun, although their predators, such as lacewings and lady bugs, cannot.

Historically there are many examples of how changing climate causes social, political, and geopolitical changes. During the Little Ice Age between 1430 and 1890, canals in Venice froze several times, and during the Thirty War (1618–1648) the Swedish army was able to cross over the frozen Baltic Sea during the winter. In 1972 a severe drought in the Soviet Union and the lack of a snow cover in the Ukraine caused major crop shortages. As a result the Soviet government bought vast quantities of wheat and other grains from the United States, resulting in the rise of American food prices, an important factor in the egregious inflation that followed. Current estimates for 2100 suggest that melting of glaciers will raise sea level some 21 feet and submerge many coastal areas, including parts of many major cities. Most of the world's cities with the largest populations are located along coasts. And if all of the glaciers melt, sea level will rise about 240 feet. In the United States, one-half of the population lives within 100 miles of the coastline and would likely be affected.

Geologists use a phrase that summarizes many aspects of geology: "the present is the key to the past;" we can also say that the "present is the key to the future."

—Sidney Horenstein

See also: Climatology; Glaciation; Habitat Tracking; Pleistocene Epoch

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Grasses

See Angiosperms

Great Apes

The closest living relatives to humans, great apes belong to the Family Pongidae and include four species in three genera: common chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*), orang-utans (*Pongo pygmaeus*), and gorillas (*Gorilla gorilla*). Like all apes, the great apes lack tails and have broad, shortened trunks (in contrast to the flattened trunks seen in monkeys). Their forelimbs are as long as or longer than their hind limbs and are equipped with mobile wrist and shoulder joints that make them good climbers. All of these characteristics reflect adaptations for suspensory locomotion, although the great apes are less acrobatic in the trees than are their smaller ape relatives, gibbons and siamangs. Great apes are very similar to humans in their reproductive biology. Females give birth to one offspring at a time and will have relatively few offspring over a lifetime. In all apes the period of infancy and maternal care is prolonged, but in great apes it can last up to four years. The average life span of great apes is exceptionally long. In the wild gorillas may live to age thirty-five, while chimpanzees can live to about fifty. In captivity, this life span is even longer.

Members of the genus *Pan*, common chimpanzees and bonobos, are found in West and Central Africa. Common chimpanzees are found north of the River Zaire, from Senegal to Tanzania, while bonobos are confined to Zaire between the rivers Zaire and Kasai. Common chimpanzees inhabit humid forests, deciduous woodland, or mixed savanna habitats. Bonobos are found in humid forests only. Both species exhibit only moderate sexual dimorphism, with females weighing in at approximately 68 lbs (31 kg) and males at approximately 88 lbs (40 kg). Captive chimpanzees are known to weigh much more than their wild counterparts. Chimpanzees (especially the young) spend a considerable amount of time in the trees but frequently come to the ground to feed. When on the ground they normally walk on all fours, supporting their weight on the knuckles of their clenched fists. Chimpanzees will sometimes move about bipedally, especially while carrying food or during male displays. Bipedal locomotion is more common to bonobos than to common chimpanzees.

Both bonobos and common chimpanzees feed primarily on fruits, but leaves make up a substantial proportion of their diet as well. As much as 5 percent of their diet consists of animal prey. This primarily includes insects (for example, ants, termites, caterpillars) but may also include small mammals. Insect prey may be taken by hand or with tools, as seen in termite fishing by the common chimpanzee. The chimpanzee is known to hunt in groups, and it will take monkeys, pigs, and antelope when the opportunity presents itself. Chimpanzee social groups range between forty and eighty individuals that include adult males, females, and their offspring.

Common chimpanzees and bonobos present an interesting contrast in social behavior for two species so closely related (they are thought to have split only 2 million years ago). Common chimpanzees are known to be quite aggressive, with incidents recorded (in Gombe) in which one group systematically hunted down and killed every member of another nearby group. Unlike common chimpanzees, which resolve issues through violence, pygmy chimpanzees (bonobos) resolve issues through sex. Another contrast to common chimpanzees is that bonobo females are occasionally dominant to males. Members of this genus are the closest living relatives to humans. Chimpanzees and humans differ significantly in only 2 percent of their genes. This evidence suggests that they share a very

Male pygmy chimpanzee (Gallo Images/Corbis)

recent common ancestor and perhaps diverged into separate species only 5 to 7 million years ago.

Members of the genus *Pongo,* orang-utans are the only great apes to live outside of Africa. Their reddish-brown fur probably helps them maintain visual contact with one another in the lowland and hilly tropical rain forests in Northern Sumatra and in Borneo. Of the three great ape genera, orang-utans spend the most time in the trees. They move slowly and deliberately, using all four limbs (quadramanus) to support their great body weight. Females and young spend much more time in the trees than do males, which is probably a consequence of the much greater size of males. When on the ground orang-utans walk resting the weight of their body on the sides of their clenched fists, a different form of locomotion from the knuckle walking seen in chimpanzees and gorillas. Orang-utans exhibit marked sexual dimorphism both in body size and in secondary sex characteristics. Male orang-utans can reach up to 200 lbs (90 kg), while females are about half their size, reaching 110 lbs (50 kg). In addition, males develop pronounced cheek flanges and throat pouches upon sexual maturity. Orang-utans are primarily frugivorous (fruit-eating) and males and females forage separately. Male and female orang-utans come together only for a brief courtship and return to their solitary lifestyle immediately after mating. Females and their single offspring form feeding groups, and the territories of males may include that of several females and their offspring.

Members of the genus *Gorilla* are the largest of all the primates: males can reach up to 5-feet-9-inches and weigh as much as 400 lbs (180 kg). The two subspecies of lowland gorilla live in hot lowland forests of west and central Africa. The other subspecies, the mountain gorilla, lives high in the cool mountains of central Africa (elev. 5,450 to 12,500 ft). Gorillas are predominantly folivorous, subsisting primarily on leaves and stems rather than fruit. Although the young spend quite a bit of time in trees, adult gorillas are primarily terrestrial, spending more time on the ground than other great apes. Consequently, they have lost much of the grasping capability of their foot. Gorillas normally walk on all fours, clenching their hands so that their knuckles take their weight. The gorilla's social group can range between two and thirty-five individuals but usually numbers five to ten. Their close-knit groups consist of one dominant male (called a silverback because the fur on their back turns silvery gray), several females, and their immature offspring. The same dominant male may lead a group for several years.

—Ken Mowbray and Shara Bailey

See also: Monkeys; Physical Anthropology; Primates

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Green Algae

See Protoctists

Gymnosperms

Gymnosperms are nonflowering seed plants that may or may not be a monophyletic group. Recent phylogenetic analyses based upon data from morphology and the chloroplast gene rbcL indicate that the gymnosperms are paraphyletic, whereas phylogenetic analyses of other gene sequences from the mitochondrial and nuclear genomes indicate that they are monophyletic. Regardless, the extant gymnosperms consist of four morphologically distinct orders: the cycads (Cycadales), the conifers (Pinales), ginkgo (Ginkgoales), and the gnetopsids (Gnetales). There are no herbaceous or truly aquatic gymnosperms, although some may grow in swamps.

Order Cycadales. Extant cycads are characterized by compound leaves; girdling leaf traces; coralloid roots containing symbiotic nitrogen-fixing cyanobacteria of the genera *Anabaena* and *Nostoc;* two unique phytochemicals, MAM glycosides (cycasins) and BMAA (a neurotoxic, nonprotein alpha-amino acid); simple cones; and pollination by snout weevils of the Curculionoidea. There is an excellent fossil record indicating a Pangean (worldwide) distribution in the Jurassic and Triassic, with considerable extinction during the Pleistocene, resulting in reduced distribution of extant genera as well as isolation by plate tectonics. The order contains approximately 300 species in eleven genera and three families. All cycads are considered endangered species, with four genera listed on CITES Appendix I and the other seven listed on Appendix II. They are pantropical, with levels of local endemism. Cycads are threatened by commercial overcollection and habitat destruction.

Family Cycadaceae. This family has a single genus, Cycas, with eighty-seven species in Asia, Australia, and Indian and southwest Pacific Ocean countries including Madagascar.

Family Stangeriaceae. There are two genera and three species in this family. Stangeria, with one species, is endemic to Natal, South Africa, and Bowenia, with two species, is endemic to the east coast of Queensland, Australia.

Family Zamiaceae. This is the largest family of cycads, with eight genera. *Ceratozamia,* with nineteen species, is endemic to southern Mexico and contiguous Belize and Guatemala. *Chigua,* with two species, is endemic to a small area in northern Colombia. *Dioon,* with eleven species, is endemic mainly to Mexico, with one species endemic to Honduras and a population in Nicaragua. *Encephalartos,* with sixty-three species, is endemic to central and southern Africa. *Lepidozamia,* with two species, and *Macrozamia,* with thirty-eight species, are endemic to Australia. The single species of *Microcycas* is found only in the Pinar del Rio area of western Cuba. *Zamia,* with fifty-seven known species, occurs in Florida and the Caribbean and throughout tropical Central and South America. Most species in the Zamiaceae are local endemics with small scattered populations exhibiting reproductive depression, often because of elimination of the pollinators where known.

Order Ginkgoales. This order is known from only a single species, *Ginkgo biloba,* which is the lone surviving species of a group with a widespread fossil record from the Permian through the early Cretaceous. *Ginkgo* plants are large trees with short spur shoots bearing fan-shaped leaves with dichotomous venation. In China, *Ginkgo* has been cultivated for centuries in temple gardens. Presumably there are still wild populations in Zhejiang province in eastern China, although that has not been confirmed. *Ginkgo* is widely cultivated worldwide in temperate areas as a street tree, with the original source being from temple gardens. The female trees bear fleshy, foul-smelling seeds, so most cultivated plants are pollen-bearing males. *Ginkgo* is wind pollinated, as evidenced by its copious seed set in cultivation in the absence of any pollinators, so its presumed extinction or at least severe range restriction in the wild is an enigma.

Order Pinales. Conifers are resin-producing, evergreen, woody shrubs or trees with scalelike or needle leaves and pollen and seed cones. All conifers are wind pollinated, and most have wind-dispersed seeds. A few exceptions occur. Larches (*Larix* and *Pseudolarix*), bald cypress (*Taxodium*), dawn redwood (*Metasequoia*), and *Glyptostrobus* are deciduous, and the yews and their relatives produce only small amounts of resin. Yews (Taxaceae and Cephalotaxaceae), podocarps (Podocarpaceae), and Araucariaceae are animal dispersed. The

A forest of white pines (USDA Forest Service)

conifers are basically a temperate group that form vast forest stands as a principal component of temperate rain forests, boreal forest, and taiga in the Northern Hemisphere, and araucaria forests in the Southern Hemisphere. When conifers occur in subtropical to tropical regions they are usually at higher, cooler elevations (for example, South America) or in very dry areas such *Callitris* in Australia. Generally they are absent from true oceanic islands. Conifers have a good fossil record. Coniferous wood is known from the Upper Carboniferous, and unequivocal conifer fossils begin in the Lower Permian, with all extant families reaching their zenith in diversity in the Lower Cretaceous and then declining in the Upper Cretaceous, accompanied by the diversification and rise of the angiosperms. As a major source of timber and wood for paper products, conifers are extremely important economically, and conifer forests are subjected to extreme habitat destruction and degradation. Conifers are cultivated in pure stand plantations, and that results in habitat degradation of mesophytic broadleaved forests worldwide.

There are eight families forming two distinctive groups (sometimes treated as orders) within the Pinales. Cephalotaxaceae, Podocarpaceae, and Taxaceae form one of these groups. Cephalotaxaceae, found in temperate habitats in Asia, has two genera: *Amentotaxus*, with four species in widely disjunct small populations in China and Taiwan; and *Cephalotaxus*, with six species ranging from the Himalayas to Japan, which is widely cultivated in temperate areas. Podocarpaceae is the largest family, with as many as 125 species in seventeen genera currently recognized. The family is pantropical, with extensions into the subtropics mainly in the Southern Hemisphere. A majority of the species occur in montane regions, and some even reach alpine areas. *Podocarpus,* with 100 species, is widespread in the tropics worldwide. The other sixteen genera are more restricted. *Afrocarpus* is centered in equatorial Africa and extends south to southeastern Africa. *Saxegothaea* is endemic to temperate South America. The two species of *Acmopyle* are endemic to New Caledonia and Fiji. The single species of *Parasitaxus,* the only known parasitic gymnosperm, is endemic to New Caledonia, where it grows on the roots of another member of the family, *Falcatifolium taxoides. Microcachys* and one species each of *Microstrobos* and *Lagenstrobos* are endemic to Tasmania. The second species of *Microstrobos* occurs in a limited area of New South Wales, Australia, and the same is true for *Lagenstrobos* in New Zealand, where *Halocarpus* is also endemic. The other genera, *Dacrydium, Dacrycarpus, Falcatifolium,* and *Sundacarpus,* are centered in the region extending from Indo-China to Australia, with three others—*Retrophyllum, Prumnopitys,* and *Lepidothamnus*—also occurring in South America. *Phyllocladus,* with five species in moist, cool habitats from Luzon to New Zealand and Tasmania, is unusual in lacking well-developed leaves and instead having flattened photosynthetic stems (cladodes or phylloclades). Taxaceae contains four genera with sixteen species that are associated primarily with old-growth forests and are becoming quite rare worldwide as a result of habitat destruction. *Pseudotaxus,* with one species, is known only from a few disjunct populations in China; *Austrotaxus,* with one species, is endemic to New Caledonia. *Torreya* (stinking yew), with six species, is highly disjunct, occurring in limited areas of California, Florida, China, and Japan. More widespread is *Taxus* (the yews), with eight species, found in temperate areas of the Northern Hemisphere and extending at higher elevations to southern Mexico and Indonesia. *Taxus* is cultivated widely as an ornamental. The bark of *Taxus brevifolia,* endemic to the Pacific Northwest of North America, is the primary source of taxol, used in cancer treatment. It has become endangered as a result of the destructive collection of the bark from mature trees.

The second group of conifer families consists of Araucariaceae (for example, Norfolk Island pine, monkey puzzle tree), Pinaceae (for example, pines, spruces, firs, larches, cedars), Sciadopityaceae (umbrella pine), Cupressaceae (for example, arbor vitae, junipers, Leyland cypress), and Taxodiaceae (for example, bald cypress, dawn redwood, redwood, sequoias). The latter three appear to be related, and current evidence strongly suggests that the Cupressaceae is in fact a component of the Taxodiaceae, with Sciadopityaceae being problematic. There are thirty-two species in three genera in the Araucariaceae. All are found in the Southern Hemisphere except in Southern Africa. *Araucaria* (for example, Norfolk Island Pine), with eighteen species, has thirteen species endemic to New Caledonia, one species on Norfolk Island, and the rest in New Guinea, Australia, and southern South America, where they form large stands. *Agathis,* with thirteen species, ranges from Malaya to Fiji, with five species endemic to New Caledonia. In 1995 a new, very locally endemic genus, *Wollemei,* was found in a national park in New South Wales, Australia. The Cupressaceae, with 125 species in twenty genera, occur primarily in cool to warm temperate areas of both hemispheres of both the Old and New Worlds. They are widely cultivated ornamentals with small leaves arranged in either whorls of three to four or in decussate pairs. The most widely distributed genera, *Juniperus*, *Cupressus*, *Chaemaecyparis*, and *Thuja* (for example, arbor vitae), are limited to the Northern Hemisphere. Other genera show high degrees of endemism. *Widdringtonia* is South African; *Actinostrobus* is Australian; *Tetraclinis* is Mediterranean and North African; *Neocallitropsis* is New Caledonian; *Platycladus* and *Microbiota* are temperate East Asian; *Pilgerdendron*, *Fitzroya*, and *Austrocedrus* are southern South American; *Diselma* is Tasmanian; *Thujiopsis* is Japanese; *Fokenia* is Indo-Chinese; and *Papuacedrus* is New Guinean, with an outlier in the Moluccas.

Callitris is primarily Australian, with endemic species in Tasmania and New Caledonia. *Calocedrus* is found in temperate rain forests of Pacific North America and far eastern Asia. *Libocedrus* is from New Zealand and New Caledonia. The Sciadopityaceae, endemic to Japan, has a single genus, *Sciadopitys*, with one species and an unusual morphology in that the leaves are actually two laterally fused leaves with inconspicuous free tips. Taxodiaceae, with sixteen species in nine genera, commonly have vegetative shoots growing from the cone tips and are mostly confined to warm-temperate areas of the Northern Hemisphere, with one genus, *Athrotaxis*, endemic to Tasmania. Other locally endemic genera are: *Sequoia* (coast redwood) and *Sequoiadendron* (giant redwood) in western North America, and *Glyptostrobus* and *Metasequoia* (dawn redwood) in central and southern China. In contrast, the more widespread genera include *Taiwania* in China, Taiwan, and northern Burma; *Cunninghamia* in northern China and Taiwan; *Cryptomeria* in China and Japan; and *Taxodium*, ranging in local disjunct populations from the northeastern United States to Florida and the Gulf States to central Mexico. Pinaceae, with 200 species in twelve genera, are confined to the Northern Hemisphere. The larger genera (*Pinus*, *Larix*, *Picea*, and *Abies*) are distributed widely across the Old and New Worlds, where they reach high northerly latitudes as the major components of boreal forests. There are concentrations of species of these genera in North America and eastern Asia. *Tsuga* (hemlock) and *Pseudotsuga* (Douglas fir) have a similar pattern but are absent from Eurasia. *Nothotsuga* and *Cathaya*, each with a single species, are endemic to southern China, where they are very rare. *Hesperopeuce* is found at high elevations in western North America from Alaska to California. *Keetelaria* is common in China but rare in the rest of the Sino-Himalayan region. *Cedrus* (cedars) ranges from the Atlas Mountains of North Africa to the western Himalayas. Pinaceae are absent from South America (except for naturalized introductions), Australasia, and Africa, with the exception of one species of Cedrus in Algeria and Morocco. The Central American and southeast Asian species are found almost exclusively at higher elevations in montane forests and above.

Order Ephedrales (=Gnetales). This is an extremely diverse order of seed plants. There are three genera—*Ephedra*, *Gnetum*, and *Welwitschia*—and each is treated as belonging to its own family. All species are functionally dioecious and have vessel elements in the wood that appear to be independently derived when compared with those found in angiosperms, as does the phenomenon of double fertilization. The three genera are easily distinguished based on growth habit, leaf features, and habitat preferences. *Ephedra* (known as Mormon tea in the western United States), with fifty species, is xerophytic, heliophilious, and somewhat cold resistant. Eurasian species are distributed from the Canary Islands through the Mediterranean and semiarid regions of inner Asia, with disjuncts in the Arabian Gulf. New World species are found in western

North America and the Andes from Peru to Patagonia. Plants of *Ephedra* are profusely branched erect to prostrate shrubs, vines, or small trees with leaves reduced to small scales and with photosynthetic stems. Seeds are enclosed winged bracts for wind dispersal or in fleshy white, orange, or bright bracts indicating bird dispersal. Pollination by Diptera has been demonstrated in some Eurasian species. They have been widely used as medicinals since antiquity, and some species are known to produce ephedrine.

Gnetum, with thirty-seven species, is found in the lowland tropics of Asia, western Africa, and the New World. Generally the plants are twining vines, but two Asian species are trees. The leaves are well developed, opposite, and exhibit a reticulate venation pattern similar to that of angiosperms. The seeds are large and enclosed in fleshy orange to red bracts and appear, at least in South America species, to be dispersed by primates. Otherwise, herbivory including insect predation are unknown in the genus, even though toxic compounds have never been identified. The mode of pollination has not been established.

Welwitschia, with a single species, is found only in a narrow, extremely xeric coastal belt of the Namibia Desert from Kuiseb, Southwest Africa, to Cabo Negro, Angola. *Welwitschia* is one of the most bizarre and unique vascular plants. Each plant is single stemmed and produces only one set of two continuously growing foliage leaves and a massive, deep-growing taproot. The leaves can reach lengths of several meters. After twelve to fifty years the axillary buds of the foliage leaves begin annually to produce highly branched cone-bearing axes. Large plants of *Welwitschia* have been radiocarbon dated at 1,000 to 2,000 years old. Pollination is assumed to be anemophilous, but there is some evidence of entomophily by Hymenoptera and mosquitoes. The seeds are lightweight and winged for wind dispersal.

—Dennis Wm. Stevenson

See also: Angiosperms; Biogeography; Botany; Extinction, Direct Causes of; Phylogeny; Plate Tectonics; Pleistocene Epoch

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Habitat Destruction

See Extinction, Direct Causes of

Habitat Tracking

The tendency for species to change their geographic ranges in response to climate and other forms of physical change on the earth's surface is known as habitat tracking. Habitat tracking in effect confers stability in times of change, for as long as a species can locate suitable habitat—which means habitat to which it is already adapted—it will tend to persist.

At the opening of the nineteenth century, when the natural sciences such as geology and biology were still very much in their infancy, most scholars saw a world of stability—one that, they thought, had been created only a scant 10,000 years earlier. Not only was stability the norm, but there simply had been no time for much change in the earth or its living species. But the science of geology began to change those traditional assumptions; the great physician/farmer James Hutton, who essentially founded geology, said that he saw "no vestige of a beginning, no prospect of an end," but rather an endless cycle of mountain uplift, followed by slow but inexorable erosion, then uplift again. He saw vast vistas of time when change, far from being possible, was instead inevitable. His intellectual successor, Charles Lyell, took Hutton's lessons and applied them systematically to the earth. Lyell established the Principle of Uniformity ("Uniformitarianism"), which said that the same processes we see operating around us today were in operation throughout geologic history. Storms, volcanoes, earthquakes—events producing large-scale effects rather suddenly—could be added to the list along with the slower actions of rivers wearing down hillsides and bringing their sediment to the sea, there to build up into thick piles that would, as Hutton saw, one day be uplifted anew into fresh mountain chains.

Lyell was able to show that a series of hills in France were actually the remnants of extinct volcanoes. The Swiss naturalist Louis Agassiz was instrumental in showing that many of the topographic features of his homeland must have been shaped by sheets of ice vastly more extensive and thicker than the glaciers that still cling to the sides of the higher Alpine peaks.

Darwin was fascinated with all the mounting evidence that the earth had undergone great changes since its inception and believed with many of his fellow naturalists that considerable spans of geologic time must have elapsed for all such changes to take place. Darwin, of course, had a deeper motive for wanting to see deep geological time established as a fact: his theory of evolution by natural selection, in which he saw changes in species slowly and gradually accumulating as the world itself changes with passing time, actually demanded a very old age for the earth and its living species. His chapter on geological time in his epochal book *On the Origin of Species* (1859) was perhaps the boldest and most creative attempt to show that the earth is not mere thousands, nor even a few millions of years old but is in fact hundreds of millions of years old. As we now know, Darwin and Lyell were quite right: the earth is 4.65 billion years old, and life goes back as far as at least 3.5 billion years—in the form of tiny bacteria that are the oldest fossils so far discovered.

Thus everything was in place for Darwin: he saw a very old earth that had a long history of complex transformation—just the backdrop required for natural selection to produce an equally long and complex history of change in the species of earth. Natural selection, Darwin thought, would simply track the climatic and geologic changes the earth was undergoing, slowly changing the adaptations of organisms to keep them matched up perfectly with their environments. If, during the great ice ages, it grew colder, then certain mammals that we associate nowadays with the tropics—elephants and rhinoceroses, for example—would adapt by evolving dense, furry coats. And, of course, there were wooly rhinos and mammoths during the ice ages. Everything seemed to fit: the earth and life were far from stable, but rather were subject to constant change as geological time went on.

But nineteenth-century naturalists, lacking the detailed paleontological and even long-term neontological (that is, modern species) studies, didn't realize one simple fact: that, when faced with events that happen relatively slowly, such as global cooling events and the growth of continental glaciers, it is not so much natural selection that tracks the change by modifying organisms to suit the changed conditions; rather, it is species themselves that move to, for example, warmer climes via habitat tracking. True, some species remain around the glacial ice fields, adapted to the new colder conditions; but these new mammals of the tundra evolved rather quickly, just under a million years ago at the dawn of the second of the four major glacial advances of the Pleistocene Epoch (Ice Age) that started 1.65 million years ago.

But most of the rest of the world's species retreated southward during the glacial advances. Even plants can "habitat track," for though a rooted tree or bush of course dies when it gets too cold (or when the ice covers it!), nonetheless plants are adapted to disperse their seeds. Thus entire plant communities move south—with the tundra ringing the margins of the advancing ice sheets, and the northern forest advancing southward ahead of it, the mixed hardwoods even further south than the northern forest. This is not to say that these large-scale plant communities simply pick up and move smoothly southward toward the equator when things get colder, and just as smoothly beat a retreat back north when the temperature warms up: nature isn't quite that smooth or simple. But as individual species track favorable habitat (each plant species needing a special combination of soil types and chemistry, water, nutrients, and temperatures, for example, not to mention the right pollinators if they depend on insects rather than the wind for reproduction), the same basic community types keep assembling as species keep on the move in the face of environmental change.

Paleobotanist Margaret Davis has become famous for the work she has performed with colleagues and students plotting the movements of plant species as the Pleistocene ice sheets waxed and waned. And paleoentomologist G. R. Coope has done the same for beetles in Europe—in one instance finding an Ice Age beetle that was living during one of the warm periods along with tropical species such as lions and hippos in what is now London's Trafalgar Square, alive and well and living in the hot climes of the southern tip of Italy.

Thus habitat tracking is real, and it helps keep species alive in the face of extinction; and species tend to survive unchanged by evolution, as they simply move to habitats to which they are already well adapted. Most of the marine invertebrate species on both coasts of North America simply moved up and down the coasts as climatic conditions (including changes in sea level) kept changing during the Pleistocene. Not only did most mollusks and other marine invertebrate species avoid extinction then, but they also remained pretty much unchanged from their condition when they first evolved, in most cases well before the Pleistocene began.

Nowadays, global warming is causing many species to track to the north. Cardinals and tufted titmice, for example, are species of birds that had been restricted to the Southern states before 1800 but are now year-round denizens in New York City and indeed even much farther north. When the study of natural history was in its infancy, the changeability of species distributions was not documented—nor was it expected in the exciting days when old notions of stability were being replaced by ideas of evolutionary change of both the earth and of life. But patient study has revealed the reality of habitat tracking—and its importance in understanding how species can remain so puzzlingly stable even in the face of massive environmental change—the phenomenon known as "stasis."

—Niles Eldredge

See also: Darwin, Charles; Evolution; Extinction, Direct Causes of; Geological Time Scale; Hutton, James; Ice Caps and Glaciers; Lyell, Charles; Natural Selection

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Haplochromine Cichlids of Lake Victoria

The haplochromine cichlid fish of Lake Victoria demonstrate both the exuberance of species radiation and the tragedy of mass extinction, the first to occur during historical times. These tiny, colorful fish, which constituted 80 percent of the fish biomass in Lake Victoria prior to 1978, now account for less than 2 percent (Kaufman, 1992). This decline has been caused by a combination of human influences.

The cichlids are a very large and diverse family of freshwater, perchlike fish characterized by certain anatomical features (such as having a single nostril on either side of the snout, and an interrupted lateral line system) and the high degree of parental care devoted to their offspring (Keenleyside, 1991). Cichlids are native to Africa, the Middle East, Madagascar, Sri Lanka, the southern coast of India, and Central and South America. Cichlids have also been accidentally or intentionally introduced in many other parts of the world, often with disastrous effects on the native fish populations because of predation or competition.

In Lake Victoria, the cichlids of the haplochromine genus form a vast "species flock," a group of species derived from a common ancestor. The haplochromines have radiated to utilize a diverse array of feeding strategies. There are bottom-dwelling detritus-eaters, algae-scrapers that feed along the rocky shoreline, snail-crushers and others that extract the snail from its intact shell, insect-eaters, zooplankton-eaters, prawn-eaters, fish-eaters, scale-scrapers, and, most notoriously, the pedophages, which specialize in eating the embryos and fry of other haplochromines (Goldschmidt, 1996). Since all of the Lake Victoria haplochromines are mouth-brooders, this means that the pedophage must wrest its meal from the mother's mouth.

The haplochromines are also notable for the rapidity with which they radiated to occupy the many niches of Lake Victoria. This lake is located in East Africa, bordered by Tanzania, Uganda, and Kenya. Lake Victoria is the second largest body of fresh water in the world (the largest being Lake Superior in North America). Although the lake existed in very ancient times, climatic changes during the Pleistocene led to its complete desiccation, which may have lasted for 5,000 years. All of the modern species of haplochromines endemic to Lake Victoria have evolved since the lake refilled, within the last 12,000 years—an example of extremely rapid evolution (Johnson et al., 1996). The diversity of adaptive speciation and niche separation among the haplochromines has earned Lake Victoria the nickname "Darwin's Dreampond" (Goldschmidt, 1996).

More than forty species of haplochromines from Lake Victoria are listed as extinct by the International Union for the Conservation of Nature (IUCN)(Hilton-Taylor, 2000), but Harrison and Stiassny (1999) caution that not enough is known about many of the species even to determine their correct taxonomy. At the current level of knowledge, it may be impossible to determine whether isolated populations of some species have survived. For now, many can be listed as "missing in action." It is safe to say that the species flock is in critical danger of losing a large portion of its diversity.

Examples of the diverse species of haplochromines that are missing in action include species occupying all of the ecological niches. *Haplochromis ishmaeli,* a green-bodied fish with splashes of red on its dorsal fin and tail, was a snail-eater. *H. ishmaeli* used its pharyngeal mill, a crushing device located in its throat, to pulverize the mollusks that it swallowed whole. In contrast, *H. degeni,* a species extinct in the wild, extracted the snail by banging and shaking the shell to dislodge its resident. *H. megalops* was a zooplanktivore, feeding on microscopic crustaceans. It vacuumed up its tiny prey by rapidly protruding its funnel-shaped mouth and sucking in water and zooplankton. Other haplochromines, such as *H. macrognathus,* an elongated fish with a silvery body, were streamlined predators that preyed upon haplochromines and other small fish. Some haplochromines, such as *H. welcommei,* which may still lurk in the waters of Lake Victoria, require only pieces of their victims. They ambush their prey and roughly scrape their meal, the scales, off of its body. *H. microdon,* with its rainbowed belly and tiger-striped dorsum, was a pedophage. It targeted a mouth-brooding female and used its body to ram into the mother with such force that the brood would be expelled from the safety of her mouth. *H. microdon* then had its meal. Many of the fish that are missing in action have not yet been assigned scientific names but are still known by colorful, descriptive monikers assigned by their discoverers, such as *H. two stripe yellow green.*

Prior to the arrival of Europeans at Lake Victoria in the 1850s, human impact was limited to subsistence fishing and low levels of agricultural and human waste runoff. Settlement by Europeans increased the demand for fish, and the volume of runoff from lakeside industry and agriculture soared. Deforestation and soil erosion also contributed to increased flow of sediments into the lake.

With increased fishing pressure, the catch of large fish (especially the tilapiines *Oreochromis esculentus* and *O. variabilis*) dwindled. To satisfy the demand, nets of smaller and smaller mesh were employed to catch the smaller and smaller fish. The result was the decimation of mature and immature populations alike. The small haplochromines were harvested to make fishmeal but were not as desirable as the larger species. In the 1950s a proposal was made to stock the lake with nonnative species, the predatory Nile perch (*Lates niloticus*) and plankton-eating Nile tilapia (*Oreochromis niloticus*). The proponents of these introductions sought to utilize the haplochromines as food for the perch that would be a more marketable fish crop. Opponents to these introductions raised sound arguments, but they fell upon deaf ears (Fryer, 1960).

The most obvious problem with the introduction of predators is based on the simple principle that an adequate prey supply must be available to support the population. In a closed system, a rapidly growing predator population can be expected to exhaust its food supply, at best leading to a boom and bust cycle. Anticipating this disastrous outcome, scientists urged caution, fearing that introductions of nonnative fish would jeopardize rather than enhance Lake Victoria's commercial fishery.

Indeed, the critics' predictions have been borne out. The native tilapine species, which had been the most important commercial species, already in decline because of overfishing, also became the prey of the Nile perch. Competition for food with the introduced Nile tilapia further strained the native tilapiines. With the diminishing catches of tilapia, human and perch appetites turned to the haplochromines (Ogutu-Ohwayo, 1990).

In the pristine Lake Victoria, diversity was advantageous for the haplochromines, enabling them to make full use of the lake's opportunities. However, populations within each species were limited, and the practice of mouth-brooding made the population more vulnerable to predation (the death of a mouth-brooding female also results in the loss of her progeny). The predatory perch, which reproduce at a much higher rate than the native cichlids, contributed to the decimation of the haplochromine populations. Having eaten themselves out of their fish food supply, they now consume prawns and cannibalize their young (Goldschmidt, 1996). It seems unlikely that a population dependent upon cannibalism can survive.

Although the Nile perch have been villainized for their role in the decline of the native fish species in Lake Victoria, the greatest share of the blame falls directly to humans. Overfishing and indiscriminate taking of young fish have diminished the breeding populations. Agriculture, industry, and deforestation have resulted in increased soil runoff and direct discharge of nutrient-rich material into the lake. Algae are nourished by this runoff, and they proliferate. The algal blooms block the sunlight, and decay of the algae consumes oxygen. This process is called eutrophication. Massive fish kills in 1984 were attributed to unusually large algal blooms following storms that stirred up nutrient-rich sediment. Deoxygenation and acidification of the water, coupled with physical clogging of the fishes' gills, killed many fish. In addition, toxins produced by the algae have been implicated in these events (Ochumba, 1990). Algae also clog the intake filters of water purification plants, increasing filtration costs to local consumers. The increased nutrient loads have also supported the proliferation of water hyacinth (*Eichhornia crassipes)*, an exotic plant that chokes waterways and further contributes to eutrophication (Baskin, 1994).

Deoxygenation of the water has made the deeper levels uninhabitable for many species. The haplochromines, which seem to be more tolerant of decreased oxygen availability than the Nile perch, may take refuge in the deeper waters. This tactic may help shield them from predation, but fluctuations in oxygen content in this already oxygen-poor environment may be fatal, and the added stresses of life under these conditions may be detrimental to growth and reproduction (Kaufman and Ochumba, 1993). Eutrophication has also led to decreased underwater light levels. Some scientists have hypothesized that closely related haplochromine species may have difficulty recognizing other members of their own kind, and thus be vulnerable to accidental interspecies breeding (Seehausen et al., 1997)

Ultimately, few have benefited from the changes in Lake Victoria, except the industrial fishing and fish export industries, and even they are now facing declining catches. From the point of view of the average local fishermen, the current state of affairs in the lake is dismal. Catching the large perch requires stronger, more expensive nets, yet the market price for Nile perch is lower than for the elusive native species. Unlike the smaller native fish, the large, oily perch must be smoked for preservation, and increased demand for firewood has contributed to deforestation (Barel et al., 1985). As fish catches have diminished, and most of the fish caught are destined for export, this primary protein source has become inaccessible to much of the local population; protein malnutrition is a growing health problem. There is also concern that loss of snail-eating haplochromines may lead to an increase of bilharzia, a parasite carried by snails, which causes severe human disease (Kaufman, 1992).

Goldschmidt (1996) found that by the late 1980s, approximately 70 percent of previously documented species were missing from a sampled area, in comparison with prior survey results. It is believed that more than 50 percent of the known species of Lake Victoria cichlids may have become extinct since their first recognition within the last 200 years. Remnant populations of some species may persist in satellite lakes and streams, but human creation of interlake waterways threatens to allow the entry of perch into those refugia (Kaufman and Ochumba, 1993). Captive breeding programs have been established for a few of the threatened species, but much of the remarkable diversity of the Lake Victoria haplochromines has already been lost. It is unlikely that human intervention will come soon enough to salvage what remains. Lake Victoria must serve as a tragic lesson about the dangers of meddling with ecosystems and the consequences of irresponsible resource management. Nevertheless, Lake Victoria is not called a dreampond erroneously. There is evidence that new species may yet be arising, selected for as a result of the current environmental pressures.

—*Julie Pomerantz*

See also: Conservation Biology; Endangered Species; Evolution; Evolutionary Biodiversity

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Herbivory

Herbivory is the process of consuming plants as food. Herbivores are organisms that eat living plants for nourishment. A monarch butterfly caterpillar eating milkweed leaves, a field sparrow eating seeds, snails grazing on lettuce in a vegetable garden, a deer browsing on woodland shrubs, Canada geese relishing the grass on a golf course, and minnows grazing on algae in a stream are all engaging in herbivory. Through their feeding activity, herbivores can have a powerful influence on biodiversity, both species numbers and distribution.

Herbivores can be selective feeders, able to survive on only one type of plant. For example, monarch butterfly caterpillars will eat only milkweed plants. Other plant eaters can be generalists, thriving on a variety of plant materials, though they may have their favorites. White-tailed deer will eat many different kinds of herbs and shrubs. Gypsy moth caterpillars prefer oaks but will do well on other trees. Most herbivores remain plant-eaters throughout their lives, but some are herbivorous only during one life stage. For example, frogs are herbivorous as tadpoles, grazing on algae in ponds; as adults, however, they are carnivorous, feeding on insects. Cecropia moth caterpillars feed on elderberry and other plants as larvae, yet do not feed at all as adults!

Herbivory can change the structure and species composition of entire plant communities, affecting biodiversity in a variety of ways. The nature of this impact will depend on the particular ecosystem and its characteristics, the species interacting in that system, and the densities of each of those species.

In terrestrial systems, herbivory can slow succession. Grazing by rabbits, voles, and other plant eaters in an old field, for example, will prevent the field from "growing up" or succeeding into forest. In aquatic systems, herbivores can accelerate change to other plant communities. This happens, for example, when grazing by marine snails clears growing space on submerged rocks along the shore, allowing later successional seaweeds to take hold.

Heavy grazing pressure can remove so much plant material from an ecosystem that diversity is severely reduced. In the northeastern United States, for example, browsing by high numbers of white-tailed deer has resulted in the disappearance of many native plants from the woodlands, reducing forest diversity. In many cases, what remains after such heavy grazing are plants that are unpalatable—those that aren't eaten because they are covered with spines or are toxic. In this way, grazing by deer can also change the plant species composition of the woodlands. That in turn affects other animals in the forest. Many bird species depend on certain woodland plants for food and as nesting sites, and these are the same plants that may be removed by the grazing deer.

If not controlled by herbivore grazing, some plants actually out-compete other plants in the area by growing over them and shading them out. This may result in lowered species diversity in a particular environment. On the other hand, a modest amount of herbivory can result in an increase in diversity in an ecosystem by removing some of the competing plants and allowing more species to find space to grow. This is particularly true if the grazing animal is selectively feeding on the competitively dominant plant species in that ecosystem.

In response to herbivory, many plants have developed antigrazing tactics. Some produce toxic or distasteful chemical compounds in their leaves to deter grazing, such as the tannin in oak leaves. Others develop leaves with hairs, thorns, or spines (for example, mullein, Japanese barberry, cactus). Still other plants have evolved strategies for seed dispersal to deter predation on seeds. Over evolutionary time, many intricate plant and herbivore relationships and strategies have coevolved, ensuring the survival of both plant and animal.

—Elizabeth A. Johnson

See also: Botany; Carnivora; Communities; Food Webs and Food Pyramids; Succession and Successionlike Processes

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Hole in the Ozone Layer

Ozone (O_3) in the atmosphere has two very different roles. On the surface of the earth it is a pollutant and a health hazard. It is found in photochemical smog that builds up during atmospheric inversions. People with lung ailments are especially susceptible to its damaging effects. When automobiles in cities release large amounts of nitrogen compounds during the summer, sunlight breaks up nitrogen oxide (NO_2) to nitrogen monoxide (NO), releasing an oxygen molecule that combines with oxygen (O_2) to form ozone (O_3). High in the atmosphere, however, ozone is beneficial, protecting life from ultraviolet radiation.

In the stratosphere, twelve to sixteen km above the surface, ultraviolet light from the sun converts the oxygen molecule to ozone. Here, the conversion process creates an ozone layer that absorbs ultraviolet radiation, protecting the earth from most of its damaging rays. Ultraviolet radiation causes skin cancer, and it is associated with cataracts in eyes, gene mutations, and immune system damage. Ozone also inhibits photosynthesis in plants.

Loss of ozone in the atmosphere was first noticed by scientists studying the atmosphere above Antarctica in the mid-1970s. This loss, which occurs during the summer, is described as the ozone hole, and scientific investigation since the loss was first noticed has shown that a number of factors are involved. During the winter polar night, sunlight does not reach the South Pole, and the air gets very cold. A strong whirlpool wind, the polar vortex, develops, causing the cold air to remain within the polar area, essentially cutting it off from the rest of the atmosphere. When the air temperature drops below -80 degrees centigrade, polar stratospheric clouds form that are composed of water ice droplets and nitric acid. Reactions take place on the surface of these ice crystals that convert benign chlorine compounds into chlorine and bromine compounds that are ozone destroyers. The source of these chemicals is CFCs (chlorofluorocarbons) and other industrial compounds containing bromine and other halogens. CFCs are used as a refrigerant in air-conditioning systems, in solvents, and in aerosols. Nitrogen compounds are produced by combustion, sources of which are jet aircraft emissions. These compounds are carried aloft by air currents and diffused into the stratosphere. Ozone loss does not occur until sunlight returns in the spring and starts a rapid cycle of ozone destruction, which usually begins in mid-September, widens in mid-October, and contracts again in December. The size and duration of the ozone hole also depends on the weather, and it exhibits the same range of variations as weather on the surface, making year-to-year variations difficult to forecast. In general, the colder the winter, the larger the number of clouds, the greater destruction of ozone, and the larger will be the hole. For example, it reached a record size in 2000, growing to three times larger than the United States and then disappearing completely by November 19.

Enough evidence has been gathered by scientists that the international community has become concerned about the hazards. The Montreal Protocol of 1987 was the result; it set provisions for the phasing out of the use of the chemicals determined to hasten ozone destruction. The agreement restricted the production of CFCs by 1995 and eventually many other halogen compounds. It was believed that these restrictions would lead to the recovery of the ozone layer by 2050. Although the ozone hole will not go away for a long time, just a few years after the phaseout program began, concentrations of CFCs have started to decline in the lower atmosphere and have leveled off in the stratosphere.

In 2000, a loss of ozone was noted over the North Pole. This is a great concern because of the substantial number of people living in the Arctic regions. Winter temperatures in the Arctic are variable, and ozone loss occurs only during very cold winters, as in the Antarctic. Using information from the TOMS (Total Ozone Mapping Spectrometer) satellite, researchers believe that Arctic ozone loss is associated with volcanic activity, which emits sulfur compounds into the earth's atmosphere and forms sulfuric acid. Volcanic sulfuric acid clouds add to the ozone-destroying power of the polar stratospheric clouds. During cold years the combination of volcanic sulfuric acid clouds below and the polar stratospheric clouds above increases the potential for creating an ozone hole in the Arctic.

—*Sidney Horenstein*

See also: Atmosphere; Atmospheric Cycles; Climatology; Global Climate Change

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Holocene

The Holocene is also called the Recent, and its boundary with the preceding Pleistocene epoch is not precisely agreed upon. However, it is defined as either when the continental glaciers in North America and Eurasia began their retreat, 15,000 years ago, or when most of the glaciated areas were free of ice, 10,000 years ago.

The Holocene is the span of time during which people have changed and dominated the environment of the world: at first by hunting while following herds of animals across the terrain, and later by settling into communities, cutting down forests for houses, and creating open spaces for farming. Later these communities expanded into large cities, necessitating large-scale mining operations, the burning of fossil fuels, and the interconnection of urban and rural areas with networks of communication and transportation.

One of the major events of the Holocene is the rapidity of climatic change and the resulting redistribution of plants and animals with migrating climatic zones. Glaciers probably reached their maximum distribution about 18,000 years ago, at the time that sea level was about 130 m lower than at the present and vast areas of the continental shelves were exposed. As the climate warmed about 12,000 years ago, glaciers shrank and sea level rose as torrents of glacial meltwater flowed into the oceans. About 12,000 years ago postglacial lakes formed over large parts of the North American continent, Lake Agassiz in the Midwest and Lake Bonneville and Lake Lahontan in Utah and Nevada. During this time the climate of the areas south of the glacial margin were much wetter. These disappeared as a result of the irregular uplift of the land surface caused by glacial rebound and changing climate. Glaciers widened and deepened river valleys, gouging deep basins that became lakes, such as the Finger Lakes in central New York and the Great Lakes of Central North America.

As the climate warmed the land was released from the grip of the ice and revegetated. In eastern North America the overall succession of tundra to boreal forest to deciduous forest is revealed at numerous sites by the study of sediments and their entombed spores, pollen, and other vegetable matter.

However, the climatic change from glacial to postglacial times was not an even transition. It was marked by warming and cooling cycles, the data for which are derived from a number of lines of evidence. For example, using radiometric dating and the position of a reef-building coral, scientists have shown that the island of Barbados in the Caribbean was involved in three periods of rapid rise in sea level between about 15,000 and 7,000 years ago. The coral grows very close to sea level today, but dead coral is also found many meters above sea level and as fossils in cores several layers well below the surface. Using radioactive dating methods and subtracting the results of tectonic rise of the island, the ages of these corals have been determined to be 14,680, 11,600, and 7,600 years. The rises in sea level that these data represent also reflect a corresponding climatic shift.

As an example, the annual snowfall layers in Greenland about 14,680 years ago doubled in thickness in the space of ten years. The rise in sea level detected in Barbados, which represents a climatic warming, increased the supply of moisture for the North Atlantic Ocean, allowing for an increase in snow accumulation in Greenland. Starting about 13,000 years ago, the Northern Hemisphere began to shift back toward glacial conditions. This cold interval is called the *Younger Dryas*, named after the plant that spread southward with colder conditions. Sea ice expanded southward, and mountain glaciers extended farther down their valleys. This cold period suddenly ended 11,600 years ago. Study of ice cores from Greenland and elsewhere indicate that this shift took place within just three years. The last sudden rise in sea level took place 7,600 years ago, perhaps as a result of the melting of large amounts of ice from Antarctica, raising the sea level close to its present level.

The Younger Dryas was also the time that large numbers of people migrated to North America. Although some archaeologists believe that small numbers of people reached

North America 30,000 years ago, it wasn't until the glaciers began to melt on a large scale in Alaska and western Canada that a route opened to the unglaciated parts of North America. It was probably about 11,500 years ago that the Clovis people developed the first widespread culture of North America. These early hunters sought out elephants and bison, using spears to kill them for food and clothing. Three species of elephants lived in North America: the wooly mammoth in tundra and grassy environments that were adjacent to continental ice sheets, protected from the cold by their long, hairy coats; mastodons in the Eastern conifer forests; and the great Southern mammoth, living in the prairies of the Midwest and Southwest.

Another feature of the Holocene is the disappearance of many species of large mammals between 12,000 and 10,000 years ago. Their demise altered the terrestrial ecosystem and left behind an enduring controversy—namely, why did they disappear? Was it the result of climatic change or the wholesale slaughter by Clovis hunters, the early inhabitants of North America? In addition to the elephants, many other large mammals disappeared, such as a giant beaver, several species of horses, a camel, two species of oxen, three species of musk oxen, a large bison, two species of giant armadillos, several species of giant sloth, the dire wolf, and three species of saber-toothed cats.

It is believed that the cats and several species of eagles, vultures, and condors died out because the large mammals no longer provided prey or carcasses for them to feed on. The cause of their extinction continues to be debated, however, and although there are merits to both sides of the debate, neither side is conclusive. Perhaps, as some have suggested, the answer is a combination of both ideas. As the Clovis population and hunting expanded in conjunction with climatic change and vegetation shifts during the Younger Dryas, the interplay of these events led to their demise.

During the last 10,000 years, climate continued to fluctuate, with warming and cooling intervals. It was at the beginning of this time frame that people began to settle down in communities and domesticate plants and animals for food, between 9,000 and 6,000 years ago in Europe. It is thought that domestication and farming emerged in the Zagros Mountains near the borders of Iran, Iraq, and Turkey, and then spread to Greece and across Europe, reaching Scandinavia some 6,000 years ago. It is believed that this expansion correlated with the beginning phase of a temperate climatic regime and the eventual disappearance of all the continental ice sheets in North America and Europe.

This warmer period is designated the hypsithermal interval, or climatic optimum, a time when the evidence from pollen and plant material indicates that the mean annual temperature of North America and Europe was about 2 degrees centigrade warmer than today. Hemlocks, for example, lived farther up mountain slopes than they do now, and dwarf birches lived where there is today only tundra. It is believed that the great civilizations of Egypt, Mesopotamia, and the Indus Valley began to flourish at this time.

Study of pollen indicates that the hypsithermal interval came to an end when climate turned colder, about 5,800 to 4,900 years ago. Another cooling occurred 3,300 to 2,400 years ago, and then again from 700 C.E. to 900 C.E. Warming and the reduction of sea ice after the last cooling event allowed the Vikings to extend their base of operations along the European coast, maintain a community on Greenland, and gain a foothold on Newfoundland. In Greenland they raised cattle and sheep, but by 1500 the colony was abandoned because extensive sea ice prevented communications and the delivery of supplies.

This cooling marked the beginning of the so-called Little Ice Age, when climate turned cold in Europe and North America, causing crop failures and the introduction of crops that could grow in shorter summer seasons. During this time mountain glaciers enlarged and extended farther down their valleys, and new glaciers formed where they had previously existed during former cold periods.

One of the effects of the advance and retreat of glaciers is the corresponding rise and fall of sea level because of the addition of water to, or its subtraction from, glaciers. Masses of glacial ice also applied great stresses to the earth's surface, depressing it as they advanced and permitting it to rebound when they retreated. Taking into account tectonic movements, shorelines can portray a very complicated series of events. Many shoreline configurations, especially locally, have dramatically changed over time as a result of these phenomena. Former river valleys, such as those of the Chesapeake and the Hudson, were converted to wide estuaries.

Such changes, both physical and social, will occur as a result of climate change; they are why many scientists and other individuals are concerned about global warming. The geologic record shows that changes to climate can occur rapidly, during the lifetime of an individual; the consequences of these changes on the reorganization of climatic belts and the resulting drowning of coastal cities and probable increased desertification of the interior of continents will have direct effects on where people will live.

—*Sidney Horenstein*

See also: Climatology; Glaciation; Global Climate Change; Pleistocene Epoch

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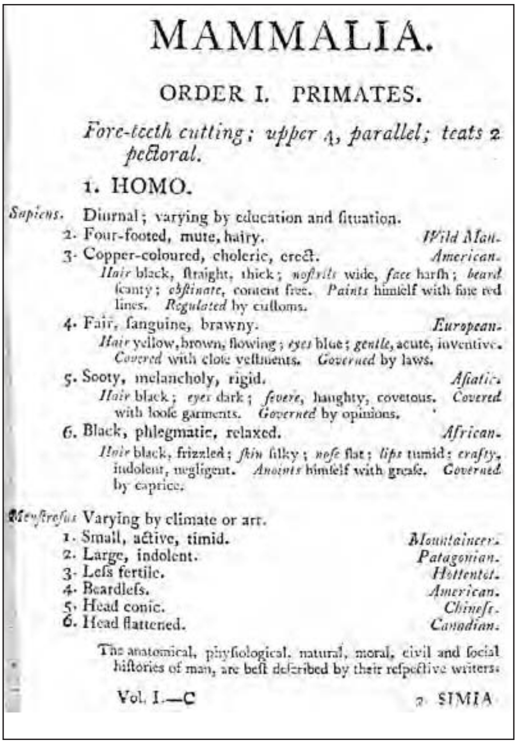
Homo Sapiens

The only surviving group within the Tribe Hominini of the Order Primates, *Homo sapiens* is the genus and species classification by which all behaviorally and anatomically modern humans are identified. The designation is derived from the Latin for "intelligent man." When Linnaeus first classified all organic organisms in their natural order using a hierarchical system with binomial nomenclature (*Systema Naturae*, 1735), he was bold enough to include humans (under the genus *Homo*) with monkeys and apes. Unable to fully describe humans at the species level, *Nosce te Ipsum* ("Know thyself") is the only clue first provided by Linnaeus to describe the human condition. He then identified four varieties based on geography and skin color; except for the peculiar category reserved for monsters, just in case tales written by Herodotus were true. Today, physical anthropologists are still unable to agree on what constitutes a human being, but we can approach the subject with systematics.

Species are in theory the most objective of all taxonomic categories. They are naturally defined by reproductive communality and phenotypic similarity. Species, and the characters that define them, may be objectively arrived at based on whether or not distinct populations maintain their distinctiveness in areas of sympatry and are diagnostically different. Among primates, closely related species usually exhibit frequency differences in specific characters, or differences in absolute size and proportions of structures, or of localized anatomy. For instance, all species have a type specimen (one specimen that universally exhibits the morphological and behavioral characters specific to that group) for which they are named. One notable exception is *Homo sapiens*. If we were to choose a type specimen, how would we go about it? Human beings are polytypic in nature, which means they have many types or varieties within a species (that is, Caucasians, Negroids, Mongoloids). Which variety would best serve as a type specimen? Until we stop looking at humans as being outside the realm of natural laws governing evolutionary pathways, we will never know the true biological meaning of *Homo sapiens*.

It is difficult to apply these rules to *Homo sapiens* without losing our objectivity. If one were to define modern humans, only a small number of unique characters stand out: (1) *Homo sapiens* are the only surviving members in the Family Hominidae committed to terrestrial bipedalism; (2) They have a relatively large brain—averaging 1,350 ml—with the most complex neocortex; (3) Their chinned faces are small compared with their neurocranium; (4) They have a bipartite brow; (5) They have a spoken language; (6) They have a relentless ability to destroy their own habitat and the habitats of others; and (7) *Homo sapiens* maintain a bizarre inability to remain bored. As you can see, it is rather difficult to describe modern humans without including culturally expressed behaviors.



MAMMALIA.

ORDER I. PRIMATES.

Fore-teeth cutting; upper 4, parallel; teats 2 pectoral.

1. HOMO.

Sapiens. Diurnal; varying by education and ſituation.
2. Four-footed, mute, hairy. *Wild Man.*
3. Copper-coloured, choleric, erect. *American.*
Hair black, ſtraight, thick; *noſtrils* wide, *face* harſh; *beard* ſcanty; *obſtinate*, content free. *Paints* himſelf with fine red lines. *Regulated* by cuſtoms.
4. Fair, ſanguine, brawny. *European.*
Hair yellow, brown, flowing; *eyes* blue; *gentle*, acute, inventive. *Covered* with cloſe veſtments. *Governed* by laws.
5. Sooty, melancholy, rigid. *Aſiatic.*
Hair black; *eyes* dark; *ſevere*, haughty, covetous. *Covered* with looſe garments. *Governed* by opinions.
6. Black, phlegmatic, relaxed. *African.*
Hair black, frizzled; *ſkin* ſilky; *noſe* flat; *lips* tumid; *crafty*, indolent, negligent. *Anoints* himſelf with greaſe. *Governed* by caprice.

Monſtroſus Varying by climate or art.
1. Small, active, timid. *Mountaineer.*
2. Large, indolent. *Patagonian.*
3. Leſs fertile. *Hottentot.*
4. Beardleſs. *American.*
5. Head conic. *Chineſe.*
6. Head flattened. *Canadian.*

The anatomical, phyſiological, natural, moral, civil and ſocial hiſtories of man, are beſt deſcribed by their reſpective writers.

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Classification by Linnaeus of man as an animal of genus* Homo *and species* sapiens, *from* A General System of Nature *by Carl von Linne, 1806 (Library of Congress)

If we were to examine our evolutionary history by examining the fossil record, we again are faced with a dilemma. About 100,000 years ago, anatomically modern humans appear in the fossil record; they have cranial and postcranial dimensions similar to those of modern humans, yet they show no evidence that leads us to believe they had incorporated a modern behavioral repertoire. Yet, 50,000 years later, with little change in the bony morphology, evidence of a dramatic change in behavior appears. Tool manufacturing technology provides the earliest evidence of a creative pulse that catapulted anatomically modern humans on an evolutionary trajectory never before witnessed in the history of life. It is not surprising that when members of different hominid groups (*Homo sapiens* and *Homo neanderthalensis*) who shared ecological niches within rapidly changing environments met, these two groups were forced to compete with each other for resources. It would only be a question of time until the advent of a flaked stone, bone, and wood technology would spawn a crucial advantage for the makers and users to out-compete one another for food and water. Tools probably helped to expand dietary breadths and contribute significantly to a group's survival during times of environmental stress.

In just a few thousand years, other behavioral changes show up in the fossil record in the form of parietal and stationary art, and body adornment (including jewelry made of seashells and teeth). Obviously, a cognitive gulf had been crossed. Soon *Homo sapiens* would start cultivating crops, domesticating animals, counting, writing, reading, and building. Just imagine, the significance of flaked stone, bone, and wood technologies lies not within its corpus of edification that results when one bashes two items together, but the necessary mental faculties and imaginative capabilities of first conceptualizing tools that possess the mechanical properties that facilitate their manufacture. When this first happened 2.5 million years ago, the overall hominid body size, brain size, and overall behavior was changing course. Brain size in hominids was increasing exponentially, and nothing short of a major hominid radiation occurred throughout the Old World. It seems that our evolutionary path was initially set in stone with the bashing of two rocks a few million years ago. Yet, it may be our desire to exemplify our own sense of purpose to others through magnificent cave paintings and portable carvings that reflexively made us who we are today: *Homo sapiens*, the last (latest?) of the hominids.

From a phylogenetic standpoint, we now know that the only uniqueness to being human is that our evolutionary history (which we believe to include dozens of extinct hominid species) culminated into a single polytypic species, *Homo sapiens*. From here we have three evolutionary choices: (1) to remain in stasis; (2) to evolve; or (3) to go extinct as all other creatures eventually do. The choice may or may not be entirely up to us.

—*Ken Mowbray*

See also: Human Evolution; Primates

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Horseshoe Crabs

See Arthropods, Marine

Human Evolution

One of the major goals of paleoanthropology—the study of human evolution—is to identify hominin species and to reconstruct a chronological sequence and evolutionary relationships among them. *Hominin* is a colloquial term used to indicate membership to the Tribe Hominini in which humans and their immediate ancestors are currently classified. This is accomplished by sorting the morphological variation within and between hominin fossil materials, taking into account idiosyncratic, geographic, and geologic parameters. Studying human evolution requires training in human and nonhuman primate anatomy, geology, ecology, taphonomy, and evolutionary biology in order to evaluate critically the fossil material and the depositional context in which it was recovered. Unfortunately, despite the enormous amount of work that goes into recovering fossil humans, the often scanty nature of fossils makes many inferences tenuous at best. This was particularly true in the early twentieth century.

Prior to 1950, inferences about evolutionary history construed from a sparse fossil record led some researchers to believe that the human lineage extended back into the Early Miocene (roughly 14 to 17 million years ago). This paradigm, and others like it, was based primarily on Darwin's suggestion in *Descent of Man* (1872) that humans were closely related to the apes—something Linnaeus had recognized a century earlier. Darwin predicted that one should look where apes live (in the jungles of Africa) if human fossils were to be discovered. He also predicted that these fossils would prove that relatively large brains evolved long before bipedal adaptations. This simple but brash hypothesis would sadly mislead human evolutionary studies for more than forty years. In 1914 leading British scientists accepted Piltdown man (a purported fossil with a humanlike cranium and apelike jaws and teeth) as the earliest human ancestor, simply because they believed in Darwin's theoretical tenet of an evolutionary link. Unfortunately, a common thread among paleoanthropologists at that time was to assume that human evolution is a unique situation, and the missing link mindset was deeply ingrained. Piltdown man seemed to be their perfect candidate for the missing link between apes and humans—perhaps too perfect. Despite having at their disposal the Javanese Trinil fossil human (*Homo erectus*), and a little later, the South African australopithecines (that is, the Taung child *Australopithecus africanus*), many scientists clung to Piltdown man as the earliest human ancestor. At the time of its discovery in 1925, the Taung child was dismissed by many as an ancient ape. Similarly, many dismissed the Trinil fossil calvaria as an extinct species of giant gibbon.

By the mid-1950s, sites from South Africa, east Africa, and Europe were generating much more fossil human material. After sober assessments of the fossils were made, the implications became clear. None of the earlier hominin phylogenetic claims could be supported. Piltdown was exposed to be a hoax—the doctored remains of a human and orang-utan; the Taung child dated to roughly 2.5 million years ago; and the Trinil calvaria dated to 750,000 years ago. With the elimination of Piltdown from the hominin family tree, both of these fossils became widely accepted as human ancestors. Even so, the human fossil record was far from being a clear picture to stand back and admire. Certain paleoanthropologists (known as splitters) had just entered a period when every fossil discovery generated a newly described species. The human fossil record became a junkyard littered with dozens of species, and it was becoming increasingly difficult to flesh out humanity's prehistory. This muddle in the middle needed to be addressed, and it took a lecture on human evolution by world-renowned evolutionary biologist Ernst Mayr to make the necessary changes. Although paleoanthropology was unfamiliar territory for the biologist, he quickly lumped many hominin species together under a single name, bringing a breath of fresh air to the field. It became very fashionable thereafter for paleoanthropologists (now known as lumpers) to do the same.

The 1960s and 1970s will be remembered as a period of enlightenment for human evolutionary studies. Protein synthesis research in primates enabled scientists to propose a molecular clock that could predict the amount of time needed to achieve the number of changes observed in certain proteins sampled from living primates. If the molecular clock is correct, the origin of the ape/human clade occurred only 5 to 7 million years ago, a much later divergence date than the previously proposed 14 to 17 million years. Despite ongoing arguments that the number of molecular changes observed in protein structures was not constant over time (or that most structural changes were neutral and have no reproductive recourse), researchers in the early 1970s uncovered bipedal apelike hominins from the Afar region of Ethiopia. These fossils led to the scientific naming of a new hominin species *Australopithecus afarensis*, dated at 3 million years. They were then the oldest known human ancestors and quickly became the basal stock to all later hominins. In just one field season, *A. afarensis* offered clarity to the longstanding question of whether the molecular clock really worked. In other arenas, many were convinced that no more than a single hominin species could have existed on earth at any given time, especially after the lumpers were finished with the fossils. This single species concept resembled earlier tendencies to perceive human evolution as being unique among mammals, but in fact, it fell short of accurately describing the nature of the variability observed in the human fossil record.

Over the next twenty-five years, hundreds more fossil human discoveries will offer fuel to feed the fires touted by contemporary lumpers and splitters. Although contemporary research and concepts quickly negated the single species hypothesis, they did little to clear up issues of modern human origins. In its place comes the long-winded debate of Multiregional Evolution versus the Out of Africa hypothesis. The Out of Africa theory firmly argues that all modern humans descended from a single African population. This is often referred to as the Mitochondrial Eve theory by some, because genetic tests were used to derive the time frame in which these African descendants would have replaced all other extant humans—a continuation of research similar to that started with the protein molecular clock. On the other hand, the Multiregional Evolution hypothesis argues simply that no one single ancient population is responsible for the origin of modern human populations.

Despite minor differences of opinion, it is clear that the human fossil record is not unique when compared with the evolution of other mammalian taxa. Hominid phylogeny is richly diversified, comprising numerous genera and multiple species—in upwards of eighteen different species—some of which shared ecological niches in both time and space. At present the multiethnic varieties of modern humans occupy the only surviving branch of what appears to have been a densely bushy phylogenetic shrub in the past (see Figure 1). Until very recently, the oldest hominins known were dated to 4.5 million years ago. However, newly announced fossil discoveries from East Africa may now extend our evolutionary history back in time to 6 million years ago. The human fossil record, which is discussed in some detail below, provides ample evidence of a rich biodiversity with multiple branching events coinciding with several extinctions. Recent modern humans just happen to occupy the last branch of a dying tribe. The worst possible reality for anyone to grasp is that extinction is inevitable, and we are the last of the hominins.

Orrorin tugenensis. Announced in 2001 by a joint Kenyan and French team, thirteen fragmented fossils belonging to at least five individuals were collected from four localities in the Tugen Hills of Kenya. Fossils include a few teeth, fragmentary leg, and arm and hand bones. Sedimentary analyses indicate an age of 6 million years, making this the oldest known fossil human. The paleoenvironment is reported as having been open woodland at the time of deposition, with patches of dense forest. Many remain skeptical because of the fragmentary nature of the fossils, as well as the reported geologic age.

Ardipithecus ramidus. Initially announced in 1994 as *Australopithecus ramidus* by a joint Ethiopian and U.S. team, this group of fragmentary fossils was renamed *Ardipithecus* in a brief erratum in a 1995 issue of *Nature*. Very little is known about this group, except that it was collected from the Middle Awash region, Ethiopia, and is reported to have thin enameled dentition and bipedal capabilities. Initial response suggests that this group is not a direct ancestor to later hominins. Initial sedimentary analyses indicated an age of 4.4 million years. A more recent and interesting announcement by an Ethiopian team member in 2001 extended *Ardipithecus* into the Miocene at 5.8 million years ago. Eleven specimens were collected, and they are purported to exhibit enough dental variability to name a new subspecies *A.r. kadabba*—thought by most to be nothing short of suspiciously miraculous. The paleoenvironment appears to have been woodland.

Kenyanthropus platyops. Announced in 2001 by joint Kenyan and British teams, this find consists of a largely complete reconstructed cranium (and two previously collected mandibles) collected from the Nachukui Formation near Lomekwi, West Turkana, Kenya. Sedimentary analyses indicated an age of 3.5 million years and a paleoenvironment of mosaic habitats, but predominantly woodland.

Kenyanthropus rudolfensis. Formally known as *Homo rudolfensis*, fossil cranium ER 1470 appears to share many facial characters with *K. platyops*. Discovered in the late 1970s, 1470 was initially thought to be a male member of *Homo habilis* dated at 1.8 million years ago; it has a cranial capacity of 750 ml. Other habiline finds prompted researchers to reassign this peculiar specimen to a different taxon (*H. rudolfensis*). Always considered a morphological sore thumb, when platyops was announced, researchers were quick again to accept the *Kenyanthropus* assignment.

Australopithecus anamensis. Announced in 1994 by a joint Kenyan and U.S. team, fragmentary fossils were collected from Allia Bay and Kanapoi localities in Kenya. Fossils include partial maxillae, mandibles, and proximal tibia. Dated at 4.2 million years ago, this species exhibits many primitive traits, making it a welcomed precursor to *A. afarensis*.

Australopithecus afarensis. Initially announced in 1978 by an international team, this group of hominins was collected from the Afar and Middle Awash Region, Ethiopia, and Laetoli, Tanzania. Fossils now include several jaws and teeth, largely complete crania and partially complete individuals (including the famous “Lucy”), as well as several individuals of mixed age and sex from the same site; they are considered a family unit catastrophically killed by flood. Sedimentary analyses indicate a lake and wooded paleoenvironment dated to 3.2 million years ago. Postcranial material suggests bipedal capabilities, and fossil footprints from Laetoli found in 1976 by Mary Leakey support bipedal behavior. Also helped to show that Darwin was wrong about big brains preceding bipedalism.

Australopithecus bahrelghazali. Announced in 1996 by a joint French and British team, a fossil mandible from this group was collected from Bahr el Ghazal, Chad. Only a partial mandible exists, dated to 3.4 million years ago. Very little is known about this specimen, except that it extends the known range of human ancestors westerly a few thousand kilometers.

Australopithecus africanus. Announced in 1925 by Raymond Dart, a subadult partial face and natural endocast were collected by miners from the Taung cave, South Africa. The Taung child holds the distinction of being the first australopithecine named. This group is known from several hundred fragmentary and partial crania, and the largely complete Sts 5—(so-called Mrs. Ples.)

Australopithecus garhi. Announced in 1999 by an international team, fossils were collected from the Middle Awash Region of Ethiopia. Fossils include partial crania, fragmentary limb bones, and several teeth. Sedimentary analyses indicate freshwater lake and open woodland, dated to 2.5 million years ago. *A. garhi* receives the distinction of being the oldest hominid associated with stone tools and cut-marked bone.

Australopithecus (Paranthropus) aethiopicus. Initially announced in 1968 by a French team, a toothless fossil mandible was collected near the Omo River in the Shungura Formation; taxa currently recognized for a largely complete skull collected from West Turkana, Kenya, in 1985 by an international team. The fossil, known as the "black skull" because it is stained by manganese-rich minerals, is striking for its tall sagittal crest and projecting face.

Australopithecus (Paranthropus) robustus. Initially announced in 1938 by Robert Broom, an adult partial fossil skull was collected at Kromdrai, South Africa. This species distinction is related to Broom's tracking down a schoolboy who had found a molar that raised Broom's interest. Because of dating difficulties with South African dolomite caves, the estimated age for this species is 1.5 to 2 million years. This species is known from hundreds of fragmentary specimens, as well as fairly complete crania and mandibles with dentition.

Australopithecus (Paranthropus) boisei. Announced in 1959 by Louis and Mary Leakey, a fossil was collected from Lower Bed 1, Olduvai Gorge, Tanzania. A massively built cranium with huge teeth (similar to those of *A. robustus*), this fossil was initially called *Zinjanthropus* (Arabic/Greek for East African Man), species nomen, pertaining to a colleague funding the project. Students of paleoanthropology know this fossil by the nickname "nut-cracker man," because of its huge cheek teeth. Dated to 1.8 million years ago, Olduvai Gorge was thought to be lake margin at the time of deposition.

Homo habilis. Announced in 1964 by Leakey and others, this fossil group was collected in Lower Beds at Olduvai Gorge, Tanzania, and East Turkana, Kenya. Fossils include complete crania and dozens of jaws and teeth. A partial individual collected much later by a U.S. team provides evidence for a more boreal way of life than previously predicted. Fossils are distinguished from those of other *Homo* fossils by the small size of the cranium and by dentition. Once thought to be the female to ER 1470. Cranial capacity is not more than 600 ml.

Homo ergaster. Fossils previously touted as *Homo erectus* were collected from East Africa in 1976 and 1985 (and maybe South Africa in 1969 from a museum find). Fossils include two complete adult crania and a fairly complete subadult individual collected from East and West Turkana, Kenya. The subadult has the distinction of being the most complete fossil human discovered from Africa.

Homo erectus. Initially announced in 1892 by French doctor Eugene Dubois working for the Dutch East Indies Company, this group has a rich history. Known from dozens of skull caps and partial mandibles from China and Java, a wide range of environments are reported for *H. erectus*. It is dated between 1.8 million years ago and 53,000 years ago. Many remain skeptical regarding the dates. Moreover, many feel that *H. erectus* is a taxonomic dumping ground, meaning that it has too wide a range of variability in skeletal morphology to be just one species. Distinction

Skull of a* Homo neanderthalensis *found in the Bouffna Bonneval Cave in the Sourdoire River Valley near the village of Chapelle-aux-Saints, 40 km southeast of Brive-la-Gaillarde, Correze, France. The skull is commonly called "La Chapelle" and is dated to about 40 thousand years ago. (KAREN/CORBIS)

for Peking Man fossils were lost during World War II. The only thing left are fossil casts made by Franz Weidenreich prior to the Japanese invasion of Peking.

Homo antecessor. Announced in 1997 by a Spanish team of researchers, this species is thought by some to be the common ancestor to modern humans and Neanderthals. Their species diagnosis is based primarily on a unique combination of craniodental traits that collectively are different from those of other known *Homo* fossils. These include a combination of primitive and derived "modern" features that show none of the derived features of later Neanderthals. So far, the fossils representing this species all come from a site called Gran Dolina in Spain, and they date from about 800,000 years ago.

Homo heidelbergensis. Discovered in 1907 by a workman at the Mauer quarry in Heidelberg, Germany, the type specimen for this species is the Mauer mandible. Fossils included in this species are found in both Europe and Africa and date to the Middle Pleistocene, ranging from about 500,000 to 250,000 years ago. Some researchers have proposed that *Homo heidelbergensis*, more primitive than modern humans and lacking many derived features of Neanderthals, represents the common ancestor to both modern humans and Neanderthals. However, with the discovery of *Homo antecessor* fossils, its phylogenetic position is currently being debated.

Homo neanderthalensis. Announced in 1864 by William King, a partial fossil skeleton was collected from inside a small cave situated about 45 feet above the Düssel River in the Neander Valley, Haan, Germany. The discovery was made in the summer of 1856 by two quarrymen. The Neander fossil became the type specimen of a newly recognized extinct human species, *Homo neanderthalensis*. Neanderthals lived approximately 150,000 to 30,000 years ago in a variety of temperate paleoenvironments. Since William King's taxonomic assessment, numerous other fossils found throughout Europe and the Middle East have been attributed to this species, including those previously discovered from Engis in 1830 and Gibraltar in 1848. Important advances in ancient nuclear and mitochondrial DNA analyses have provided solid genetic support for what William King had proposed more than a century earlier—that Neanderthals are taxonomically distinct from modern humans.

Homo sapiens—Nosce te ipsum.

—*Ken Mowbray*

See also: *Homo Sapiens;* Physical Anthropology; Primates; Great Apes

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Humans and Biodiversity: Examples from the Hoofed Mammals

Mammoths and Mankind

Coevolution with *Homo sapiens* proved adaptive for large hoofed mammals. As humans spread out and populated the earth, megafauna outside of Africa rapidly went extinct. Some twenty species of mammoths lived for about 4 million years. They thrived in Eurasia and North America until a sudden global extinction event occurred, approximately 10,000 to 12,000 years ago, overlapping with human migration into North America. In the Americas, the Ice Age ungulates—megafauna including mastodons, woolly mammoths, and giant bison—died out shortly after the first humans moved into the hemisphere from northern Asia. This fact suggests that they were possibly hunted to extinction. The New World megafauna's extreme vulnerability to human predation may have been partly the result of their having evolved, like the dodo in Mauritius, in the absence of any natural predator species. Thus they never learned to fear man: "They did not have that aversion to our two-legged profile that seems to be part and parcel of every single large African mammal's take on life" (Eldredge, 1998, pp. 35).

American Museum of Natural History paleomammalogist Ross MacPhee, postulating that the mammoths were as well adapted to survival as are modern elephants, hypothesizes that a "hyperdisease" could have been the real agent responsible for their sudden dying off. Mammal extinctions as a whole were distributed unevenly, with far greater losses occurring outside of Africa and Eurasia. MacPhee reasons that neither the brief period of human predation nor massive climate change alone can fully account for the sudden, simultaneous, widespread, and thorough mammoth extinction event. Since even small numbers of surviving mammals can rebound from sharp population decreases within a few generations, he theorizes that megaherbivores like the mammoth could have been the victims of a deadly, highly contagious disease, perhaps something like the recent outbreak of Ebola virus, with humans or human-associated hosts acting as vectors bearing the lethal pathogens into new environments. This model, which might explain the rapidity and ubiquity of the mammoth extinction, has yet to be fully tested against competing hypotheses.

Ungulate Hunting and Pastoralism

Throughout prehistory and history, human interactions with hoofed mammals (or ungulates) including deer, horses, cows, pigs, llamas, buffalo, sheep, and goats have been more consequential for both mankind and the environment than those with any other group of animals. In ancient Egypt, domesticated cattle were kept for their milk and as draft animals, while large herds of grazing ungulates roamed freely in the Nile River delta. Beef consumption was reserved for the elite, except on ceremonial occasions, while sheep, goats, and pigs were raised for their meat. Pastoralism was a practical solution to desertification in northern Africa, even though ancient livestock was frail and thin compared with modern breeds, readily succumbing to environmental stresses. Milk rather than meat was the staple protein for most of the annual cycle. Pastoralism evidently became an important means of human survival in the Sahara Desert some 7,000 or 8,000 years ago. Cattle, sheep, and goats were imported by herders migrating from the once fertile crescent of southwestern Asia and Arabia, areas that had become desiccated at an earlier period. Pastoralism in Africa was largely limited to open savanna areas, since the heavy canopy in equatorial forest shut out sunlight, preventing the growth of the grasses necessary for foraging. Farming on the scale of Eurasian agriculture was simply not possible under these environmental conditions.

South of the Sahara, the raising of cattle was at first limited to regions without the blood-sucking tsetse fly, common in the forest boundary zones, which spread trypanosomiasis. But in modern times, eastern and southern African societies are widely characterized by what anthropologists call the cattle complex. Cattle serve important socioeconomic functions, not only in providing milk, meat, horn, and hides but also as property, bridewealth, and an instrument for the maintenance of kinship ties. Dependence on cattle complexes has occasionally led to disastrous consequences for humans, however, along with the benefits. During the 1890s a historic epidemic of rinderpest, a deadly viral cattle plague carried by beasts imported from India, struck and killed some 90 percent of domesticated cattle and buffalo, as well as many of the wild ungulates then extant in southern Africa; it led to economic collapse and widespread famine. The San people of Botswana found that the cattle industry, supported by European colonialists, encroached on their wild grazing lands, which were converted to pasture for domesticated livestock. During the 1950s more than 60 percent of the remaining big game in Botswana's Kalahari region, including wildebeests and hartebeests, perished (ibid., pp. 37–39). The ecological pressure of roaming livestock grazing on open land has nearly wiped out the indigenous ecosystems of the Okavango delta, as cows crowd out the once plentiful herds of elephant, buffalo, and red lechwe (ibid., p. 4). Modern Kalahari people descended from the historical intermingling of Khoekhoen (Khoikhoi, or Hottentot) herders and San hunter-gatherers are designated by the anthropological term *Khoisan*. Today, most Khoisan people in the Kalahari have adapted to herding and agriculture, with only about 5 percent still subsisting primarily by hunting and gathering.

The North American Great Plains, this continent's largest biome and today one of the world's most abundant granaries and cattle pasturages, was the ancestral home of large herds of bison (also known as American buffalo). Estimated at some 30 million in 1800, the bison were nearly destroyed in a period of just fifty years. During the nineteenth century the expanding Euroamerican fur trade grew increasingly dependent on Indian hunters providing food and hides for the influx of settlers. The introduction of guns, diseases, and new markets for leather products in eastern North America upset the ecological balance traditionally maintained by native peoples and quickly led to the demise of the bison or American buffalo in the West (ibid., pp. 35–36). By the end of the nineteenth century, the great bison herds of the Plains had diminished to fewer than 1,000 animals.

The horse is indigenous to North America, but it had long been extinct on the continent when it was reintroduced by the Spanish conquest of Mexico in 1519. West of the Great Lakes, the Indians upon whom the fur traders would come to depend began hunting bison on horseback. Horses were used to advantage in war, as well as in hunting and for transportation, communication, and trade. Those cultures with horses consequently became highly mobile and expansive, as their herds increased. In the Southwest, the Apache obtained horses sometime after 1630. Another seventy years would pass before they began supplying horses to the Comanche and Ute. Horses spread northward from the Plains during the early part of the eighteenth century as Shoshonean peoples traded them to the Blackfoot (Siksika), and the Kiowa obtained them from the Comanche. The Lakota, the first mounted hunters to shoot bison with guns, used the military advantage conferred by the combination to gain control of the northeastern plains.

Anthropologist Julian Steward's influential theory of cultural ecology emphasized the role of adaptation to the environment in causing cultural change, while stopping short of an absolute environmental determinism. Thus, by changing their way of life, Shoshonean peoples, who had previously lived in small hunting bands, were able to amalgamate their tribes and become successful warriors, following the acquisition of horses and the occupation of their lands by Euroamericans (Steward, 1955). Martin (1987) ran simulations of the populating of the New World showing that in prehistoric times, Paleoindians had quickly hunted the American megafauna to extinction, but attributing the much later demise of the American buffalo solely to the incursion of whites into Indian territories. This has become the generally accepted view of the herds' demise. However, Isenberg (2000) and Krech (2000) recently reconsidered the destruction of the bison, arguing against the romanticized image of Indian societies having lived in perfect ecological balance prior to the invasion of the white man. Diamond (1999) has mapped out the major role played by the introduction of germs, evolved inside domesticated Eurasian livestock serving as hosts and carried with them across the Atlantic, in the European conquest of indigenous societies in both the Old and New Worlds.

Reindeer and Caribou

The Eurasian reindeer and the North American caribou are actually varieties of a single species, *Rangifer tarandus*. The semidomesticated reindeer and the more wild caribou exhibit some differences in appearance and behavior. On both continents herds fall into three major groupings selectively adapted to marine, tundra, and forest environments.

Reindeer provided a major part of the Upper Paleolithic diet for tens of millennia. They were first domesticated in Eurasia more than 7,000 years ago. Their thick hair and wide hoofs are well adapted to the cold, snowy environment of the Arctic. They conserve body heat and energy through their consumption habits of eating less and shedding excess weight during the long winters. The reindeer's preference for a low-mineral diet of lichens and snow enhances its water-retention capacity, decreases thirst, and conserves body heat by eliminating the energy expenditure inherent in long treks in search of drinking water.

In prehistoric times, the ancestors of today's indigenous Saami (or Lapp) people of Scandinavia and northwestern Russia hunted wild reindeer, tracking the herds northward as the continental ice shelf retreated. During the 1500s, with the wild herds diminishing and migrant human populations exerting pressure from the south, Saami herders moved into the mountainous tundra and tended their domesticated stocks as pastoral nomads. Reindeer provided for many of their basic subsistence needs. The twentieth century brought a movement toward cash commoditization as government economists using efficiency models attempted to reorganize the reindeer husbandry industry along modern production lines. In Sweden the number of herders is now tightly restricted, and the descendants of Saami who have turned to other means of livelihood are legally barred from returning to their ancestral occupation.

At the time of the 1986 Chernobyl nuclear accident in the Soviet Union, some 7,000 Saami people in Finland and Scandinavia still made their living by herding a half-million reindeer. This traditional ecology and mode of economic life was already threatened when the windborne release of radioactive elements over northern Europe created a catastrophic situation in the hardest hit areas of central Sweden and Norway, contaminating berries, fish, animals, and milk. Lichens, the rootless organisms that are the main fodder of grazing reindeer, are entirely fed by airborne nutrients and therefore especially absorbent of radiation. Reindeer herds were relocated to safer areas and slaughtered at normal levels, but the contaminated meat was not fit for human consumption (Stephens, 1987). Reindeer products remain inedible more than fifteen years later, as the economic and lifestyle pressures on Saami herders continue to mount.

Rangifers were introduced into western Alaska during the 1890s, when Presbyterian missionary Sheldon Jackson, observing starvation among the Inupiat people, organized a U.S. federal government assistance program for the importation of Siberian reindeer and the training of native apprentices by immigrant Saami herdsmen. In fact, the historical evidence suggests that starvation was not particularly rampant in Alaska and that there was no pressing economic need for reindeer herding. But the discovery of gold near Nome at the turn of the century and the ensuing Gold Rush created a market demand for Rangifers to be used as draft animals. An incipient Eskimo aristocracy arose, in which a local woman known as Sinrock Mary became for a time the largest herd owner and the most powerful economic player in Arctic Alaska. From 1915, large seasonal gatherings of people and animals known as reindeer fairs flourished for a few brief years, until the devastating influenza epidemic of 1918. When the Gold Rush subsided and the attendant economic boom collapsed, there was little incentive remaining for native people to continue the commercial enterprise of reindeer herding. However, with efficiency reforms in management on terms somewhat more favorable to the natives, the number of Alaskan reindeer continued to increase to a high of some 640,000 at the beginning of the 1930s. With growth came the problems of overstocking, increasing neglect by herders, carnivore predation, and the loss of domesticated animals through attrition when they went feral, joining wild herds of wandering caribou. A drastic decline in the

Alaskan reindeer population ensued, their numbers falling rapidly to 250,000 by 1940 and to 25,000 by 1950 (Olson, 1969).

Meanwhile, in the modernizing Soviet Union, native reindeer trackers living a subsistence hunting life were organized into cooperative herding brigades by the state. They gradually found their livelihood and culture threatened by government-mandated boarding schools that took their children away from the tundra for most of the yearly cycle, and by the increasing social undesirability of the lonely nomadic life, with its hardships and deprivations. With the Soviet system's collapse in the early 1990s came the economic failure of the reindeer brigades. As large-scale husbandry became less viable for native people, large numbers of reindeer were exterminated in the Transbaikalia region. In the first decade of the post-Soviet era, the movement for native Evenk autonomy and land reform has somewhat improved the prospects for Rangifer survival. At the end of the twentieth century, the falling number of semidomesticated reindeer in the Russian Federation stood at some 1.5 million, while the rising number of wild reindeer reached 1.3 million (Circumpolar Ph.D. Network in Arctic Environmental Studies).

The Future of Hoofed Mammals

The number of reindeer and caribou will in all likelihood continue to fluctuate dramatically from year to year with seasonal variations, local climatic conditions, and development projects. The outlook for maintaining traditional reindeer husbandry in northern Russia remains precariously dependent upon the perpetuation of a delicate balancing act weighing national economics and ecological preservation with the social rights and responsibilities of the thirteen aboriginal peoples presently engaged in the traditional occupation. For the Gwi'chin of northwestern Canada—as for the Evenk of northeastern Siberia—although they no longer depend solely on caribou for sustenance, their traditional way of life and cultural identity are integrally tied to the ecology of Rangifer herding. The prospect of new oil and mineral exploration and pipeline construction in the Arctic may threaten the annual migration route of the Porcupine River caribou herd in the Northwest Territories, a possibility that the Gwi'chin are lobbying against. Scandinavian reindeer herds exposed to radiation from Chernobyl will probably remain tainted by high levels of radioactivity for years to come. New initiatives in international scientific and governmental cooperation seek to integrate indigenous, private, and governmental methods of herd management for optimum sustainability throughout the circumpolar north.

In 1997, Dolly, the first cloned sheep, was created in the laboratory by substituting the genetic material of one sheep's egg cell nucleus for that of another, followed by implantation in the uterus of a surrogate mother. With the genomic revolution underway, the idea that extinct species might be cloned for future reintroduction is currently the object of much speculation. However, the improbability of even the most well preserved ancient DNA remaining viable makes the challenge of reviving extinct species far more problematic than that of cloning living animals. Russian and native northern scientists are engaged in attempts to clone a live mammoth using genetic material taken from Dima, a frozen baby mammoth unearthed in northern Yakutia, and other Siberian fossil deposits found in remote areas of the Taimyr Peninsula, Wrangel Island, and the Kolyma River basin. They hope to attain a live birth by stripping an elephant egg of its genetic material, replacing it with mammoth DNA, and implanting the egg into a female elephant. If this process should ever become feasible, their plans call for the resulting animals to be kept in a zoological park and eventually allowed to roam free in herds grazing on the steppes, filling the approximate ecological niche of the ancient megafauna. Based in part on the ecological model of the former bison cultures in the American West, these apparently quixotic efforts to restore the Pleistocene "big hairies" in Siberia are aimed initially at creating a "Jurassic Park" style tourist attraction, and ultimately at revitalizing the indigenous hunting cultures of the tundra. However, most Western scientists still firmly believe that the deterioration and fragmentation of ancient genetic material, along with many other formidable obstacles, render cloning the mammoth a distant, farfetched dream at best, and in all likelihood an outright impossibility.

The history of human introduction of exotic ungulate species to new environments is rife with cautionary lessons. Many imported animals have subsequently adapted all too well to their adopted ecosystems, destroying habitats and driving out endemic species. Mountain goats (*Oreamnos americanus*) imported to the mountain ranges of Washington's Olympic Peninsula during the 1920s were so successful at colonizing the territory that efforts are now being made to eradicate them from Olympic National Park. Barbary sheep native to North Africa were introduced to New Mexico during the 1950s in the hope of providing big game animals to serve as prey for sport and trophy hunters. They soon decimated the local plant life and threatened to spread parasites to other hoofed mammals, including ranchers' domestic livestock and the endemic Rocky Mountain bighorn sheep (Laycock, 1966). However, ungulate importations do not always lead to failure or ecological disaster. Today, for example, imported musk oxen are thriving at an experimental station run by the University of Alaska in Fairbanks; they may someday be released into the wild.

Domesticated livestock coexisting with human society is subject to culturally varied modes of exploitation and protection. Among Hindus in India, according to religious custom cows are sacred and protected from slaughter. Throughout the world, observant Muslims and orthodox Jews adhere to religious taboos banning the consumption of pork, while among indigenous peoples of New Guinea pigs are important forms of wealth and signs of prestige, conferring socioeconomic status on their owners. The industrial revolution wrought profound ecological and socioeconomic changes in nineteenth-century England and Scotland with the large-scale enclosure of formerly common lands for private sheep pasturage, to supply wool for rapidly expanding textile production. The displacement of peasants and rural smallholders from crop land to make way for livestock gave rise to the mournful popular saying that "sheep eat men." Strategies of rural development and production comparable to the enclosure movement in method if not in scope were applied to colonial India by British administrators, with long-range ecological and socioeconomic consequences that are still being felt at the turn of the twenty-first century.

New dangers associated with growing human dependence on hoofed mammals, including threats to human and animal health, continue to arise. During the 1990s, bovine spongiform encephalopathy (popularly known as mad cow disease) appeared in the United Kingdom, evidently as a result of the cost-cutting practice of cannibalistic feeding. This modern cattle plague is now threatening the European mainland and could soon appear on other continents. In 2001 an outbreak of contagious hoof-and-mouth disease necessitated the massive extermination of sheep in England and Scotland to halt the spread of the epidemic, a financially ruinous development for farmers and shepherds.

The nutritional benefits of the additional protein supplied by a diet rich in beef products may be offset in the long run by the tremendous resource expenditures needed to keep pace with the consumption patterns of a rapidly expanding global population. With millions of people—especially in the industrialized West—relying on cattle for meat and milk, more and more grassy rangelands will be required to raise more and more animals. The pressure for clear-cutting rain forests to make room for grazing acreage intensifies as a hungry population continues to increase in numbers. The huge amounts of land and biomass required for animal fodder could be far more efficiently utilized to raise soybeans and other much less energy-intensive crops. Other environmental side effects of ungulate overbreeding, such as a massive increase in bovine methane gases with the potential to significantly accelerate atmospheric global warming, are already ensuing. In the age of globalization and fast food, the ecological pressure exerted on the earth by the voracious human need for grasslands to sustain large herds of hoofed mammals is only likely to increase.

—*Thomas R. Miller*

See also: Alien Species, Introduction of; Artiodactyls; Coevolution; Cultural Survival, Revival, and Preservation; Extinctions, Direct Causes of; Herbivory; Land Use; Lichens; Mammalia; Mass Extinction; Order Uranotheria; Subsistence

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Hutton, James

Many historians credit the eighteenth-century Scottish geologist James Hutton with introducing the concepts of actualism and deep time to geology. Actualism is the assumption that the earth's past can be explained in terms of natural processes observable in the present. Deep time—stretches of hundreds of millions of years—pushed the geological time frame radically beyond the 6,000 years that theologians had allotted. Almost half a century after Hutton published the first edition of his *Theory of the Earth* (1788), another Scot, Sir Charles Lyell, made actualism the keystone in his cluster of ideas later known as Uniformitarianism—the foundation of modern geology. Lyell, in turn, became a major influence on Charles Darwin, who applied the notion of small, steady changes acting over immense periods of time to the evolution of life.

Born in 1726 in Edinburgh, James Hutton was apprenticed to a lawyer while in his teens, but he was constantly disrupting the law office with amateur chemistry experiments. His strong bent for science led him to medicine, which was the only scientific profession recognized at the time. After earning an M.D. from the University of Edinburgh, he then pursued studies in chemistry and medicine in Paris and Leyden. After returning to his home city, Hutton's efforts to establish a practice were thwarted by a clique of older physicians, and he decided to earn his living as a "scientific" farmer and chemical manufacturer instead. He also became known as a leading light among Edinburgh's brilliant natural philosophers.

Studying rocks on his own farmland and in the volcanic hills around Edinburgh inspired Hutton to tour Europe and northern Scotland to study granite formations and mines. Since his three sisters ran his household like clockwork, he had time to write, conduct experiments, and spend long evenings with his cronies, who included the geologist and mathematician John Playfair (1748–1819) and Joseph Black (1728–1799), a physician who was one of the founders of modern chemistry.

Hutton's two-volume version of his *Theory of the Earth; or an Investigation into the Laws Observable in the Composition, Dissolution, and Restoration of Land upon the Globe*, published by the new Royal Society of Edinburgh in 1795, blasted the catastrophist tradition, which held that the earth's history was a series of cataclysms or upheavals unlike anything known today, caused by drastically different processes.

As far as Hutton was concerned, geologists should not attempt to theorize about "the origin of things," since we can only attempt to understand processes that we can observe (Lyell, 1854). Field geologists could see for themselves that the earth was in a constant state of change. Floods eroded hillsides, weather cracked and crumbled rocks, and avalanches changed the shape of mountains. A history of past depositions, upheavals, and erosions could be read in so-called unconformities—fossil surfaces of erosion, gaps in time separating two episodes in rock formations. Some sequences of strata or deposited layers, he recognized, had been tilted or upended by later earth movements. Hutton was also the first to correctly understand how metamorphic rocks were formed from sedimentary ones by compression. He did not, however, believe that all these processes acted to evolve the world or modify it in any particular direction. Instead, he saw the building and wearing down of geological features through such processes as deposition of sediments, intrusion of lava, and erosion by wind and water as part of the steady maintenance of a planet that has "no vestige of a beginning, no prospect of an end" (cited in Gould, 1987). He believed that time and geological events moved in great cycles,

James Hutton inspects a rock outcropping. (Corbis)

and that the "purpose" of it all was to sustain life—with human dominion over all other forms of life.

Hutton was a poor writer, whose key ideas were often lost among his meanderings and repetitions. He was lucky, however, in his choice of friends. John Playfair interpreted and summarized Hutton's discoveries in *Illustrations of the Huttonian Theory of the Earth,* a small and very readable book published in 1802, five years after Hutton's death. Playfair's successful popularization kept his friend's ideas alive; a few decades later, they inspired Charles Lyell and Charles Darwin to revolutionize the natural sciences.

—*Richard Milner*

See also: Deposition; Geological Time Scale; Lyell, Charles

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Hydrologic Cycle

Heat from solar energy causes water to evaporate off the surface of the sea and the land. The vapor rises and condenses to form clouds from which rain and snow fall back to the surface. On the land, rivers return the water to the sea to be evaporated once again. The endless cycle is called the hydrologic cycle. When rain falls to the surface, some of it is immediately evaporated back to the atmosphere, a portion flows into streams, and the rest soaks into the ground. How much water goes to each depends on temperature, humidity, and the nature of the soil and bedrock. The portion that moves underground through soil and rock may enter aquifers (underground reservoirs), where water may take decades or more to be returned by seeping into streams and lakes and then to the atmosphere or the sea. However, some water that soaks into the soil may be utilized by plants and is returned to the atmosphere by transpiration, the loss of water through leaves. Studies have shown that transpiration contributes more water to the atmosphere than does direct evaporation from lakes, rivers, and soils. In many places snow usually melts and evaporates, returning the water quickly to the atmosphere; but in colder climates some snow remains and may be converted to glacial ice, where it is reserved for hundreds or thousands of years. If all of the glacial ice on earth were to melt, sea level would rise about 240 feet.

One important aspect of the hydrologic cycle is that the evaporative process purifies water. All of the materials in water—whether they are sea salts, clay particles, micro-organisms, or dissolved materials—are left behind. However, as water condenses and precipitates, it may pick up pollutants on the way down, and after reaching the surface may dissolve additional unwanted chemicals on or below the ground.

—*Sidney Horenstein*

See also: Atmosphere; Climatology; Freshwater; Lakes; Oceans; Rivers and Streams

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I

Ice Caps and Glaciers

Glaciers are masses of ice in motion that move slowly over the surface of the earth, under their own weight and through the action of gravity. For a glacier to form there must be sufficient precipitation, and it must be cold enough for the snow and resulting ice to remain throughout the entire year; that is a function of latitude and altitude.

The formation of a glacier is similar to the formation of a monomineralic metamorphic rock (a rock made of one essential mineral). Minerals are naturally occurring, crystalline, inorganic substances with a usually precise composition. Snowflakes clearly fit the definition: their composition is H_2O, they form hexagonal crystals, and they are naturally occurring. Snowflakes accumulate as a fluffy mass of loose crystals, similar to the way in which sediments are deposited on the seafloor. Instead of having water trapped between the grains, however, snowflakes contain air.

As more snow falls to the surface the overlying snow presses down, forcing some of the air out and causing the points of the flakes to melt. The resulting water tends to migrate and refreeze toward the center of the flake, producing rounded grains called firn. These granular particles stick to each other as the melting and refreezing process continues, forming a mass similar to a sedimentary rock. With further snowfall and pressure more air is driven out, gradually transforming firn to a metamorphic rock, glacial ice, a rock that has been formed by the addition of heat and pressure and contains interlocking crystals of ice. The ice has a blue color because all of the other colors are absorbed and only blue is reflected. This process of ice formation may take a few years or hundreds of years or even more, depending on the amount of melting and recrystallization and snow accumulation.

When the ice mass grows large enough in weight and thickness to flow down slope, it is called a glacier. Glaciers generally move slowly, perhaps 15 m a year, a speed that cannot be seen while standing in front of the ice front. However, some glaciers, especially those that are not frozen to the underlying rocks, can surge forward at 10 km a year, lubricated by water at their base.

Glaciers are classified by their size and where they occur. As the term describes, alpine glaciers, also known as valley or mountain glaciers, are found within mountain valleys. Where several alpine glaciers emerge from adjacent valleys onto a plain in front of the mountain, they coalesce forming a piedmont glacier like the Malaspina Glacier in Alaska, which is larger than Rhode Island. Large glaciers that cover parts of large land masses but are 50,000 square kilometers or less in size are called ice caps, while large ice masses are termed ice sheets and are usually a kilometer or more in thickness.

A glacier is not a rigid mass of ice. Glaciers behave more like warm wax, or thick honey or molasses, slowly moving at different rates within different levels of the ice mass. As a glacier travels down a valley its flow is retarded at the sides and bottom of the ice where it is in contact with bedrock. But within the glaciers the flow is not held back, and it flows more rapidly. Ice caps are so thick that the bedrock usually does not play an important role. They flow from the higher parts of the ice to their periphery, from the thicker part, to the thinner edge even on a flat surface. If you pour molasses, or almost any other liquid, note how it spreads away from the center. When you increase the pouring rate the speed of the flowing molasses will also increase. Ice caps behave in a similar way.

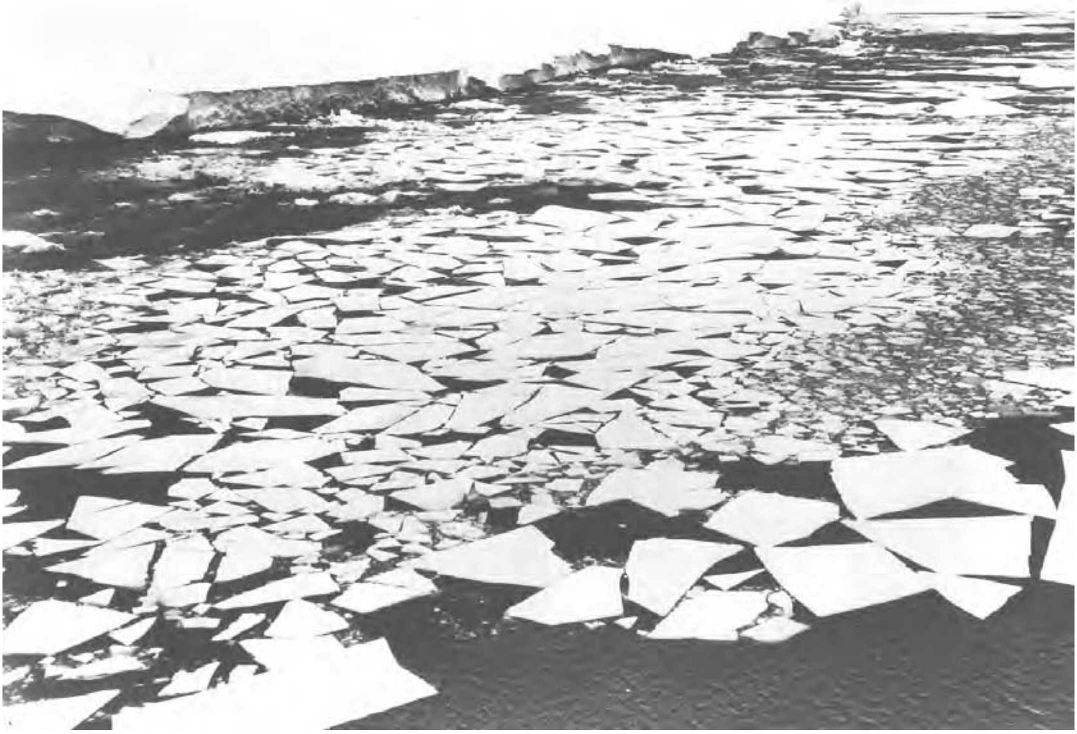
Many glaciers develop crevasses or cracks as they flow over an irregular bedrock configuration. Glaciers terminate where melting and evaporation, termed ablation, is equal to or greater than the forward motion of the ice: it has gone as far as it can under the current climatic conditions. Where glaciers enter the sea, they break off in pieces as a result of the up and down movements of the tide and the crevasse pattern. This calving process gives rise to the icebergs that float with the currents in the northern and southern seas and are a hazard to ships. The number and range of icebergs are determined by climate; during the Little Ice Age, 1540–1890, they were able to float farther away from polar areas than they do today.

The ice sheets on Antarctica and Greenland contain about 75 percent of the freshwater on earth, an amount equivalent to about sixty years of worldwide precipitation. If the earth continues to heat up this resource will be lost, most of it mixing with seawater and becoming unavailable for human consumption. In addition, complete melting will cause sea levels to rise 80 m worldwide, drowning most coastal cities.

The Greenland ice sheet covers about 80 percent of Greenland's land mass and has an area of about 1,800,000 square kilometers, containing some 2,620,000 cubic kilometers of ice that is more than 3,200 m thick at the center of the island. This accounts for 8 percent of worldwide ice, and if all of it melted it would raise sea levels by about 6.5 m. The mass of ice flows from the center toward the perimeter of Greenland, where it encounters high mountains at its periphery, forcing the ice sheet to squeeze through narrow valleys to the sea, where they calve and produce most of the icebergs of the North Atlantic.

On the other hand, ice on Antarctica covers about 90 percent of the continent, about 13,586,000 square km, and in places it is more than 4,200 m thick. As a result there are 30,109,800 cubic kilometers of ice, a little more than 91 percent of the total. If it all melted, it would cause sea levels to rise by 73.44 m. Bedrock configuration mapping shows that the land below the ice is mountainous, and because of the weight of the ice, parts of West Antarctica may be 2.5 km deep. In a number of places the ice has flowed into the sea as a contiguous mass, forming an ice shelf that floats in the sea. The Ross Ice Shelf is about the size of the state of Texas and approximately 400 m thick.

The rest of the ice, valley glaciers, and ice caps cover 680,000 square km and have a volume of 180,000 cubic kilometers; if it were to melt it would cause sea level to rise about a half-



The edge of the Ross Ice Shelf, Antarctica (broken up by a U.S. Coast Guard icebreaker during the Byrd expedition), 1947 (Library of Congress)

meter. Nevertheless, at this time about 80,000 glaciers have been inventoried, and some estimates indicate that there may be twice as many.

It has been suggested that rapid melting of glacial ice can cause the thermodynamic balance of ocean currents to be altered, resulting in a change of climate for adjacent continents. It has also been suggested that rapid melting of the Greenland ice cap would pour so much cold water into the ocean that the warm Gulf Stream would be altered, causing Europe to become much colder.

Glaciers are important tools for determining the nature of past and present climate change. By taking cores from glaciers and examining the trapped gases and particles, scientists determine the composition and climatic parameters as well as the geologic processes going on at the time. Numerous cores some thousands of feet long have been taken from Greenland, Antarctica, and many other glaciers from around the world. Some contain records as old as 500,000 years.

Antarctic glaciers are storehouses of meteorites. Thousands of meteorites have been discovered embedded in the glacial ice. Usually black, they stand out clearly in the white ice and are not easily lost among rocks strewn across the surface.

—Sidney Horenstein

See also: Glaciation; Pleistocene Epoch

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Indigenous Conservation

Definitions of so-called first peoples as aboriginal, indigenous, autochthonous, or native are made in relation to later immigrant population groups occupying the same or adjacent territories. Although there is no universally accepted definition of indigenous peoples, the term is generally understood to refer to those tribes, nations, or ethnic groups historically inhabiting lands before the advent of colonizing settlers. In addition, they are usually minorities within larger societies, discriminated against in socioeconomic life, at a comparative disadvantage in terms of power and opportunity in their respective states, and linguistically or culturally distinct from the majority. A further criterion, which is replacing older racial parameters in many censuses and official classifications, is self-identification by individuals as indigenous or of mixed heritage. According to language adopted by the United Nations in 1987, the term *indigenous* refers to peoples experiencing colonialism during the past 500 years. Some ancient European peoples such as Basques are thus classified as ethnic minorities rather than as indigenous peoples. In Asia indigenous status applies to more than 150 million tribal, semitribal, and nomadic peoples, many of them in India, Russia, the Philippines, and Malaysia.

Throughout history, battles of conquest have been fought over territory and the control of natural resources. Historically, the global incursions of European colonization and imperialism from the sixteenth to twentieth centuries placed local peoples in a subordinate position throughout much of the world. In the nineteenth and early twentieth centuries, European military and economic power both enabled and was achieved through colonial domination, leaving a trail of economic dependency in its wake. In the postcolonial era, structural inequality has had drastic effects on poverty and wealth, mortality, and health. Indigenous locals are typically marginalized and dispossessed. In recent generations, people tied to the land by tradition have been uprooted and dispersed, through decentralizing policies like transmigration in Indonesia and the acceleration of globalization at the turn of the twenty-first century.

The Caribbean ecosystem encountered by Columbus has been entirely transformed over the past 500 years by the introduction of alien species and plantation systems of cultivation. The eastern woodlands of North America have also been radically transformed by patterns of habitation and exploitation in the postcontact era. Yet ethnohistorical research has revealed that landscapes once thought to be "pristine" at the time of European settlement had already been greatly affected by indigenous occupation, landscaping, and harvesting practices. Environments that are taken for natural, meaning unmodified by man, often turn out to have undergone transformation by humans. Even the vegetation of some old-growth forests has long been affected by the controlled use of fire. The stated goal of some conservationists to restore a particular habitat to a prior state before colonization and technologically driven modification thus selects a somewhat arbitrary point in the history of climate change, species diversification, and the coexistence of man and nature.

Acknowledgments of indigenous impact on the ecosystem and traditional techniques of resource management mean that the establishment of baselines for change and the strategic planning for preservation and restoration must always take human development into account. However, loss of traditional knowledge, as in the native southwestern United States, produces another kind of extinction, that of the firsthand experience of rare and endemic species. The disruption of generational transmission of ecological knowledge from elders to youngsters severs cultural continuity from the biodiversity with which it has coexisted in some places for more than 10,000 years.

In southern Africa, small indigenous cultures have been dominated by larger African tribal groups, settlers, and colonialists. As much as one-quarter of South Africa's vast land area has been affected by development, with a high cost to wildlife. Over several centuries, extinctions in South Africa have included fifty-six known plant species, two bird species, and two mammal species. In Madagascar, a megadiversity hot spot, international conservation leaders are becoming increasingly aware of the need to include local people in endangered species preservation and forest management efforts for the long-term sustainability and viability of both people and the environment, which is home to many endemic species including the world's only lemur populations. The training and employment of Malagasy rangers, wildlife biologists, and guides provides an economic alternative to continued degradation of the forest habitat in one of the world's poorest nations, and is key to the success of internationally directed antipoaching and land conservation efforts.

Anthropogenic, or human-formed, landscapes are far more pervasive than was previously assumed. The mounds built by woodland Indians in prehistoric Mississippi and Ohio are one example of anthropogenic landscapes; the "forest islands" created by Kayapó people in Brazil in the midst of savanna land are another. New studies are showing that many areas once thought to be original wilderness are actually characterized by overgrowth conforming to older landscaping patterns. Some are old growth forests; others, like the Ojibway wild rice fields in Ontario, are plantations gone to seed and still providing sustenance. The anthropogenic character of such landscapes is often invisible to planners from outside native communities. Many "natural" areas and resources have been shaped by human activity, but the term *wilderness* suggests that they are formed entirely by forces of nature, with the connotation that they should belong to everybody equally. In practice, this means that marginalized local and tribal peoples, the traditional stewards of these lands and resources, are denied property rights and usage permits on many such territories.

In the Amazon, internationally organized efforts to promote indigenous stewardship over biodiversity are being incorporated at the policy level into initiatives to establish protected biosphere reserves and sustainable development zones. Unique ecological knowledge and cultural resources are rooted in the histories and oral traditions of indigenous peoples, linking them to their traditional lands. In some places the narratives of folklore, mythology, and genealogy are being considered by legal and state authorities as admissible evidence of ancient title to the tribal ownership of sacred sites. As stewards of the land, indigenous peoples have engaged in the theory and practice of conservation as sustainable environmental knowledge for millennia. For Maasai people and other East African pastoralists, sacred oases are protected zones that can save lives in times of drought.

Conservation of the natural ecology of sacred sites according to indigenous principles has roots in ancient ritual practices held in ancient sacred groves of India, Ghana, Sierra Leone, Côte d'Ivoire, Australia, Canada, Siberia, and other places. The 1972 UNESCO Convention Concerning the Protection of the World Cultural and Natural Heritage (The World Heritage Convention) introduced the category of "cultural landscape." The designation of landscapes as World Heritage sites recognizes that ecosystems are shaped by long interaction with humans as well as evolution and the elements. Since 1978 the World Heritage List has inscribed more than 700 properties for protection in 124 states. Only about 20 percent are natural sites, with the rest designated as cultural or mixed sites. The first protected site was Tongariro National Park in New Zealand, a region held sacred by the Maori people. In New Zealand, bicultural heritage resource management is resulting in cooperative programs and institutions run by Maori and non-Maori together according to the cultural practices and sensitivities of both groups. Indigenous conservation and curatorial traditions are valued and used in combination with scientific and museological methods and standards.

Despite greatly uneven development, indigenous activists the world over face common challenges and are largely agreed on issues of concern. Rain forest peoples in Ecuador, Brazil, Indonesia, and other tropical zones find themselves dealing with many of the same problems associated with deforestation and negotiating with many of the same multinational corporate logging interests. Mining activity in Australia and the southwestern United States has often raised issues of native land rights, as well as pollution and environmental controls. Grassroots organizing and international activism by indigenous peoples' movements to defend and promote their common interests have arisen in the past few decades. The first networking initiatives were taken during the 1970s, when native American activists formed alliances with their counterparts in the circumpolar Arctic and Oceania. At a meeting called by the American Indian Movement in 1974, more than 5,000 local representatives of native peoples from throughout the Western Hemisphere gathered to form the International Indian Treaty Council. The following year, the National Indian Brotherhood of Canada founded the World Council of Indigenous Peoples.

Many local, regional, and transnational community organizations have followed. Land and water rights are major issues for indigenous peoples everywhere, especially in the developing world, where they must compete with mining, logging, and commercial interests to sustain their traditional territories, and with them their modes of economic subsistence and their cultures. The rights of self-determination for indigenous peoples in former colonies are tied to the persistence of ecological lifeways. A combination of indigenous practices and new approaches must ensure that local notions of conservation and associated knowledge are sustained together with the coevolved species of a continuously preserved environment.

—Thomas R. Miller

See also: Conservation; Cultural Survival, Revival, and Preservation; Ethnoscience; Land Use

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Industrial Revolution/ Industrialization

The transformation from an agricultural to an industrial society began only about 250 years ago, but its consequences for the natural world are almost unprecedented. The major innovation that marks the industrial era is the exploitation of the earth's vast stocks of fossil fuel. The availability of more energy per capita has led to undreamed of material wealth for a significant percentage of the world's population, but it has also put tremendous pressure on land and natural resources. The major negative effects of industrialization on biodiversity are: (1) population growth and the consequent destruction of natural habitats, (2) the commercialization of society and the treatment of nature as a commodity, and (3) the increase in income disparity both within and among nations.

Modern humans have inhabited planet earth for several hundred thousand years. In terms of the impact on biological diversity, human history can be divided into three broad categories of economies: the hunter-gatherer or foraging economy, which represents more than 95 percent of our time on earth; dependence on agriculture as the primary food source, beginning about 10,000 years ago; and the modern industrial economy. The economic organization of these three broad epochs differed dramatically.

Hunter-gatherers lived on direct flows from nature within the confines of local ecosystems. Although the case for hunter-gatherer "harmony" with the natural world can be overstated, the fact that they depended on direct flows from specific kinds of ecosystems gave rise to institutions and technologies that preserved those flows. Agriculture made our dependence on other species less direct and exacerbated the conflicts between humans and the rest of the biological world. After the widespread adoption of agriculture, we depended upon far fewer species, and we began our continuing war on biological "pests" that threaten our crops and livestock.

Agriculture brought two new threats to biodiversity: settled communities that made it possible to amass individual possessions; and the explosive growth of the human population. The total human population 10,000 years ago was about 4 million; as the agricultural way of life became dominant, it mushroomed to 200 million by 3,000 years ago. The industrial revolution further removed humans from the constraints of local ecosystems, and the population growth rate continued to increase. As in the case of the agricultural revolution, industrialization made us less dependent on biological variety but more dependent on technology to manipulate a few crops and animals.

Industrialization is usually defined in terms of technology, but it was even more an institutional and social revolution. Technological advances in the Middle Ages (500–1500 C.E.) including the wheeled plow, the water wheel, and the horse collar, and steady improvements in the organization of agricul-

A shepherd watches thick, dark smoke pour from a large chimney at a fertilizer complex at Homs, Syria. (Christine Osborne/Corbis)

ture paved the way for the remarkable flowering of commerce and technology from 1750 to the present. Social transformations include the rise of the nation state, the rise of the consumer society, and global economic integration controlled by supranational economic units. The consequences of the industrial revolution for the human condition and for the natural world have been profound. During the past two and a half centuries, the human population has increased from 1 billion to more than 6 billion. The worldwide dominance of the market economy has created an ever-increasing output of economic goods and services going to a smaller and smaller percentage of the world's population.

It is hard to comprehend the magnitude of the impact of industrialization on the environment. It is now accepted that human activity has changed the earth's climate worldwide with largely unknown but likely negative effects on biodiversity. Large-scale human management of freshwater has significantly changed stream flows around the globe. Human movement of earth for agriculture, road and building construction, and mining rivals the impact of natural erosion, earthquakes, and volcanic activity. It has been estimated that humans directly use or impound about 40 percent of the earth's "net primary productivity"—that is, the solar energy captured by photosynthesis minus that used by organisms for respiration. All the world's ecosystems are now dominated by human activity.

The following are some of the main adverse consequences for biodiversity associated with industrialization:

Population growth. The sheer numbers of people on the planet mean more direct use of land for habitation and food. Habitat loss is the main contributor to biodiversity decline, and habitats for other species shrink in proportion to the expanding human population. The concentration of people in cities means more direct pressure on soil resources in outlying areas to feed the growing population, and the increased use of fertilizer and pesticides upsets the nutrient balance of rivers and streams. Fragmentation of the land has led to the extinctions of large carnivores in many areas of the world. It also enhances the introduction of alien species through the "edge effect" of making interior patches of habitat more accessible to invading species.

In an industrial society, the human population depends on maintaining large energy and resource flows to produce a steady throughput of consumer goods. Many of the harmful effects associated with industrialization are not new. But the increase in population that came with industrialization vastly increased the use of resources going into the economic process, as well as the amount of pollution coming out of it. Although population growth is not the whole story behind biodiversity loss, sheer numbers of people do matter, and the fact that the human population is projected to reach 10 billion by the middle of this century—most of that increase occurring in developing countries—does not bode well for biodiversity preservation.

The commercialization of society and the commodification of nature. The industrial market economy is a relatively recent development, although its roots go back to the origins of agriculture. In only the past few decades, however, this rather unique system of economic organization has spread across the globe. All of the earth's ecosystems are now under the power of a single type of human society based on buying and selling. This can affect species directly, as seen in the illegal market for wild animals and their parts. A single animal of some endangered species can sell for tens of thousands of dollars, a large sum anywhere but a fortune to residents of some impoverished countries. Black bear gall bladders reportedly sell for $10,000 a kilo in Japan; a Siberian tiger can fetch $25,000 when its various body parts are sold on the black market; and an Indian rhino horn can bring $100,000 in some Asian countries when ground into powder and sold as an aphrodisiac. Globalization means that if a demand for an animal exists anywhere in the world, that animal's life is in danger.

Equally serious are the indirect effects of commercial activity on biodiversity. In the global economy, the environmental effects of economic change are far reaching and impossible to predict. For example, the near-extinction of the rhino can be traced in part to the oil price increase of the 1970s. The new oil money flowing into the Middle East sharply increased the demand for ceremonial rhino horn knives used by indigenous cultures there. Logging and mining activities in once remote areas in equatorial Africa are threatening many endangered species with extinction, especially rare primates, as animals are being hunted for "bush meat."

One particular aspect of the commercial economy particularly threatening to biodiversity is the practice of "discounting." Discounting means simply that most people would rather have something now than a few months or years from now. Suppose we are indifferent between having $100 today and $110 a year from now. That would indicate a discount rate of about 10 percent. Put another way, it means that an offer of $100 delivered a year from now is worth only $90 to us today. We discount the future in market transactions. This makes perfect sense for individuals making market transactions. But is it sensible for society as whole to discount things like biodiversity or a stable climate? Discounting means that it may make economic sense to cut down a rain forest if it yields a greater stream of income sold as timber and the proceeds invested in something else than as an intact forest. In the logic of the industrial market economy, everything—including the irreplaceable features of the biological world—is treated as a consumer good.

Increasing income disparities. Increasing income stratification is apparently accelerating and occurring within almost every geographic, economic, and social category. According to World Bank estimates, the world's poorest countries are getting absolutely poorer, while the growth rate of per capita income in the richest countries is accelerating. All these changes have negative consequences for the variety and richness of the biological world. The disparity between the richest and poorest is remarkable. It has been estimated that the wealth of the 350 richest people on earth is almost equal to the annual income of the poorest half of the world's population.

This aspect of industrialization puts pressure on biodiversity from both the wealthy at the top and the poor at the bottom. The richest 20 percent or so of the world's population consume enormous amounts of resources, and their appetite for consumer goods puts tremendous pressure on the environment. The average U.S. citizen consumes about thirty times as much energy and forty times the quantity of other natural resources as does a citizen of a poor country. Furthermore, it is the wealthy countries (and wealthy individuals within those countries) who make the decisions about environmental protection and resource use; these are the people who can best isolate themselves from the adverse effects of the economic growth they promote. At the bottom, impoverished people contribute to biodiversity loss through hunting wild animals to supplement their meager diets, clearing tropical forests for small-scale agriculture, and cutting trees for fuel.

Some make the claim that only with increasing industrialization can poor countries afford the costs of environmental cleanup and create reserves for wildlife protection. Many economists use this logic to argue that economic growth is good for the environment. In some cases, it is true that in the early stages of industrial development there is a decline in environmental quality, but when per capita income reaches a certain level it improves. That is true for a number of specific environmental pollutants. For example, some indicators of water and air quality are higher in the industrial north than in the poor countries. For other environmental indicators, however, the relationship between economic growth and environmental integrity is negative. Greenhouse gas emissions rise steadily with economic output. Biodiversity loss is irreversible, so once a species or ecosystem is lost, or within-species genetic diversity is reduced, no recovery is possible even in the wealthy nations.

Technology, substitution, and biodiversity loss. Much of the debate about the industrial economy and the environment has centered on the "limits to growth." In general, biologists argue that humans are subject to the same carrying capacity constraints as other species, and that we have reached or passed those limits. Most economists argue that the key difference between humans and other species is that we can, through our advanced technology, substitute one resource for another as a particular resource becomes scarce. If we drive one species of fish to extinction, we can switch to another. The problem is that as we use up biological resources and move from one species or ecosystem to another, we steadily impoverish the tapestry of life upon which we depend. The result will most likely not be "overshoot and collapse," but rather a steady erosion not only in the richness of the biological world but also eventually in human living standards.

The growth in material wealth made possible by industrialization depended upon an ideology of progress and unlimited faith in technology. In many ways this ideology has served us well, but it has put the human species on a collision course with the rest of nature. Unless we can find a way to reconcile the rules of the global market, which gives us material well-being, and the rules of the biophysical world, which gives us our very existence, the long-term prospect for the industrial age is not bright.

—John Gowdy

See also: Agriculture, Origin of; Economics; Population, Human, Curbs to Growth; Population Growth, Human; Sustainable Development; Valuing Biodiversity

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Insects

See Arthropods, Terrestrial

Interior Wetlands

Interior wetlands occur from the Arctic Circle to the equator and support a vast array of life forms. There are six major types of interior wetlands: swamp, marsh, fen, bog, wet meadow, and shallow water (aquatic). In all wetlands the soil, plants, and animals are adapted to an environment of flooding. The distinctive soils are often anoxic, because water contains less oxygen than air, because oxygen diffuses slowly through water, and because oxygen is rapidly consumed by soil microorganisms. The plants in wetlands often have hollow stems to permit movement of atmospheric oxygen downward into the soil; simultaneously, gases such as methane may move from the soil back into the atmosphere. Wetland plants often grow rapidly, supporting numerous animal species including invertebrates (plankton, shrimp, clams), fish, amphibians (salamanders, frogs), reptiles (turtles, snakes, alligators), birds, and mammals.

Interior wetlands occur in the interior of continents, and, being isolated from the saline oceans, normally have freshwater. (Occasionally, in arid regions where evaporation exceeds rainfall, such as in western North America, northern Africa, and central Eurasia, interior wetlands may become saline.) These six types listed above are produced by different combinations of flooding, soil nutrients, (see Figure 1) and climate. Within each type of wetland, smaller differences in conditions produce further differences in plant and animal communities. Hence the more kinds of conditions, the greater the biological diversity. The other factors that increase biological diversity are large area, low latitude, seasonal changes in water levels, low nutrient levels, and the effects of fire or wild grazing animals. In landscapes heavily altered by humans, diversity also declines with loss of adjoining forests and stabilized water levels, or with increased nutrients (eutrophication).

Wetlands in the northeastern United States. The soil, plants, and animals found in wetlands are adapted to flooding. (USGS/W. C. Rasmussen)

Six Types of Wetlands

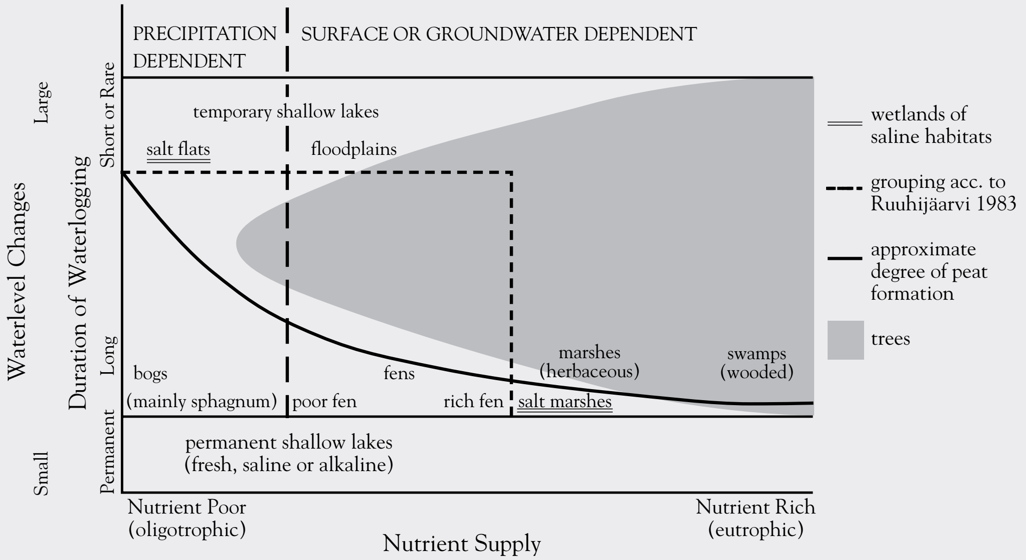
Swamps and marshes have mineral soils with sand, silt, or clay. Swamps are dominated by trees or shrubs, whereas marshes are dominated by herbaceous plants such as cattails and reeds. Such wetlands tend to occur along the margins of rivers or lakes, and they often receive fresh layers of sediment during annual spring flooding. Marshes are among the world's most biologically productive ecosystems.

Fens and bogs have organic soils (peat), formed from the accumulation of partially decayed plants. Nutrients such as nitrogen and phosphorus are therefore scarce. Many bog plants are shrubs with small evergreen leaves (sclerophyllous shrubs or ericaceous shrubs). Carnivorous plants obtain nitrogen and phosphorus from the bodies of captured invertebrates. Most peatlands occur at high latitudes in landscapes that were glaciated during the last ice ages. In fens the layer of peat is relatively thin, allowing the longer roots of the plants to reach the mineral soil beneath. In bogs plants are entirely rooted in the peat. As peat becomes deeper (the trend from fens to bogs), plants become increasingly dependent upon nutrients dissolved in rainwater, eventually producing an ombrotrophic bog. Peat has been a traditional fuel in many European countries. The large amounts of organic carbon stored in peatlands help reduce global warming.

Wet meadows occur where land is flooded in some seasons and moist in others, such as along the shores of rivers or lakes. This often creates particularly high plant diversity, often including carnivorous plants and orchids.

Figure 1

Creation of Interior Wetlands by Varying Water Regimes and Nutrient Supplies



Source: Gopal, B., J. Kvet, H. Loffler, V. Masing, and B. C. Patten, B. 1990. "Definition and Classification." In *Wetlands and Shallow Continental Water Bodies*. Vol.1. *Natural and Human Relationships*. Edited by B. C. Patten. The Hague, The Netherlands: SPB Academic Publishing. p. 14, fig. 4. (Reprinted with permission).

Note: Different kinds of interior wetlands are created by different kinds of environmental conditions. The water regime and nutrient supply (upper left) are the most important factors. The more combinations of environmental conditions in a landscape, the more biological diversity that will occur.

Examples of wet meadows include wet prairies, slacks between sand dunes, and wet pine savannas. Pine savannas may have as many as forty species of plants in a single square meter, and hundreds of species in a hundred hectares.

Aquatic wetlands are covered in water, usually with plants rooted in the sediment but possessing leaves that extend into the atmosphere. Grasses, sedges, and reeds emerge from shallow water, whereas water lilies and pondweeds with floating leaves occur in deeper water. Aquatic wetlands provide important habitat for breeding fish and migratory waterfowl. Animals can create aquatic wetlands: beavers build dams to flood stream valleys, and alligators dig small ponds in marshes or wet meadows.

The two largest interior wetlands (of more than 750,000 square kilometers) are the Amazon River basin and the West Siberian lowland. The Amazon is a tropical lowland with freshwater swamps and marshes containing more kinds of trees and fish than any other region of the world. The West Siberian lowland consists largely of fens and bogs, many of which drain by way of the Ob River north into the Arctic Sea.

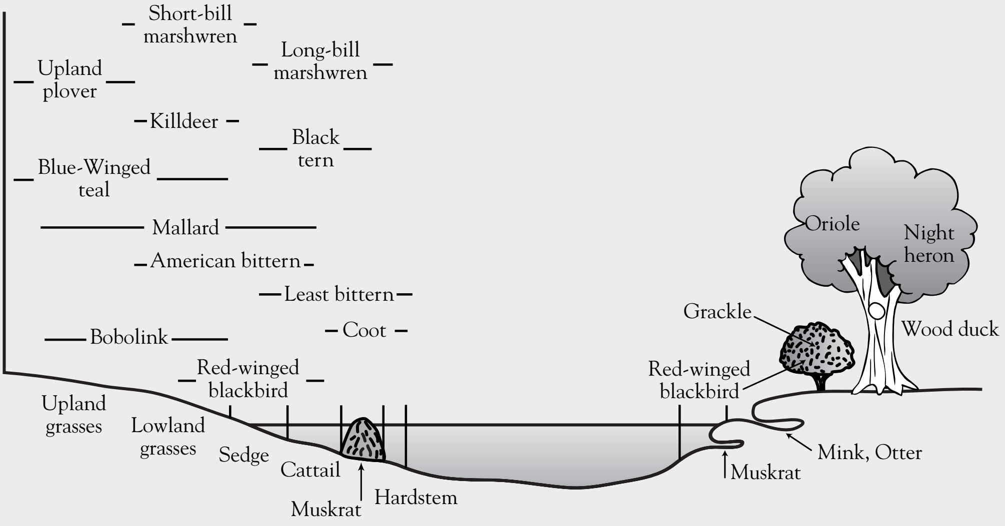
Environmental Factors Controlling Diversity

Water level is a critical factor in all wetlands. Since each kind of plant and animal can withstand only certain amounts of flooding, wet-

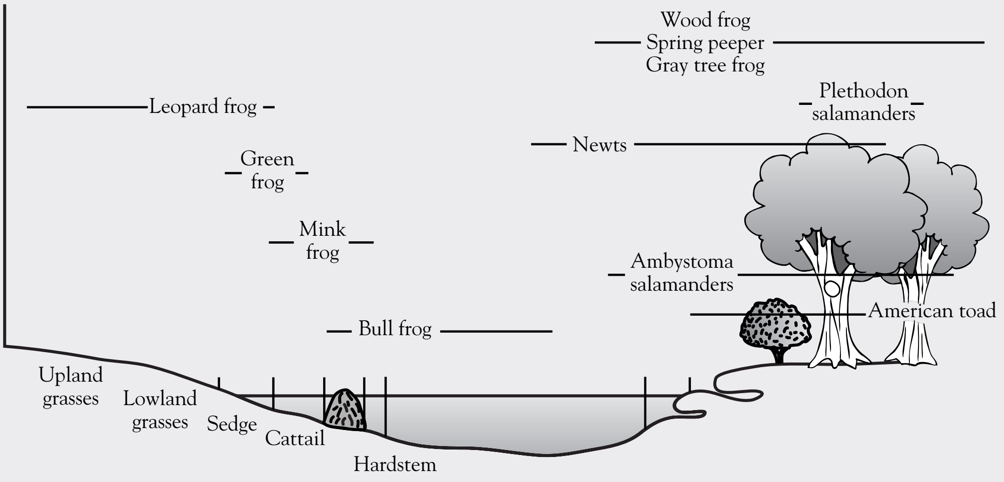
Figure 2

Zonation of Birds, Mammals, and Amphibians in Relation to Water Level and Vegetation

A. Birds and Mammals



B. Amphibians



Source: Keddy, Paul A. 2000. *Wetland Ecology*. Cambridge: Cambridge University Press. fig. 2.3, pp. 88–89. (Reprinted with permission)

Note: Different water levels create different plant communities, which in turn generates diversity in birds, mammals, and amphibians.

lands with different water depths will support the most kinds of species (see Figure 2). A typical shoreline marsh on lakes will often show distinct bands of vegetation (so-called zonation), with each kind of plant occupying a narrow range of water levels. Most animals, including frogs and birds also have their own preferred set of water depths.

Seasonal changes in water levels are normal; spring floods alternate with midsummer droughts. Spring floods enlarge marshes and swamps by killing terrestrial plants at higher elevations. Droughts allow some species of plants to regenerate from buried seeds. Humans often reduce these seasonal changes with dams. Spring floods are retained by the dams (see Figure 3), then released later to augment periods of low water. This almost invariably reduces biological diversity.

Nutrients (principally nitrogen and phosphorus) enhance productivity, but, paradoxically, added nutrients often reduce diversity. The high productivity is channeled into a few dominant species; rarer species disappear. Humans often increase nutrient levels in watersheds and wetlands. This process (called eutrophication) can be the result of either point sources (such as sewage from cities, runoff from feedlots) or diffuse sources (for example, erosion from farmland or logging operations).

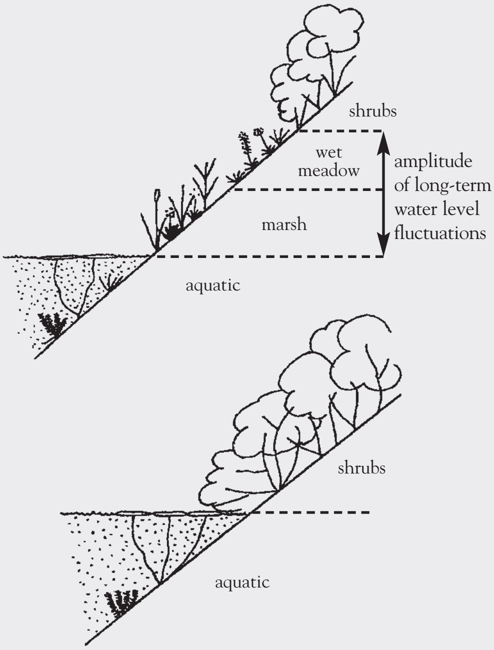
Natural disturbances may remove biomass and increase diversity. In interior wetlands, disturbances include waves on lakes, fire, grazing, or, in the north, scouring by winter ice. Disturbances create gaps in the vegetation, allowing new kinds of plants to establish themselves from buried seeds. Most interior wetlands have buried seeds; in fact, densities may exceed 1,000 seeds per square meter. Gaps resulting from disturbance can also provide different kinds of food or nesting conditions for wildlife.

—*Paul Keddy*

See also: Coastal Wetlands; Dams; Freshwater; Lakes

Figure 3

Effects of Water-level Variation and Stabilization on Wetland Zones



Source: Keddy, Paul A. 2000. *Wetland Ecology*. Cambridge: Cambridge University Press. fig 4.9, p. 195. (Reprinted with permission)

Note: Variable water levels (top) generate diversity in plant communities, particularly extensive areas of marsh and wet meadow. Changes in water level over decades, perhaps associated with changes in rainfall, are particularly important on large lakes such as the Great Lakes in North America. If dams stabilize water levels, the two types of wetland are lost, and the shoreline has only aquatic and shrub zones.

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International Trade and Biodiversity

The effects of international trade on biodiversity are hotly debated topics. On the positive side, international trade accelerates the transfer of ideas, environmental awareness, efficient and environmentally friendly production technologies, and breakthroughs in biotechnology and medicines worldwide. International trade and globalization has increased public awareness of the existence of biodiversity "hot spots" of intact ecosystems rich in biodiversity in remote corners of the world that are threatened by the destructive effects of uncontrolled economic development. This international public awareness may ultimately strengthen national and international laws to protect regional and global biodiversity, and increase international support for stricter environmental standards to maintain strong trade relations.

On the negative side, international markets may have the perverse effect of bidding up prices of critical habitat and endangered species, thereby accelerating their demise. The growing international demand for old growth timber from equatorial rain forests, for bushmeat, and for exotic species are examples. The opportunity for negative social and environmental consequences as by-products of trade also increases with international movement of goods and services, because consumers are generally unaware of the distant environmental and socioeconomic impacts of their market choices. More liberalized trade policies have also resulted in relaxed customs and quarantine rules that allow increased intercontinental migration of alien species. When introduced in countries lacking natural predators, the imported species may quickly multiply and crowd out native species, resulting in extinctions and biodiversity loss.

Economic policies promoting international trade are based largely on the principle of comparative advantage, which says that countries should specialize in producing those products that they can produce most efficiently. In theory, if all countries do this, more total economic output can be produced and all countries will be better off. International trade is promoted as beneficial to all trading partners as well as the environment, because, in theory, it creates economic growth, brings lower prices to consumers in industrialized countries (as manufacturing relocates to lower-cost countries), and creates jobs and export earnings in cash-strapped developing countries, thereby enhancing their ability to safeguard environmental resources. There is considerable controversy, however, among economists about the assumptions necessary to support that position. Specialization based on comparative advantage has a shaky foundation that can be quickly reversed when currencies are devalued or revalued, when prices change dramatically, or when international demand for a product changes. Specialization also makes countries more vulnerable to international price fluctuations, which may force the adoption of least-cost production methods, regardless of the environmental consequences.

Liberalized trade between countries promoted by the World Trade Organization may accelerate habitat destruction and biodiversity loss, by taking away national sovereignty. WTO rules restrict the ability of member countries to impose national environmental standards on imported goods. In order to compete against imports, countries have the choice of relaxing national environmental regulations that make domestic goods more expensive to produce, or losing that domestic industry. Prices established in international markets are more likely to underestimate the marginal value of resource stocks and biodiversity preservation because they are set based upon international supply and demand, and do not take into account declining resource stocks and relative scarcity, which may be apparent only at the national or regional level.

—*Marsha Walton*

See also: Economics; Industrial Revolution/Industrialization; Sustainable Development; Valuing Biodiversity

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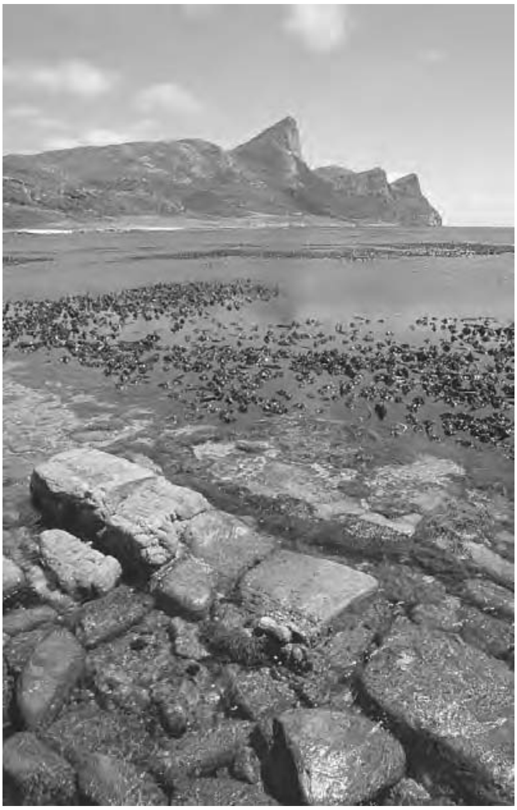
Intertidal Zone

The intertidal zone, also sometimes referred to as the littoral or eulittoral zone, refers to the part of the marine, benthic environment (see Benthos) between the maximum high and minimum low tide levels. The width of this zone may vary tremendously—from a few centimeters to kilometers—depending on both the amount of tidal exchange and the underlying slope of the shore. In addition, the character of the intertidal zone will depend on whether the shoreline is composed of muddy or marshy embayments, sandy beaches, mangroves, or rocky bedrock, boulders, or walls. These diverse intertidal zones all play important ecological roles as habitats in their own right, as well as being a series of transitional "ecotone" habitats between true terrestrial and true subtidal areas. What unites these disparate environments is the periodic cycling between exposed, terrestrial conditions and submerged, marine conditions.


An intertidal zone with kelp beds, South Africa (Gallo Images/Corbis)

Because intertidal organisms may spend portions of their daily lives exposed to both marine and terrestrial environmental factors—such as direct solar radiation, wind, waves, and water with a wide range of salinities—they must be more physiologically tolerant than most marine organisms. The degree of environmental tolerance will determine in part the portion of the intertidal zone that individual species can inhabit. For example, those that are especially resistant to heat and desiccation may live higher in the zone in the upper intertidal, while those that are more susceptible to those stresses will be limited to lower levels (that is, the lower intertidal).

In addition, the ecological processes of competition and predation will also influence which parts of the intertidal zone various species inhabit. Stress-tolerant but competitively inferior species, for example, may be forced to occupy higher, less preferable levels of the intertidal when dominant competitors are present. Similarly, the tidal range of predators can also cause the range of their prey to shift within the intertidal zone. The combined action of physical (that is, abiotic) and biotic pressures may contribute to the patterns—both subtle and striking—of species zonation that are frequently apparent in many intertidal habitats.

The presence of strong, consistent environmental gradients across short tidal distances—combined with other environmental gradients, such as the degree of wave exposure—have made intertidal zones extremely important ecological systems for scientists. Temperate, rocky intertidal habitats containing many fixed (sessile) or slow-moving organisms (such as mussels, barnacles, rockweeds, and kelps) that must compete for limited space within their narrow, preferred ranges in the overall intertidal zone, have been particularly important to ecological research.

—Daniel Brumbaugh

See also: Ecological Niches; Ecology; Ecosytems; Oceans

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L

Lagomorpha

Order Lagomorpha is represented by two living families: Ochotonidae (pikas), and Leporidae (rabbits and hares). The thirteen genera and eighty-two living species of lagomorphs are terrestrial herbivores. Their natural distributions covered most major land areas except Antarctica, southern South America, Madagascar, the Australian–New Guinea region, New Zealand, and many islands. One species now occurs worldwide through human introduction. Certain species are exploited by humans for food, recreational hunting, clothing, and medical and commercial research; others are detested for their exploitation of crops and grazing lands, and their deleterious impact upon the indigenous fauna.

Preceding the nineteenth century, lagomorphs were arranged as a suborder within Order Rodentia, but by the early 1920s lagomorphs and rodents were placed in different orders. At different times they have also been allied with marsupials, primates, insectivores, and artiodactyls. Currently the circle has closed, and rodents are again regarded as the closest living relatives of lagomorphs. The first true lagomorphs have been found in Eocene sediments, so the origin of the group probably extends into the Paleocene.

Lagomorphs share a suite of morphological features setting them apart from other mammals. All have long, dense, and soft fur, haired foot soles, and a tail that is short and furred in rabbits and hares but not visible externally in pikas. There are five digits on each front and hind foot (the first is very small in rabbits and hares, so each hind foot appears to have four digits). The testes are located anterior to the base of the penis, instead of behind as in most other mammals. Facial and back regions of the skull are composed of thin, highly perforated bone (fenestrated). All lagomorphs have one pair of ever-growing lower incisors but two pairs of ever-growing uppers, the second situated just behind the first (a third pair is present at birth but is quickly lost). Between incisors and premolars is a long, toothless gap (diastema) without canine teeth. The cheek teeth (premolars and molars) are high-crowned and without roots (ever-growing). Cheek teeth occlude in such a way that food can be masticated by sometimes vertical, but usually transverse (side-to-side) movements on only one side of the jaw at a time. Jaw movement is powered by two sets of large jaw muscles: the masseter, responsible for vertical movement;

and the pterygoids, important for side-to-side motion. The clavicle (shoulder bone) is prominent in pikas but hardly developed in rabbits and hares. Configuration of the elbow joint (tongue and groove articulation of ulna and humerus) restricts movement of anterior limbs to a front-and-back-plane (no side-to-side or rotary movements are possible). Fecal pellets are reingested (coprophagy).

Living lagomorph species are classified into two families. Ochotonidae (pikas) consists of *Ochotona*, with twenty-five living species; and *Prolagus*, with one species endemic to Mediterranean islands (Corsica, Sardinia, and smaller nearby islands) that is now extinct but persisted until possibly the late 1700s. These two genera are remnants of a recorded fossil diversity of twenty-four extinct genera. Ochotonids are rooted in Late Eocene sediments in Asia; Oligocene in Europe and North America; Early Miocene in Africa; and Middle Miocene in the Mediterranean region. By the Miocene, pikas were living in Eurasia, North America, Africa, and the Mediterranean area. Living pikas are not found in western Europe or Africa, but they do occur in western North America, Eastern Europe, and most of Asia south to Iran, Afghanistan, Pakistan, northern India, Nepal, and Sikkim, and, until historical times, on some Mediterranean islands.

Leporidae (rabbits and hares) consist of eleven recent genera and fifty-five living species; thirty-one extinct genera are represented by fossils. The earliest records are from Eocene sediments in Asia, Africa, and North America. Leporids first appear in the Mediterranean region during the Miocene and have been in Central and South America since the Pleistocene. Their present natural distribution includes most major land masses in the Old and New Worlds. The European rabbit (*Oryctolagus cuniculus*) was originally endemic to the Iberian Peninsula and southern France but has now been introduced on all continents (except Antarctica, Asia, and many islands) and has been domesticated throughout its introduced range. Several species of hares (*Lepus*) have been introduced to regions where they do not occur naturally.

The desert cottontail rabbit is one of the fifty-five living species of rabbits and hares. (D. Robert and Lorri Franz/Corbis)

Pikas are small, with a head and body averaging 200 mm, and weighing 125 to 400 gm. They have short limbs and small, rounded ears. Fur ranges from grayish to buffy brown. Pikas are most active in early morning and evening but may forage at all hours. North American pikas live in talus slopes where they shelter in chambers and crevices among the rocks. They forage in adjacent meadows, cutting grasses, sedges, and forbs that are hauled to the talus, where it is stacked until dry and then stored within the rocky labyrinths for later use. Some Eurasian species also live in talus and rock-strewn terraces, but others inhabit plains, desert-steppes, and forests where they excavate burrows for shelter. Pikas do not hibernate, even though they live in regions subject to long, cold winters.

Body size of leporids ranges from 275 mm (weighing up to 462 gm) in the pygmy rabbit (*Brachylagus idahoensis*) to about 700 mm (weighing up to 5 kg) in some of the larger species of hares (*Lepus*). Fur color ranges from gray to brown, and two species (*Nesolagus*) are patterned gray and white. Front legs are much shorter than the elongate hind legs. Ears are short in some species but very long in others, and those species also have very long hind feet. Leporids inhabit savannas, deserts, steppes, tundra, boreal to tropical forests, alpine meadows, and a variety of regrowth formations. Scampering species usually shelter and seek safety from predators in burrows, but swift and strong runners shelter in surface depressions (forms) and rely upon their speed to escape predators. Two species of *Lepus* in the southeastern United States are amphibious.

Lagomorphs are an important element in natural ecosystems. In temperate and boreal regions some leporids undergo population cycles of impressive abundance alternating with extreme scarcity, often influencing the population densities of their predators.

—Mary Ellen Holden

See also: Alien Species; Artiodactyls; Deserts and Semiarid Scrublands; Food Webs and Food Pyramids; Herbivory; Mammalia; Primates; Rodents

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Lagoons

Lagoons are almost completely or partially enclosed bodies of water located between the coastline and offshore structures such as sand spits, barrier islands, and coral reefs. They connect with the open ocean through narrow breaks in the barriers. Coastal lagoons are abundant landforms, and like barrier islands, which they are associated with, form a little more than 10 percent of the world's coastlines. Most commonly they are found along coasts bordering lowlands such as the East and Gulf coasts of the United States; they are complex features in that they frequently adjoin one or more estuaries. Because they are protected from attack by ocean waves and currents, lagoons are low-energy environments and accumulate mud, sand, and organic material. Deposition is the dominant action ultimately causing the lagoon to fill up over a long period of time. Occasionally, in coastal lagoons, large storms send seawater over the protective barrier island, bringing large volumes of coarse sand into the lagoon. Large storms may also break through the barrier forming narrow tidal inlets, which results in the creation of a localized delta. Because the gaps in the barriers are narrow, currents flowing through them are usually strong near the inlets. Tides and winds are the most important ecological factors.

Lagoons are water bodies that generally vary greatly in salinity and temperature, even within an individual lagoon. They have a greater temperature range than the adjacent open sea and are warmer in the summer and colder in the winter. As a result, lagoons contain a biota of low diversity, although individuals may be abundant. Lagoons with restricted inlets and large evaporation rates develop highly saline waters and accumulate crystalline salt. When subsidence is slow, thick deposits of salt can be produced, similar to the ancient deposits found in many parts of the world.

Because they are shallow, waves, even small ones, can stir lagoon sediments vigorously. Where sediment is abundant, coastal lagoons fill up, creating intertidal flats around their edges and developing extensive marshes. The decaying plant material as well as skeletal remains enrich the sediment. Under these conditions, deposits of peat can develop. In tropical climates, coastal lagoons are often covered with algal mats that trap sediment. As the algae grow upward more sediment is trapped, eventually producing finely laminated structures called stromatolites. Stromatolites are found frequently as fossils, and were first illustrated in the scientific literature in 1825; it wasn't until 1914, however, that their blue-green algal origin was suggested.

Where there is little or no input of sediment, as in coral reef lagoons, skeletal material covers the lagoon floor; sediment in these environments may also include calcium carbonate mud precipitated under high saline conditions. Shallow coral reef lagoon floors are frequently covered by vast patches of coral, while deeper lagoons are more open. Rocky islands associated with some coral reef lagoons inhibit coral development and create murky water because they are the source of sediment detrimental to coral growth. Many coral reef lagoons have very deep inlets eroded when sea level was lower, during the height of the last glaciation.

—Sidney Horenstein

See also: Barrier Islands; Beaches; Coral Reefs; Estuaries; Oceans

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Lakes

Lakes occur where depressions on the surface allow water to accumulate. Landslides blocking rivers, subsidence or collapse of the surfaces, glacial erosion and deposition, and volcanic activity are some of the common geological processes that can create the necessary basins.

Water filling the lake basin is usually derived from rivers, overland flow and direct precipitation, while groundwater is an important component in many regions. Although most lakes have inlets, not all have outlets; some do not have inlets or outlets.

Location and climate determine the chemical nature of lake water. Essentially, lakes are found in all regions of the world, from polar to equatorial, and where precipitation varies from abundant to minimal, resulting in water that varies considerably in salinity as well as acidity.

Lakes have one characteristic that is common to them all. They are relatively short-lived. Although tectonic movements may extend their lifespan, lakes gradually fill with sediment carried in by streams from within their watersheds. In arid environments a considerable amount of sediment may be blown onto the surface, then sinking to the lake floor. Vegetation growing along the edges and lake bottoms adds to the accumulation and helps to diminish the lifespan of the lake.

Groundwater has several roles in the life a lake; the most important is the position of the water table, the upper surface of the zone of saturation. The surface of a lake is also the surface position of the local water table, which rises and falls with the amount of precipitation that, in turn, determines the elevation of the lake surface. Groundwater in limestone areas dissolves the rock and produces caves, which sometimes contain underground lakes. In addition, as caves enlarge, the roofs often collapse forming depressions on the surface. Where the water table is high enough, lakes called sinkholes form in the depression.

After volcanic activity has ceased, even temporarily, rainwater fills some craters at the top of volcanic edifices. Where large calderas form, large lakes, sometimes many miles wide, may develop. A good example is Crater Lake in Oregon, where a major eruption occurring 6,600 years ago destroyed most of the volcano, scattering the rocks over great distances and forming a basin that is now occupied by a lake.

In arid regions, lake basins may receive water during a short rainy season and leave dry lakebeds as evaporation continually reduces the volume of water. The Great Salt Lake of Utah is a mere remnant of a vast lake that covered most of Utah some 8,000 years ago, when precipitation was greater. As the climate became drier, the decrease in rainfall caused the lake to shrink to its present size.

In cold climates soil is frozen most of the year, except for a short summer season when it thaws, leaving, in places, numerous lakes. Lake sediments are important tools that geologists use to determine past climate. By dating the sediments collected on the lakebed and identifying the spores and pollen, and thus the nature of the ancient vegetation contained within it, geologists can determine the local climate.

Crater Lake in Oregon occupies the caldera of Mount Mazama, an extinct volcano. (Library of Congress)

Lakes can also be created by people, as their activities modify the surface of the earth by blasting out rock quarries, digging pits for gravel, creating lakes for farms, and the damming of stream and rivers for water supply, flood control, and recreation.

—*Sidney Horenstein*

See also: Freshwater; Rivers and Streams

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Land Use

In land issues, land is defined as geophysical earth, as territory, or generally as food and economic resources. Resource-driven notions of land have typically predominated in legal discourse. Older definitions of land were often topographic, yet they tended toward an emphasis on economic use-value. More recent definitions take ecological factors into greater consideration, including the subsurface sphere of biota, hydrological characteristics, populations of plants and animals, and settlement patterns and other human effects on the landscape. In the broadest sense, land issues and land rights cover geological strata and mineral deposits, bodies of water and subsurface hydrology, as well as terrestrial surface areas. Natural land units, as environmental entities bounded by geographical features, differ from administrative land units. Frequently the latter are divided according to historical, colonial, or political criteria that can be arbitrary from a geophysical standpoint.

Changes in land exploitation, settlement, and socioeconomic patterns are mutually interdependent. A classical notion derived from John Locke holds that resources should belong to those who add value to nature, an idea that has been interpreted as legitimizing the property rights of capital. Historically, economic and governmental systems have tended to alienate laborers, who occupy and work the land, from possession. Peasant land reform movements in the twentieth century aimed at a redistribution of ownership and control over land and profits from harvesting resources. Stakeholders in questions of land disposition and care include individual owners and title holders, corporations, transportation interests, international and regional associations, nongovernmental organizations, established residential communities, migrant workers, nomadic peoples, and indigenous tribes. Land use management and planning seek out ways of reconciling conflicting interests and agendas, and establishing guidelines and policies for rational exploitation. Zoning for production, conservation, mixed use, and other purposes allocates subdivisions of arable land, forest, and water resources into discrete parcels.

Approximately a quarter of a million plant species are known; some 7,000 out of 30,000 edible varieties have been documented as used for food and other purposes. In the southwestern United States, an estimated 375 plant species are used by American Indians. In some cases, plant species have greater importance for their cultural and spiritual associations and meanings than for food, energy, medicinal, or commercial uses. Throughout the world, sacred groves or other sacrosanct lands and waters are set aside by indigenous peoples and protected from exploitation and development. Many of these sacred sites are rich in biodiversity, and they often serve key functions in maintaining balance within the overall ecosystem.

In the Sacred Valley of Peru, the heartland of the Inca empire, researchers are mapping changes in the geophysical landscape with the help of new tools and old data. The area's natural vegetation has nearly disappeared, along with the original agroforestry practices of the indigenous inhabitants. Upon the arrival of the Spanish in 1532, the mostly Quechua-speaking planters in the highlands abandoned the terracing system of farm landscaping under which they had grown maize and potatoes (the potato, a starchy tuber, is indigenous to the Andes). The social structure of these Inca people, forced to work on Spanish plantations, was reorganized through forced relocation, and the population was decimated by smallpox; only since the late twentieth century has the indigenous Peruvian population approached precontact levels. During the nineteenth century, Europeans introduced eucalyptus trees. Planted at first for ornamental purposes on the haciendas, they gradually became an important source of firewood. In 1969 the Peruvian government began funding reforestation, and today eucalyptus plantations have replaced many of the native trees such as *aliso, buddleja incana,* and *molle*. Replacing these indigenous species with eucalyptus trees has had negative environmental consequences. The toxicity of the aromatic leaves leeches into the soil, the trees require a high level of water consumption, and wool-bearing camelids will not feed off the leaves, necessitating the planting of alfalfa and grasses for alpaca and llama fodder.

Nongovernmental agencies have successfully restored native-style terracing in the town of Cajamarca, and international research teams are now using remote-sensing tools including satellite imagery, geographical information systems for mapping, simulation modeling, and comparison with aerial photography from the 1930s to evaluate and plan further conservation efforts in the region. These new techniques combine ethnographic information with comparisons over time for areas where archival photographs or other historical data exist, and they utilize remote sensing technologies to plot the course of changing patterns of forestation and land use. Amazonian models are being adapted and applied in other regions where deforestation threatens to reach crisis proportions, as in Sierra Leone, Kenya, and other parts of sub-Saharan Africa.

The toll of species lost when megadiversity hot spots like Amazonia undergo massive, rapid deforestation is incalculable. The uncontained sprawl of new urban and suburban development projects like Brasilia, Brazil's planned capital city built in the midst of cleared jungle, is a dramatic reminder of the need for appropriate conservation measures as part of development packages. The incorporation of indigenous knowledge and local native people into projects is a required element in achieving a sustainable balance of biocultural diversity. Urban residents are also stakeholders in the land and in the maintenance of genetic diversity; the long-term viability of settlement depends on the maintenance of sufficiently rich biomass, as is found in mangrove swamps for example, as a check on climatic change and carbon dioxide—based global warming.

An important question for current research is whether biodiversity itself is vulnerable to climate change. Some one-quarter of climate changes result from human land use. Human activities affecting climatic conditions include the consumption of natural resources, deforestation and desertification, and the emission of fossil fuel waste. Larger populations in some developing countries can have more of an effect on global climate change than developed countries with smaller populations and more land. For example, the global climatic effect of resource consumption by India's middle class is greater than that of the entire population of Australia. With industrial carbon dioxide emissions rising and the pressure of economic demand driving a dramatic increase in clear-cutting of timber worldwide during recent decades, forest retention areas—sometimes called carbon sinks—are considered vital safety valves, serving as oxygen pumps for the entire atmosphere. Options for land use projects to act as a brake on global warming include reforestation (or "afforestation" in the language of the Kyoto Protocol), the large-scale avoidance of deforestation (as in Belize's Rio Bravo Preserve), and agricultural plantation development.

Current projections by the Nature Conservancy suggest that tropical forest regeneration, slowed tropical deforestation, and sustainable agroforestry plantations could offset fossil fuel emissions by 12 to 15 percent. Projects of this sort must take into account the social needs of local populations, especially in the poor rural south and other parts of the underdeveloped Third World, in order to be ethically justifiable, socially nondestructive, economically viable, and ultimately sustainable. Nongovernmental organizations like the Nature Conservancy purchase tracts of land to save them from development, thus saving forest resources as well as preserving wildlife by conserving its habitat. The Atlantic Forest Project in Brazil has purchased 20,000 acres of water buffalo ranch in order to restore it to forest land, while the Noel Kempff Project in Bolivia includes funding for the economic and community development of the poverty-stricken forest area there.

The sociological concept of diaspora has been adapted by ecologists and biologists to characterize the migrations of animals and plants, which often accompany or influence human societies. The biocultural process known as biological and cultural diaspora refers to the phenomena of parallel migrations by humans and other species, or of displacement from one environment to another, whether the movements are of urban migrant populations or transplanted flora and fauna. These migrations affect biocultural diversity and landscapes. The draining of swamplands affects wildlife populations through habitat loss, sometimes with drastic results for the food web. Aquatic wetland preserves sheltering migratory fowl are found in densely populated areas of the northeastern United States, where the need for preservation may be especially acute. The Jamaica Bay wildlife preserve near John F. Kennedy International Airport in New York City is one such area, providing needed protection for wildlife in a place where humans and birds need to share the same flyway. Vector-borne diseases such as malaria can be deadly side effects of human-engineered climate and landscape change. In Malaysia and elsewhere, the clearing of tropical forests for road building, timber extraction, and other development projects has created open pathways for insect carriers of human disease.

Corporate and governmental policies aimed at maximizing profit through large-scale exploitation of resources conflict at times with the preservationist ethos of environmentalists or indigenous communities. Attempts to open dialogue and reach agreement among these constituent groups are still in the early stages. In Clayoquot Sound on the west coast of Vancouver Island in British Columbia, Canada, forestry companies are collaborating with First Nations (aboriginal groups) in an experimental effort in the practice of sustainable logging, returning control of the forest to its original managers. Corporations employ local Indians as loggers and forest managers, who in turn limit timber yields to small batches of premium product. This harvest will be sold in the high-end marketplace, while the bulk of the rain forest acreage is devoted to preservation and regeneration. Whether such efforts can gain a foothold in industry remains to be seen. A small but burgeoning movement to promote fair trade products in the marketplace, such as the wholesale importation to the United States of organically raised coffee beans from experimental worker-owned plantations in El Salvador, is seeking alternatives to the inequalities of globalization. Such efforts are presently testing the marketplace to see how much of a premium environmentally and politically motivated consumers are willing to pay for products certified organic and for fair-trade labor practices. Whether the potential of this niche will be considered economically worthwhile by producers is very much an open question. Supply and demand will depend not only on price competition but also the general level and tone of interest in the mass media and social spheres, which can be generated through public relations and campaigns to raise consumer awareness.

—Thomas R. Miller

See also: Agricultural Ecology; Biogeography; Conservation, Definition and History; Cultural Survival, Revival, and Preservation; Hydrologic Cycle; Indigenous Conservation; Organizations in Biodiversity, Role of; Population, Human, Curbs to Growth; Sustainable Development

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Late Devonian Extinction

The Late Devonian extinction destroyed the largest reefal marine ecosystem ever seen in earth history, reefs that constituted almost ten times the areal extent of reefs present in today's oceans. It was one of the five largest biodiversity crises to have occurred in geologic time. The extinction appears to have been triggered by a rapid drop in global temperatures during the Late Devonian, but the ultimate cause of this lethal period of global cooling remains controversial.

Biodiversity Loss in the Extinction

Our best data compilations from the fossil record indicate that 21 percent of all of the marine families, and 57 percent of all the marine genera, of animals present in the world's oceans did not survive this biodiversity crisis. Global tallies of species-level data for the extinction are incomplete, but they indicate that a minimum of 70 percent of marine species perished; some estimates suggest that the species kill may have been as high as 82 percent.

The Late Devonian extinction is unusual in that the diversity crisis does not occur at the end of the geologic period, as is the case with the other "Big Five" mass extinctions (the Late Ordovician, Permo-Triassic, Late Triassic, and Cretaceous-Tertiary). The Late Devonian Period is divided into two geologic stages: the Frasnian and the Famennian, from older to younger. The diversity crisis occurred within the Late Devonian in a series of extinction pulses during the latest Frasnian and the earliest Famennian (Figure 1).

After the extinction pulses ceased, the Late Devonian world had lost more than three-quarters of its species.

Causes of the Biodiversity Crisis

The principal cause of the Late Devonian extinction appears to have been rapid global cooling. The Frasnian world was quite hot, with extensive shallow seas covering much of the continental landmasses. In these warm seas the great Devonian reefs, and other high-diversity marine ecosystems, proliferated. The

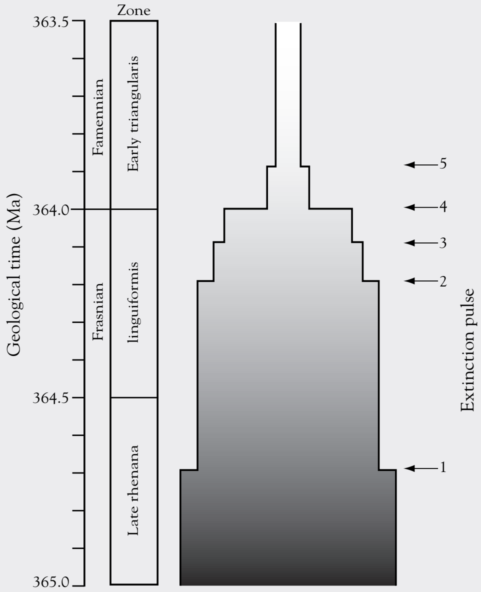

Figure 1

Temporal Pattern of Biotic Diversity Loss in the Late Devonian Extinction

Source: McGhee, G. R., Jr. 2001. "Late Devonian Extinction," in Briggs, D. E. G., and P. R. Crowther, eds., *Palaeobiology II*. Oxford: Blackwell Science. figure 2.4.3.1, p. 224. (Reprinted with permission)

Note: Five pulses of extinction (numbered in the right margin of the figure) occurred in latest part of the Frasnian stage and the earliest part of the Famennian stage within the Late Devonian.

earth's first forests evolved in the Middle Devonian and spread across the continents in the hot climates of the Frasnian, from tropical to almost subpolar regions. The first true woody trees, the *Archaeopteris* progymnosperms (ancient relatives of modern nonflowering evergreens), towered some 30 m high in these early forest landscapes. They were accompanied by strange sphenopsid trees, which looked like gigantic reeds, and lycopsid trees 10 to 20 m tall, towering trees that are survived today only by tiny club mosses.

In contrast to Frasnian climates, the Early Famennian world appears to have been cold and arid. The great forests shrank and were confined to low-latitude equatorial regions. The uplands and high-latitude regions of the earth supported only a very sparse vegetation in conditions that were not only very cold but also very dry, without perennial snow. In the oceans, huge reef tracts died out all over the world during the latest Frasnian. The few reef organisms that managed to survive into the Famennian were confined to what few warm waters still existed on the earth, in restricted regions along the equator.

Causes of Global Cooling

It is still not clear what triggered the collapse of the Frasnian hot climates and the rapid fall of global temperature into the cold Famennian world. The temporal structure of the Late Devonian extinction (Figure 1) consists of a series of extinction pulses that occurred on multiples of 100,000-year scales over a period of 1 to 2 million years, and it is thus similar to the temporal pattern seen in the glacial cycles of the Pliocene and Pleistocene. However, all attempts to find geologic evidence of glaciation in the Late Frasnian to Early Famennian interval of time have failed.

At the present, two alternative theoretical scenarios have been proposed to explain the rapid global cooling that apparently triggered the Late Devonian extinction. Both of these hypotheses are catastrophic: one proposes that an interval of major flood basalt volcanism occurred during the Late Devonian, while the other proposes that an interval of impact bombardment occurred during the Late Devonian, during which a series of asteroids or comets struck the earth.

In the catastrophic impacts scenario, the earth is envisioned to have been impacted by a series of asteroids or comets, impacts that occurred sequentially over a span of 1 to 2 million years. One of the climatic effects of the impact of a large asteroid with the earth is rapid global cooling, caused by the vast amount of dust and debris injected into the earth's atmosphere by the explosive vaporization of both the asteroid and the earth's crust at the impact site. An impact-produced global dust cloud would block light from the sun from reaching the earth's surface, triggering a planetwide "impact winter" and lethally cold temperatures, even at the equator. A string of such impacts is hypothesized to have produced a series of cooling pulses during the Late Devonian, and it is thought that these triggered the observed extinction pulses (Figure 1).

The catastrophic volcanism scenario is based upon the recognition that there have been flood basalt episodes in earth's history, during which enormous amounts of lava, gasses, and volcanic dust have been produced in volcanic eruptions of almost unimaginable magnitude. These flood basalt fissure eruptions are produced by gigantic plumes of molten rock that originate deep in the earth's mantle and that slowly rise to produce paroxysms of volcanic eruptions over huge geographic areas when they intersect the earth's surface. Several flood basalt episodes are known to have occurred in other times of biotic crisis, such as the eruption of the Siberian flood basalts during the Permo-Triassic extinction and the Deccan flood basalts during the Cretaceous-Tertiary extinction. It has been hypothesized that the enormous volume of volcanic gasses and dust injected into the earth's atmosphere during such events would produce catastrophic climatic effects very similar to those produced by the impact of an asteroid with the earth—a "volcanic winter" scenario rather than an "impact winter" one.

Vast regions of the bottoms of the earth's oceans were depleted of oxygen during the Late Devonian. It has been argued that the great geographic extent of these anoxic water masses was produced in part by extensive submarine volcanism, and hence might be evidence for catastrophic volcanic episodes during the Late Devonian. In addition, a major continental rift system is now known to have been active in the Ukraine region of Europe during the Late Devonian (the Pripyat-Dnieper-Donet rift), and many of the earth's flood basalt fissure eruptions are associated with rifting and spreading of the earth's tectonic plates. On the other hand, the volume of volcanic material erupted in the Pripyat-Dnieper-Donet rift appears to be relatively small (less than 10,000 cubic km); thus the intensity of the volcanism associated with the rift was not near the magnitude associated with the Siberian or Deccan flood basalt fissure eruptions (both of which produced well over a million cubic km of volcanic material).

In contrast to the catastrophic volcanic scenario, much more evidence exists for the hypothesis that the earth was impacted by a series of asteroids or comets during the Late Devonian. This evidence consists of craters blasted into the earth's surface by an impact event: eight impacts are known to have

Table 1
Late Devonian Impact Craters

Crater	*Diameter (kilometers)*
Known Late Devonian Impact Events	
Woodleigh (Western Australia)	120
Alamo (New Mexico)	70
Siljan (Sweeden)	52
Charlevoix (Quebec, Canada)	46
Flynn Creek (Tennessee)	4
Probable Late Devonian Impact Events	
Taihu Lake (China)	100
Aorounga (Chad)	13
Panther Mountain (New York)	10

occurred during the Late Devonian (Table 1), and another three impact events are probable.

These impacts all occurred on the earth's continents; thus an unknown number of additional impacts may have occurred in the earth's oceans, for which we have no geologic record.

The Aftermath of the Extinction

The Late Devonian extinction precipitated a permanent change in the structure of the global metazoan reef component of marine ecosystems in geologic time. Metazoan reef ecosystems were virtually destroyed in the extinction, shrinking in geographic extent by a factor of 5,000 from the Frasnian world to the Famennian. The stromatoporoids were a keystone taxon in the ecological structure of Devonian reefs, and the three-dimensional physical structures created by the stromatoporoids provided the reefal niches crucial to the existence of many other benthic taxa. The failure of the previously diverse tabulate corals to recover following the Late Devonian extinction was directly linked to the loss of the spatial heterogeneity and structure provided by the stromatoporoids.

Other ecological effects of the Late Devonian extinction are not as dramatic as the demise of benthic reefal ecosystems but are just as permanent. In the marine zooplankton, all of the cricoconarids were lost, representing an extinction at the class level in the taxonomic hierarchy. The cricoconarids were tiny cone-shaped animals, similar to modern planktic snails, and their extinction eliminated a major element of the Devonian zooplankton. In the nekton, the collapse of the hot climates of the Frasnian struck the marine fish much harder than their freshwater relatives, which were better adapted to seasonal temperature fluctuations; fully one-third of all placoderm fish families were driven out of the world's oceans by the climatic effects of the Late Devonian extinction.

—George R. McGhee, Jr.

See also: Coral Reefs; Cretaceous-Tertiary Extinction; Global Climate Change; Mass Extinction; Permo-Triassic Extinction; Volcanoes

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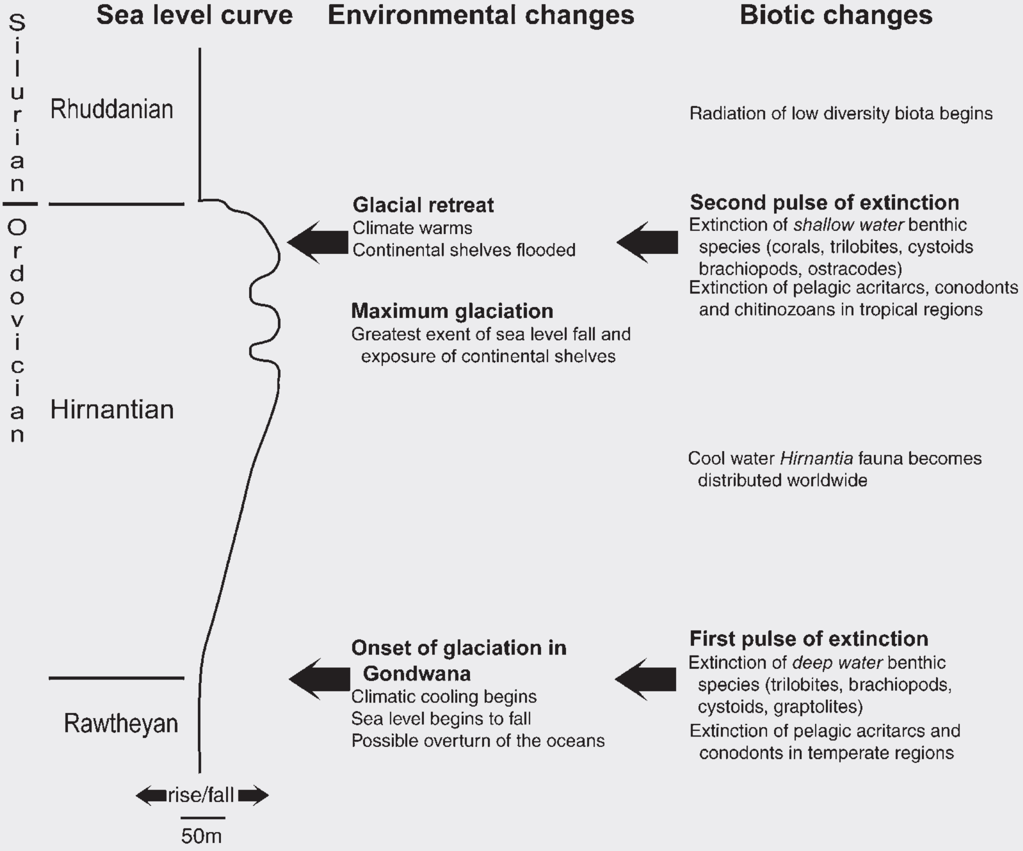
Late Ordovician Extinction

The second largest mass extinction of the Phanerozoic Era occurred during the Late Ordovician, about 445 million years ago. During that time, 22 percent of all families and more than 60 percent of genera became extinct. The Upper Ordovician extinction occurred in two pulses during the Ashgill (the latest part of the Ordovician), separated by about 500,000 years. The first extinction event occurred at the boundary between the Rawtheyan and Hirnantian stages and is related to changes in climatic cooling and changes in oceanic circulation related to the start of glaciation in Gondwana (the supercontintent composed of Africa, South America, Australia, India, and the Middle East).

The second wave of extinction occurred in the middle of the Hirnantian stage and is related to melting of the Gondwanan ice cap and the concomitant spread of anoxic bottom waters over the continental shelves. Although taxonomic losses were high dur-

Figure 1

Extinction Horizons, Sea Level, and Environmental and Biotic Changes in the Late Ordovician



Note: The major pulses of extinction occurred at the boundary between the Rawtheyan and Hirnantian stages (correlated with the onset of glaciation) and the halfway through the Hirnantian stage (correlated with melting of the polar ice cap).

ing the Late Ordovician, the ecological severity of this event was not as great as for other mass extinctions, such as the Late Devonian extinction, inasmuch as only community-level changes occurred across the extinction boundary.

The Pattern of Extinction

Each of the two pulses of extinction affected different parts of the biota. The initial pulse of extinction at the Rawtheyan-Hirnantian boundary primarily affected deeper water benthic organisms. Those taxa that were hardest hit include the trilobites (45 to 75 percent generic loss), brachiopods (25 percent generic loss), cystoids, a group of primitive echinoderms with 70 percent generic loss, and graptolites. In addition to those benthic groups, the pelagic acritarchs and conodonts became rare in temperate regions.

Following the extinction of many of the previously dominant Ordovician biota, a residual fauna, the *Hirnantia* fauna, became well established in temperate regions. The *Hirnantia* fauna is considered a cool-water fauna that ranged from circumpolar to subtropical latitudes. The *Hirnantia* fauna was composed of brachiopod-dominated communities of low diversity that had a global distribution. Some additional extinction of shallow-water brachiopod and coral species may have occurred during the interval between extinction pulses.

The *Hirnantia* fauna became extinct during the second pulse of extinction in the mid-Hirnantian stage. During this phase of extinction, shallow marine benthic organisms suffered heavy extinction, including 40 percent of brachiopod genera, 70 percent of the coral genera, and several trilobite and cystoid families, as well as many ostracode genera. Pelagic groups such as the conodonts, acritarchs, and chitinozoans also experienced mass extinction within the tropical latitudes at this time.

Causes of Extinction

Major environmental changes occurred in the Late Ordovician that correlate with the two extinction pulses. For the majority of the lower Paleozoic Era, the earth was in a "greenhouse" or ice-free condition. However, a short-lived glaciation event occurred during the Hirnantian stage. Unlike other major Phanerozoic glaciations, which may have lasted in excess of 40 million years, the Hirnantian glaciation lasted less than 1 million years, with full glacial conditions existing for as little as 200,000 years. The change from a "greenhouse" to "icehouse" world would have had dramatic effects on climate, sea level, and oceanic circulation and could have precipitated the observed extinction pulses.

The first pulse of extinction coincides with the onset of glaciation at the South Pole in Gondwana (over modern Saharan Africa). The formation of a polar ice cap caused a number of environmental changes in the oceans. First, sea level was lowered by as much as 100 m. This would have reduced the area available for shallow marine organisms to inhabit. Secondly, the change from a greenhouse to an icehouse climate caused a shift in climate belts and may have removed some climates completely. The climate change can be observed in the fossil record by the expansion of the cool-water *Hirnantia* fauna during the Early Hirnantian into areas formerly inhabited by warm-water species during the Rawtheyan. Changes in ocean circulation and ocean chemistry were also caused by the onset of glaciation. The mid-Ordovician oceans were stable and characterized by slightly stratified, warm, saline, and deep waters in the low to mid latitudes, whereas, the development of glacial conditions promotes the development of cold, dense, deep waters with strong bottom circulation. This change in oceanic conditions may have resulted in oceanic overturn that caused upwelling that would have been toxic for some shallow-water biota.

Determining whether fall in sea level, climatic cooling, or oceanic changes contributed the most to the first pulse of the Late Ordovician extinction is not simple. Sea level fall, however, is a slow process, and the maximum sea level fall, or regression, did not occur until well after the initial extinction pulse had been completed—so it probably did not play a major role. Oceanic overturn, while a promising mechanism, has not yet been supported by direct evidence from the fossil record, although it may be supported by carbon isotope data. Climatic cooling, on the other hand, can occur rapidly and is evidenced by the spread of the *Hirnantia* fauna as well as extensive glacial deposits; therefore it may be considered the best explanation for the first extinction pulse.

The mid-Hirnantian extinction pulse coincides with the melting of the Gondwanan ice cap and a very rapid transgression or sea level rise. The warming conditions may have caused oceanic circulation to decrease and return to the weakly stratified state of the mid-Ordovician. Consequently, the transgression caused the flooding of continental shelves with anoxic or dysaerobic (that is, oxygen-poor) waters that are toxic to benthic faunas. This resulted in the second extinction phase, which included the extinction of much of the benthic shelf biota, including the *Hirnantia* fauna. Rapid changes in oceanic surface temperatures probably account for the extinctions among the pelagic realm.

—*Alycia Rode*

See also: Arthropods, Marine; Benthos; Brachiopods; Chordates (Nonvertebrate); Cnidarians; Communities; Echinoderms; Ecosystems; Extinction, Direct Causes of; Geological Time Scale; Glaciation; Global Climate Change; Ice Caps and Glaciers; Mass Extinction

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Late Triassic Extinction

The last two geological divisions of the Triassic Period, the Carnian and Norian stages, are marked by high rates of extinction and include at least one and possibly two episodes of mass extinction, separated by 12 to 17 million years. The Late Norian (the terminal period of the Triassic) is marked by one of the five largest mass extinctions of the Phanerozoic Era. At least 23 percent of all marine and terrestrial families and 54 percent of marine genera became extinct during the latest Triassic. This extinction, which occurred about 200 million years ago, had a dramatic impact on both terrestrial and marine organisms, although the effects may have been felt on land several hundred thousand years before the effects were felt in the sea. Although the cause of this event is unclear, it is likely to be related to marine regression and widespread anoxia (that is, lack of oxygen) in the oceans. In addition, the boundary between the Middle and Late Carnian stages marks a dramatic faunal turnover in terrestrial vertebrates as well as some marine groups, and it may represent an important extinction event. This event may have been climatically induced.

Carnian Extinction

Extinction within the Carnian is pronounced in many groups, including both marine and terrestrial organisms. In the marine realm, ammonites, crinoids, echinoids, bryozoans, scallops, conodonts, calcisponges, fish, and marine tetrapods exhibit large diversity declines. Meanwhile on land, peaks in the extinction rates of pollen and spores suggest that many species of plants became extinct. In addition, up to 42 percent of tetrapod families, including 66 percent of tetrapod species, became extinct during this interval. The extinctions that occurred during the Carnian are also important because they signify a change in the terrestrial realm from the dominance of groups such as rhynchosaurs and mammal-like reptiles prior to the extinction to more modern groups, such as turtles, dinosaurs, and mammals following the extinction. It has been suggested that this extinction may be related to climate change, such as increased rainfall.

Although this event appears to have been dramatic, it has been argued that the Carnian extinction is local and not global in extent, or that it may be an artifact of a poor fossil record, since sea level was low at that time and few marine rocks are preserved. Indeed some groups, such as the majority of bivalves, do not suffer elevated extinction during this interval. Therefore, although some extinction certainly does occur during the Carnian stage, it is uncertain how widespread or dramatic the effects of this event were globally, and whether it should be considered as important an event as the extinction that occurred at the end of the Triassic Period.

End Triassic Extinction

The mass extinction at the end of the Triassic Period heavily affected life on land and in the seas. In the oceans, taxa that were a major component of Paleozoic biota but survived the Permo-Triassic extinction—such as conodonts and several key groups of brachiopods—reached their demise. In addition, more than 40 percent of marine bivalve genera, including up to 92 percent of species and all but one genus of ammonoid cephalopods, became extinct. Gastropods and reef organisms were also severely affected. In the terrestrial realm, the end of the Triassic Period is marked by a dramatic floral turnover, in which 60 percent of Triassic pollen species share their last stratigraphic occurrence at this horizon. Insects, freshwater bony fishes, mammal-like reptiles, and labyrinthodont amphibians also experienced severe extinction across the Triassic-Jurassic boundary.

The duration and timing of this event has been examined in some detail. Based on comparisons of pollen data with Milankovitch cycles, cycles of variation in the earth's orbit, the Late Triassic extinction has been estimated to have lasted less than 500,000 years, and it may have occurred in as little as 40,000 years. Additional radiometric dating has shown that the mass extinction boundary may be at least 700,000 years older for continental deposits than for marine deposits. This suggests that the extinction event may have affected the terrestrial ecosystem prior to affecting the marine realm. The End Triassic extinction is the only mass extinction in which this dichotomy of timing is currently recognized.

The constraints on the timing of the mass extinction also provide some limitations on potential causes. The difference in timing of extinction on land and in the sea argues against a single, short-lived, catastrophic cause such as a meteorite impact, but does not rule out the possibility of long-term environmental change, for which the threshold of tolerance for terrestrial ecosystems is less than that of marine systems. Examples of this type of disturbance include volcanism, sea level change, and climate change. In fact, the occurrence of either volcanism or sea level change is likely to have induced some form of climatic change. A rapid, geographically widespread regression, or drop in sea level, coupled with a transgressive event, or increase in sea level, has been documented during this interval. The regression would affect marine species by reducing available habitat, resulting in changes in the terrestrial setting including increased seasonality and converting of coastal swamplands to low plateaus. Conversely, the transgression would result in habitat loss for terrestrial species and an anoxic event in which marine organisms could not survive because of lack of oxygen in the bottom waters flooding the continental shelf. This regressive-transgressive couplet could therefore cause terrestrial extinctions first by climatic changes, and then marine extinctions as a result of anoxia. The onset of extensional tectonics within the supercontinent Pangea (in the area of modern eastern North America and Europe) including associated volcanic activity also appears to correspond in timing to this change in sea level. Therefore the combination of these factors may have triggered the End Triassic Extinction.

—Alycia Rode

See also: Brachiopods; Bryozoa; Chordates (Nonvertebrate); Cnidarians; Echinoderms; Extinction, Direct Causes of; Geological Time Scale; Global Climate Change; Mass Extinction; Mollusca

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Leeches

See Annelida—The Segmented Worms

Lemurs and Other Lower Primates

Primitive primates are typically known as prosimians and consist of lemurs, lorises, pottos, galagoes, and tarsiers. Many refer to this group as lower primates because they are most similar to the earliest primates, which lived tens of millions of years ago. Technically, this group belongs to two suborders: the Strepsirhini (wet nose) and Haplorhini (dry nose). Within Strepsirhini is the infra-order Lemuriformes, which is composed of several superfamilies: Lemuroidea, Indrioidea, and Lorisoidea. At one time, tarsiers were classified as Strepsirhini, but recent studies in genetics and biochemics suggest that tarsiers are more closely related to monkeys and apes than they are to other prosimians. However, if you compare their bony anatomy with that of other primates, they appear to fall within the range of normal variation among the prosimian group. Since they are morphologically more similar to other prosimians, we have chosen to discuss tarsiers in this group of lower primates. Phylogenetically, tarsiers fall under the hyporder (Tarsiiformes), further divided into the suborder of Haplorhines. This suborder has several superfamilies within it, only one of which pertains to the living group of tarsiers (Tarsioidea).

Compared with higher primates (tarsiers, monkeys, apes, and humans), prosimians have a greater reliance on their sense of smell (olfaction). Their longer, foxlike, wet nose reflects this adaptation. In addition, their eyes are located more laterally on the face, and their vision is not stereoscopic as it is in monkeys, apes, and humans. Most have large, mobile ears and eye sockets with a ring of bone (the postorbital bar) rather than the enclosed eye sockets that characterize the higher primates, which are more visually oriented. Most lemurs have long, fuzzy tails (the Indri excepted). They use this tail for balance when leaping from tree to tree, and unlike many New World monkeys, their tails are not prehensile.

Lemurs are found only on the island of Madagascar, located off the southeast coast of Africa, and on the neighboring Comoros Islands. There are twenty-two living species of lemurs, but, at one time, many more species existed in Madagascar and elsewhere. The others became extinct after humans began to inhabit the island region. Living lemurs range in size from the tiny pygmy mouse lemur, which weighs 30 grams (1 oz), to the Indri and the Sifaka, which weigh well over 7 kg (15 lb). They can be found in a wide range of habitats,

Ringtail lemur (Kevin Schafer/Corbis)

from the lush, wet, rain forest in eastern Madagascar to the dry desert in the southwest. With the exception of the ringtail lemur, lemurs spend most of their time in the trees. The ringtail is the most terrestrial of all the lemur species, spending as much as half of its day on the ground. The smaller lemur species tend to be nocturnal, while most of the larger species are diurnal. Lemurs feed primarily on leaves and fruits, although some nocturnal lemurs feed primarily on inscets.

Lorises are found in Southeast Asia and the islands of Malaysia. They live in forested and woodland regions, and most lorises are slow-moving arboreal (tree-dwelling) quadrupeds. Some lorises maintain a grooming claw on their second metatarsal (foot bone). Lorises are nocturnal creatures that live semisolitary lives, but within small groups. Their diet consists mainly of insects. Their slow and deliberate quadrupedal walk is a convenient weapon when used as a stealth tactic for sneaking up on insects.

Pottos are the African version of the Asian lorises. Nocturnal creatures of habit, they are generally found in a closed canopy environment. Unlike their Asian kin, pottos eat mostly fruit, leaving a very small percentage of their diet to animal protein (insects, ants, termites). Like the Asian lorises, the pottos also have a specialized hand in which the thumb is rotated 180 degrees in divergence from the other digits. This specialization allows them powerful grasping capabilities. In addition to the thumb specialization, the index finger has been reduced to a nub. Pottos have one unique specialization not found in any other primate: their lower cervical vertebra and first thoracic vertebral spinous processes are elongated, giving the potto a great degree of protection of the vertebral column and blood supply from predators.

Galagoes are found in the forests and woodland savannas of the Sahara Desert in Africa. Also nocturnal, galagoes in forested regions occupy the lower levels of the canopy. *Galago alleni* eats mainly on the ground. Its diet consists mainly of fruit and gums, but it will eat up to 25 percent animal protein when available. The true bushbaby, *G. senegtalensis*, eats mainly insects and gums off the ground. The locomotion of galagoes is by means of vertical clinging and leaping. Their social groups consist of small groups of neighboring galagoes. Some sleep in leaf nests, others in holes in trees.

Tarsiers are found in the forested regions of Indonesia. Although they look and act like other prosimians, biochemical studies indicate that they are probably more closely related to monkeys. They are small, nocturnal creatures with large, mobile ears, but they lack the wet nose that characterizes prosimians. They may be very similar to the ancestors of the first anthropoids (the taxonomic group that includes monkeys, apes, and humans). Tarsiers have the unique ability to rotate their heads 180 degrees.

As is the case for most mammals, the kind of social group that a prosimian belongs to depends on several factors: whether they are nocturnal or diurnal, whether they are small- or large-bodied, and where they live. Most nocturnal species are solitary (for example, the potto). Diurnal species with large bodies live in larger social groups (for example, the ringtailed lemur). Many wild populations of lemurs and other prosimians are under the threat of extinction. This is primarily because of extensive habitat loss and human hunting. Since humans reached Madagascar, about 2,000 years ago, the once extensive forests have been reduced by more than 90 percent. Many of the other lower primates—lorises, galagoes, and tarsiers—also face the threat of extinction as humans continue to alter and destroy their natural habitats.

—Ken Mowbray and Shara Bailey

See also: Great Apes; Monkeys; Primates

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Lichens

Although usually green, lichens also show up as a yellow or orange "moss" that grows on naked rocks and logs. The oldest fossils of plants contain fossils of fungi: the joining together of members of separate living kingdoms, fungi and algae or monera (bacteria) to make lichens, is part of an ancient tendency for life to settle land by a combination of partners. (Similarly, if human beings were to settle space, we could not with present technology do it alone, but would require food plants to eat, and microbes such as bacteria and fungi to recycle air and turn our wastes into drinking water and soil.)

Perhaps the most famous example of symbiosis, or living together, lichens are synergistic associations between fungi and either algae (a protoctist) or cyanobacteria (a bacterium). In reproductive sex the two sexes come together briefly, contribute part of their genomes, and an offspring arises. In lichens, by contrast, the two components—fungus (mycobiont or fungal life form) and phycobiont (photosynthetic life form)—have per-

Lichen-covered rocks, Glacier National Park, Montana (David Muench/Corbis)

manently merged. The fungus is usually an ascomycete. whose name derives from a saclike reproductive organ, the ascus. Yeasts, morels, and familiar molds are ascomycotes. The spores of ascomycotes can remain viable for years while dry, and some ascomycotes are responsible for tree diseases such as blight and Dutch elm disease. Of the approximately 50,000 ascomycote species, 20,000 are found only in association with photosynthetic green organisms—that is, as the fungal part of a lichen partnership. More rarely, the fungal partner in lichens will be classified as a basidiomycotes, the other great phylum in the Kingdom Fungi.

Symbiotic Advantage

On their own, ascomycotes and cyanobacteria—or ascomycotes and fungi—are not able to grow in some places that they can grow in while teamed up as lichens. Lichens, for example, are a common sight on bare rock; over hundreds and thousands of years, the lichen partnership can erode rock into rich soil, changing geology into biology. The symbiosis between fungus and algae or green cyanobacterium is to the advantage of both: the photosynthetic component provides the fungus with the organic nutrients, access to which it might not otherwise enjoy; the fungus, for its part, retains water for both partners, dissolving mineral nutrients, and sensitizing the partnership to environmental change. Reproduction in lichens is via soredia, which are propagules composed of cells of algae surrounded by the fungal reproductive threads known as hyphae. Thus the lichen symbiosis—or rather, lichen symbioses, since many different species have come together to reinvent lichen—is not optional but hereditary; it makes a lichen a lichen. Lichens, which may also reproduce when bits are blown about to new locations, are among the first organisms to colonize barren areas. Very sensitive to air pollution (such as sulfur dioxide), lichens are also useful as markers of ecosystem health, a kind of herbal equivalent to the canaries that coal miners used to gauge gas leaks before they could become fatal to humans. Breaking down rocks, lichens release into nearby puddles, ponds, and streams the phosphate and nitrate compounds required by organisms, thereby generating nutrients for soil microbes and the roots of plants. All other things being equal, forest environments rich in lichens can be assumed to be healthy with a rich allotment of biodiversity.

Classification

In a five-kingdom classification system, lichens are put somewhat awkwardly into the kingdom fungi. Although the fungal components of lichens are in fact ascomcetes and basidiomycetes, the role of these fungi in the lichen collective has physiologically changed them to the point where they deserve their own taxon. Together lichen partners produce acids and pigments that neither can produce on its own; together they make the "tissuelike" substance that turns rock to soil and expands the domain of the living.

In contrast to the diverse fungal members of lichens (estimated at 25,000), the photosynthetic partners are relatively few. Most common are Trebouxia and Pseudotrebouxia: walled, immobile cells that can no longer survive without their fungal brethren. Made of members of two separate kingdoms, one or two (depending on if the photosynthetic component is algal) also have a symbiotic history from bacteria coming together; the existence of fungi as a phylum, while logical, shows that branches on the tree of life merge as well as split.

—Lynn Margulis and Dorion Sagan

See also: Classification, Biological; Coevolution; Conservation Biology; Five Kingdoms of Nature; Pollution; Soil; Topsoil Formation; Topsoil, Loss of

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Linguistic Diversity

There are an estimated 5,000 to 7,000 spoken languages still extant in the world at the turn of the twenty-first century. Ten languages account for nearly half the world's people. The first language, or mother tongue, with the largest speech community is Mandarin Chinese, with 16 percent of the world population. English is in second place, with 8 percent, followed by Spanish (5 percent) and Arabic (4 percent). Four mother tongues—Hindi, Bengali, Russian, and Portuguese—are spoken by 3 percent each of the world's people, with French and Japanese each accounting for 2 percent. The remaining 51 percent speak other tongues as their first languages. Some 3,406 languages were found to have fewer than 10,000 mother-tongue speakers in 1995; 553 of these languages had 100 or fewer individual speakers. One-third of the world's living languages are spoken predominantly in Asia, and nearly as many—just over 2,000 languages—are found in Africa. Some 19 percent of languages occur in the Pacific, 15 percent in the Americas, and around 3 percent (some 230 languages) in Europe (UNEP, 1999, p. 23).

Actual or threatened language loss, environmental degradation, loss of habitat and species extinctions, and loss of cultural tradition are all intimately connected and interdependent phenomena. The continents with the greatest surviving linguistic diversity are Asia and Africa, but the largest number of endangered languages are spoken in the Americas and in the Pacific islands (Oceania), where the prospect of further language loss is disproportionately acute. Although different methods exist among linguists of counting and determining which dialects are distinct enough to constitute separate languages, *Ethnologue* tallied 6,809 spoken languages in the year 2000. Of these, 417 are considered to be "nearly extinct," defined as having "only a few elderly speakers" left alive. Some 161 of these languages are found in the Americas and 157 in Oceania. In extreme cases such as Eyak, a language of southern Alaska, only a single native speaker survives.

Linguistic diversity, often devalued as archaic and even retrograde in periods of rapid assimilation and socioeconomic change, can have a positive value for the maintenance of traditional communities and ways of life, sustaining distinct indigenous identities, the promulgation of self-determination and human rights, and the preservation of environmental knowledge and ecological balance. Biotic diversity is reflected in specialized lexica and classificatory variations. Smith (in Maffi, 2001) has found a regular pattern of correlations between ethnolinguistic diversity and biodiversity in native North America. Environmental knowledge encoded in linguistic repertoires may be lost under circumstances of colonization, migration, or widespread occupational change. Language indirectly affects ecology through the formation and maintenance of speech communities; social domination of one ethnolinguistic group over another; discourse about landscape, resources, and technology; and conceptual specialization of terminology linked to climate, pharmacology and medicine, land, plant cultivation, and animal husbandry. Linguistic diversity and biocultural diversity are crucial for the preservation of local environmental knowledge and the maintenance of traditional ecologies in endangerment zones and megadiversity hot spots where much of the indigenous biota remains unknown to Western science.

Archaic forms of language hold valuable clues to history, prehistory, ethnogenesis, and environmental change. Greenberg's controversial protolanguage hypothesis is an attempt at reconstructing common ancient tongues from which modern languages branched off and evolved. This is a kind of linguistic archaeology, done through a constituent analysis of shared features found in related living languages, using necessarily speculative methods such as glottochronology to date the earliest forms. This complex form of educated guesswork is based on a wealth of data but inspires skepticism among many scientists. There may be some correlation among biological and linguistic relationships, but linguistic adaptation can and does occur independently of either biological or cultural assimilation. Borrowing, loan-words, and hybrid word forms are generally more reliable if less sweeping evidence of historical mixing among populations. Mufwene (in press) proposes an evolutionary model of linguistic ecology based on population genetics, with each language at the equivalent functional level of species, and personal variations on local dialects analogous to individual organisms. Through the language contact that takes place within polyglot individuals, distinctive features of languages undergo competitive selection and adaptation to survive within speech communities.

In South America, nearly two-thirds of the pre-Columbian languages spoken by an estimated 1,200 different indigenous peoples before European contact have been lost. Today there are approximately 422 indigenous ethnolinguistic groups on the continent, comprising a population of some 10 million (as compared with an estimated 24 million in 1492). About one-third of those still surviving have fewer than 1,000 speakers left, placing their future viability in doubt. Excluding Spanish, Portuguese, French, English, Dutch, and Quechua, there are 146 South American languages still spoken by more than 1,000 people each. This figure indicates that about 12 percent of the estimated pre-Columbian linguistic diversity still exists (Lizzaraldo in Maffi, 2001). Economic and cultural change are major factors accounting for the erosion of indigenous South American languages. Continued shifting away from traditional subsistence practices is likely to result in further loss of environmental knowledge as encoded in linguistic terms for plants and of other biotic information.

In Mexico, ethnolinguistic diversity underwent drastic decline in the decades following conquest by the Spanish, as the indigenous population fell from some 22 million to under 1 million in less than a hundred years. Some 54 of the 120 indigenous languages spoken before the invasion are still spoken in Mexico, representing 8 million people (7.5 percent of the Mexican population in the 1980 census). For the past fifty years, the number of native speakers of indigenous languages in Mexico has been rising (Minnis and Elisens, 2000, pp. 46–47). In California, an area of former linguistic megadiversity, a multitude of native tongues has dwindled to a mere handful of moribund languages, some down to their last speakers, replaced principally by English and Spanish.

Greenberg (1966) classified 730 African languages in four large groupings labeled Congo-Kordofanian, Nilo-Saharan, Afroasiatic, and Khoisan; these are divided into sixteen language families composed of forty-six subfamilies. Botswana, home to the greatest number of Khoisan languages, is also a contact zone where eastern and western Bantu languages meet and interact. As the biodiversity of the Okavango delta is threatened by pastoral and agricultural activities, so too are its indigenous languages being replaced by Tswana. Recent efforts at preservation have begun to succeed in changing negative attitudes toward minority tongues and stimulating regional policy to encourage the maintenance and transmission of local knowledge and minority languages in Botswana. This need must be balanced with the enhanced educational opportunity and economic benefits that minority individuals can indisputably gain by adopting more widely spoken languages.

The teaching of an indigenous language as a second language in school contrasts with primary language acquisition in the home. School-based instruction may be the next best option after home instruction. Such formal teaching can preserve and perpetuate language structures and vocabularies, but it can never substitute for the habitual use of native tongues among parents and children in the household. In the northern Soviet Union, government policies took the children of native reindeer herders away from the pastoral environment to boarding schools where they spoke only Russian. As a result, many minority languages are now familiar mainly to older people and may die out within a generation. Native language loss in Siberia was comparable to that experienced in western North America during the first half of the twentieth century. In Canada, for example, Indian children in government-run missionary schools were beaten for speaking their mother tongue. Revival efforts are aimed at reinstating indigenous languages at the elementary school level through classroom instruction and the publication of primers.

In northeastern Siberia, Sakha (Yakut) was spoken regionally and used for interethnic communication by Russians and minority peoples, as well as Sakha people before the Russian revolution. The Russian language and Cyrillic-based orthographies became more dominant in all the Soviet republics under reforms begun during the 1920s. Since the 1990s and the collapse of the Soviet Union, Sakha and other native languages are on the increase through conscious cultural revitalization efforts, including school instruction, radio and television broadcasting, and official government use. The Sakha are the most populous non-Russian group in the region, and their language has consequently been able to withstand the pressure of Russianization. Smaller minority languages in the north, however, continue to fade through attrition and lack of generational transmission. In Siberia and Kamchatka, elementary school readers and folk tale collections in the native languages of the small peoples (indigenous peoples with unique languages and cultures) of the north including Even, Evenk, Itel'men, and Yukagir appeared in the 1980s and 1990s. Continuity of native language and land rights are among the most vital threads necessary to ensure the long-term survival of small populations such as the Yukagir and the Itel'men as distinct ethnic peoples. There is hope that under favorable circumstances, northern languages will survive. In Chukotka and neighboring regions of far northeastern Asia and the northern Pacific, all indigenous languages have reached the endangered status; some, however, have undergone unusual adaptations to Russian grammar and structure while retaining native morphology and vocabulary (a reversal of the more typical pattern whereby native grammar and structure are retained and applied to imported vocabulary), resulting in special regional dialects that continue to exist (Vakhtin in Kasten, 1998).

Alaska is the birthplace and cradle of diversity for Eskimo-Aleut and Na-Dene, two of North America's largest indigenous language families. In Alaska, four Eskimo-Aleut languages have almost disappeared in the past half-century. Two Yupik languages are still spoken by children in certain villages, while Alutiiq and eastern Aleut are in decline. Alaska's fifteen Indian languages face a similar urgent situation (Iutzi-Mitchell in ibid.). Eyak and the western Aleut dialect of Attuan are probably the most moribund of those that remain, with each retaining as little as a single elderly native speaker (Krauss, 1980). As elsewhere in the western United States and Canada, during the early twentieth century native languages in Alaska were repressed by missionaries, and children were punished for speaking their mother tongues in school. The Federal Bilingual Education Act of 1967 permitted but did not mandate instruction in languages other than English in the United States. Experimental programs in bilingual education began in Alaska in 1970. Shifts in the valuation and prestige of native languages, combined with school-based instruction and dissemination of mass media in indigenous tongues, offer some hope for linguistic revival in the form of second languages, at least among those still retaining a critical mass of speakers. Linguists continue to believe that parents speaking a language to their children in the home is ultimately the only way that true language survival can take place.

Sociolinguistics, or the sociology of language, focuses on the speech community, rather than the specific languages or dialects spoken within a group, as the basic unit of analysis. Language contact occurs in individuals who may practice bilingualism, multilingualism, diglossia (the use of more than one variety of a single language in different circumstances), or code-switching (alternating use of more than one language or dialect within a single speech situation). These deviations from monolingual speech, which linguists term interference, are the locus of language change in intercultural contact. As such, they are intimately bound up with other phenomena of acculturation and syncretism. In actual practice, the use of elaborated or restricted codes by a single individual can range widely across complex social and environmental variables, including the relative status of the speaker and the addressee, the cultural setting of the interaction, and the specific function of any given communication. Language planners designate ten different situations, which can overlap, for education: Indigenous Language, Lingua Franca, Mother or Native Tongue, National Language, Official Language, Pidgin, Regional Language, Second Language, Vernacular Language, and World Language (Eastman, 1975). Language planning takes place at the policy level to determine standardized use among national populations. Such legislation has profound effects on the degree of sociopolitical unity or disunity among diverse populations. Modern examples include the institutionalization of Swahili in Kenya and Bahassa in Indonesia (based on a Malay trade dialect of the Indonesian archipelago). Language planning and policy typically work against linguistic diversity in the interest of fostering national unity, but they can also be applied in the reverse direction. Combined with computerized database inventories, the development of instructional media tools, and conscious preservation efforts, planning and policy are being implemented to help stem the tide of loss of linguistic diversity in the twenty-first century.

—Thomas R. Miller

See also: Biogeography; Cultural Survival, Revival, and Preservation; Ethnoscience; Indigenous Conservation; Organizations in Biodiversity, Role of; Population Growth, Human; Valuing Biodiversity; Why Is Biodiversity Important?

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Linnaean Hierarchy

Scientific names are strange and rather intimidating to the layman. Why in the world would a scientist prefer to use the name *Felis domesticus*, when there is a perfectly good common name: "domestic cat"? The reason lies in the need to have a universal system of names that can be understood by all scientists regardless of their native language. In fact, the reason that all scientific names are either Latin (*felis* means "cat" in Latin) or latinized (frequently classical Greek) is a historical remnant of the way European scientists communicated with each other across national borders. Latin was the universal language of the Western educated world until the nineteenth century. By continuing to use Latin, scientists have adopted a "neutral language." Perhaps it is inconvenient to modern scientists who lack training in classical Latin and Greek, but at least we do not have to fight over whether *Felis domesticus* should be called cat (English), *chat* (French), or *neko* (Japanese Romanji).

Some curious features of the name for the domestic cat might strike you. Why is the name in italics, and why is one part of the name capitalized and not the other? That is another convention. The names of species (*Homo sapiens*) and the names of genera (*Homo, Felis*) are always "set apart" from the other words, and the first part of the name is always capitalized while the second part is not, even when named after a person. Why are there two words for a species? A bit of background is needed to understand this and other mysteries of scientific nomenclature.

The scientific classification of living organisms has a long history that began with Aristotle (384–322 B.C.E.) in such works as the *History of Animals* (350 B.C.E.). Carl Linnaeus (1707–1778), a Swedish botanist/naturalist/physician, devised the major features of the classification hierarchy that we use today. Working at first alone and then with colleagues, Linnaeus attempted to organize all known biological diversity, both plant and animal, into "natural" systems of classification. He produced a groups-within-groups system, organized using more or less inclusive categorical ranks that still characterize biological classification today.

One reason for the success of Linnaeus's system was his way of naming species. Taking his clue from Aristotle, Linnaeus proposed that each species of plant or animal should be given a two-part name, called a binomial. All species belong to a genus, so the first part of the name (*Felis*) was formed from the name of the genus; the second part was the specific epitaph (*domesticus*). The name of the cat species became *Felis domesticus*, while that of the chimpanzee became *Homo troglodytes* (since changed to *Pan troglodytes*). This idea became popular, principally because it replaced the long and rather cumbersome descriptive names attached to species with a short and highly functional name. Another reason for success was the fact that Linnaeus produced a flexible and expandable system that utilized categorical ranks to organize larger and more inclusive group of species. Many species could be grouped into a genus; many genera could be grouped into a family; and so forth. What is more, these ranks could be reused. For example, there are more than 400 taxa of fishes classified at the family rank. Some of the basic categories, and an example of a group at each rank, are shown below:

- Kingdom Animalia
  - Phylum Chordata (lancets, fishes, amphibians, etc.)
    - Class Mammalia (mammals)
      - Order Primates (lemurs, monkeys, apes, humans)
        - Family Hominidae (great apes and humans)
          - Genus *Homo* (fossils and recent humans)
            - Species *Homo sapiens* (us)

Note that each line contains the name of a group (Animalia, Primates, and so forth). Such groups are called "taxa" (singular, taxon). Second, each taxon is associated with a rank category (kingdom, order, and so on). The taxon name refers to an actual group of organisms, while the categorical rank refers to the position of the taxon in the classification relative to other taxa. So, the Order Primates has a position in the hierarchy that is equivalent to the position of other orders, such as Carnivora (bears and lions), or Coleoptera (beetles). Third, each level, from lowest to highest, contains more of these groups of organisms. Mammalia contains many orders (Ungulata for hooved mammals, Carvinova for bears and cats, and so forth). From the layperson's point of view, taxa seem to have impossible names. That is because all of the names, not just the species names, are either Latin names or latinized Greek or modern names. Sometimes we recognize the Latin root (such as "carnivore"), but usually we are stuck. Do you know what the name for the monkey family—Cercopithecidae—is derived from? Answer: It is a compound name derived from the classical Greek for "tail" (*cerco*) and "monkey" (*pithecus*), along with the ending used for families of animals (*idae*).

The Linnaean system provided European scholars with a flexible and powerful tool for organizing the ever-growing list of newly discovered species flowing into the universities and museums of Europe. However, it did not solve one major problem: the use of different names for the same taxon in different countries or by different scientists. A rose by any other name might smell as sweet, but how could a botanist in Sweden and another in England effectively communicate, if the same rose species had two different names? Beginning with A. P. Candolle in 1813 and extending to H. E. Strickland in 1843, taxonomists attempted to formulate rules that would govern the use of names internationally. This process evolved over the years to become the three major Codes of Nomenclature that now govern the names of plants, animals, and bacteria (there are other codes for viruses and cultivated plants).

The codes are an effort to formalize and standardize the naming of organisms in a manner that would ensure uniform use of names across international boundaries, languages, and cultures. The codes are simply sets of rules for naming and the use of names. As such, they do not speak to particular philosophies of classification, such as classifying strictly according to descent with modification, or exclusively by overall similarity, or even classifying by fives. They explicitly avoid setting rules for the actual practice of science, and that is why they have survived. In other words, the codes do not specify what you must name, only how you must form the name if you wish to name something, and what names you should use once they are formulated.

The general principles of Linnaean classification as embodied in the current Rules of Nomenclature are relatively simple, even if the practice strikes some seasoned scientists as arcane. Each specifies a beginning for the nomenclature of the group, and each is independent of the others. For example, all zoological nomenclature begins with the publication of Linnaeus's tenth edition of *Systema Naturae*, considered published on January 1, 1758. Earlier names (even those in Linnaeus's earlier editions of the *Systema*) are considered invalid. The rules differ among the three major groups of organisms, but all share some general principles.

1. Forming names. All taxa are given Latin or latinized names, a uninomial name for taxa ranked as genera and above and a binomial for species. Specific rules may also

apply to taxa or certain ranks. For example, the names of taxa ranked as families in botanical classifications must end with the suffix "aceae." Thus the taxon Rosaceae requires no categorical rank to show its position in the hierarchy; it is immediately identifiable as a taxon ranked as a family, the Linnaean family of roses.

2. Taxa assigned to certain categories can have only one correct name, and that name is usually the earliest name applied to the taxon. The use of the earliest names is termed the Principle of Priority. For example, *Homo sapiens* is the only correct name for humans, and we use that name because it appears in the tenth edition of the *Systema* and thus is the oldest name available for our species. You can give humans another name if you wish, but no one will use it if they follow the rules. The Principle of Priority can be set aside, but only by submitting a petition to the appropriate International Commission of Nomenclature and only upon acceptance of the petition.
3. Two taxa cannot have the same name unless they are governed by different codes. It is possible for a plant species and an animal species to have the same name, but not for two plants species or two animal species. Two names for the same species of animals would be termed synonyms, and the older named is usually used.
4. Certain taxa are "objectively defined" in reference to actual specimens. For example, every new species named today is objectively defined in reference to a type specimen or series of type specimens. (In some cases it isn't a specimen of the actual organism, but some "work" done by a specimen, such as a fossil track or burrow made by an extinct worm.) These specimens are usually deposited in natural history museums where other scholars can examine them. Type specimens are not meant to be "typical" of the species. Rather, they document that the original systematist actually examined that particular specimen as he or she was formulating the name. Sometimes, especially in early works, a type specimen was not designated. It is common for a systematist who later studies the group to name a type specimen in such cases.

Each of the various codes goes on for pages, outlining how names should be formed, what names are to be used, and how names should be changed. The appropriate international commission, a body of scholars who can draft revisions and pass judgment on problems that arise, regularly reviews each code. Systematists who regularly name new species and other taxa are expected to know these rules. Reputable journals publish the names of new taxa only if the applicable code is followed. Most of this scholarship is uninteresting to those who use the names, but it is a necessary part of systematic scholarship and minimizes chaos.

Alternatives to Linnaean Classification

Many systematists and taxonomists have doubted that the Linnaean system and the formal Codes of Nomenclatures are capable of handling the numbers of organisms and groups of organisms that continue to be discovered. For example, Willi Hennig, the German entomologist who founded the dominant systematic paradigm Phylogenetic Systematics, suggested several alternatives, such as providing separate classifications for each geologic time period, or using a numerical prefix system as a substitute for Linnaean categories such as class and family. Others have advocated "rankless" classifications in which subordination is expressed simply by indenting, while still others have suggested that numerical codes be used. These doubts spring from a single principal source. Pure Linnaean classifications require ranking to express subordination (that is, the position in the hierarchy). The more detailed the phylogenetic tree, the more rank categories are needed to express completely the relationships through the classification. However, the Linnaean hierarchy and its attendant Rules of Nomenclature have great historical inertia, and it remains to be seen if some alternative system will replace it.

—E. O. Wiley

See also: Classification, Biological; Systematics

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Many standard texts contain brief to extensive discussions of the various rules of nomenclature. However, details change with the adoption of each new Code, so caution is encouraged.

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Lizards

See Reptiles

Lycopod

See Pteridophytes

Lyell, Charles

Portrait of Sir Charles Lyell (Library of Congress)

A child of privilege as the eldest son of a well-off Scottish laird, Charles Lyell was born at the family estate Kinnordy, in the mountain country of eastern Scotland. While he was still a toddler, the family moved to New Forest, near Southampton, England, and he grew up collecting butterflies and aquatic insects in the woods near his home. His father, an amateur naturalist and literary man, had opened up the world of nature to him, although he pushed him to become a lawyer. At nineteen, Lyell entered Oxford University, where his interest in geology was encouraged by his teacher, the famed geologist William Buckland. Eventually, Lyell became a lawyer, but he usually spent his summers hiking throughout Europe, exploring geological formations wherever he went.

During a visit to Paris in 1823, he met the famous naturalists Alexander von Humboldt and Georges Cuvier and then spent weeks studying the geology of the French countryside. Although he was admitted to the bar in 1825, he never practiced. With his father's blessings and financial support, he turned all his energies to making his mark in geology.

Between 1830 and 1833, Lyell published his *Principles of Geology,* which was vastly influential in shaping the modern earth sciences. He established the principle that the geologic past can be understood in terms of natural processes we can still observe today, such as rivers depositing layers of silt, wind and water eroding landscapes, and glaciers advancing or retreating. This idea, known as actualism, had first been put forward by another Scots savant, James Hutton, in his *Theory of the Earth* (1778), some fifty years earlier. Like Hutton, Lyell thought that major geological changes are generally slow and steady, and obey constant, eternal natural laws, operating at about the same intensity in the past as they do today. His development of the idea, and methods of applying it, later came to be known as Uniformitarianism—as opposed to Catastrophism, the then widely accepted view that the earth had been shaped by supernatural forces that were different from any that could be observed today.

In 1831, just before young Charles Darwin embarked on his five-year voyage aboard HMS *Beagle,* a Cambridge professor gave him the first volume of Lyell's *Principles of Geology* (1830) to "read it for the facts and ignore the wild theories." Darwin devoured the book, which was brilliantly written, thoroughly grounded in fieldwork, and seemed to place the study of geology on a new and sensible footing. If slow, small forces operating over immense spans of time had reshaped the earth many times over, why couldn't living creatures develop in a similar manner? "I am tempted to extend Lyell's methods even farther than he does," Darwin wrote. Later, he said, "I really think my books come half out of Lyell's brain. I see through his eyes."

But Lyell, who became Darwin's friend and mentor after the voyage, had a hard time returning the compliment. Although for years he privately encouraged Darwin's evolutionary work, Lyell could not bring himself to endorse his friend's theories in his own popular geology books. Nevertheless, later in life he grudgingly acknowledged the growing evidence. Darwin was frustrated and angry with Lyell's reluctance to support evolutionary ideas wholeheartedly in print, though he did so in private conversations. Lyell simply could not, as he put it, "go the whole Orang."

Lyell subtitled his great work *An Attempt to Explain the Former Changes of the Earth's Surface by Reference to Causes Now in Operation.* His systematic observations of erosion, sedimentation, and volcanic formations enabled him to clarify many long-standing mysteries about the earth's features. What was really peculiar to Lyell, however, are two ideas rarely associated with his *Principles of Geology*—the older ideas that earth and water trade substances and shape each other, maintaining some kind of long-range balance (the steady-state earth), and that time and life proceed in planetary cycles.

Lyell continued to revise his *Principles of Geology* through thirteen editions. It had started out as a long, connected argument, but later became a jumble of bits and pieces added to include newer research. Finally, the book itself became a career and produced substantial revenues for its author.

By 1840, Lyell's uniformitarian principles (encompassing actualism, progressionism, vast geological time scales, a steady-state earth, and more) had exerted a huge influence. It was not until 1863, however, in his book *The Antiquity of Man,* that he publicly supported Darwin's ideas about the continuity of life in the natural world—though he still skirted the issue of humankind. "Perhaps," he grudgingly conceded, "community of descent is the hidden bond which naturalists have been unconsciously seeking while they often imagined that they were looking for some unknown plan of creation."

Inasmuch as Sir Charles Lyell's uniformitarian geology strongly influenced Charles Darwin, it is commonly—and mistakenly—assumed that Lyell believed that the earth itself had "evolved," undergoing progressive or directional change. Oddly enough, Lyell never questioned the very old idea of a "steady-state" earth, and he wove it into his uniformitarian doctrine. Paleontologist Stephen Jay Gould has argued that Lyell's famous books appear in hindsight as a mixed bag of seemingly irreconcilable ideas. For instance, Lyell believed in a steady-state earth, resisted Darwin's demonstrations that evolution had taken place, and believed that time moved in great recurrent cycles. He thought that perhaps, given enough time, the flying reptiles and dinosaurs would one day return.

—Richard Milner

See also: Darwin, Charles; Deposition; Evolution; Geological Time Scale; Glaciation; Hutton, James

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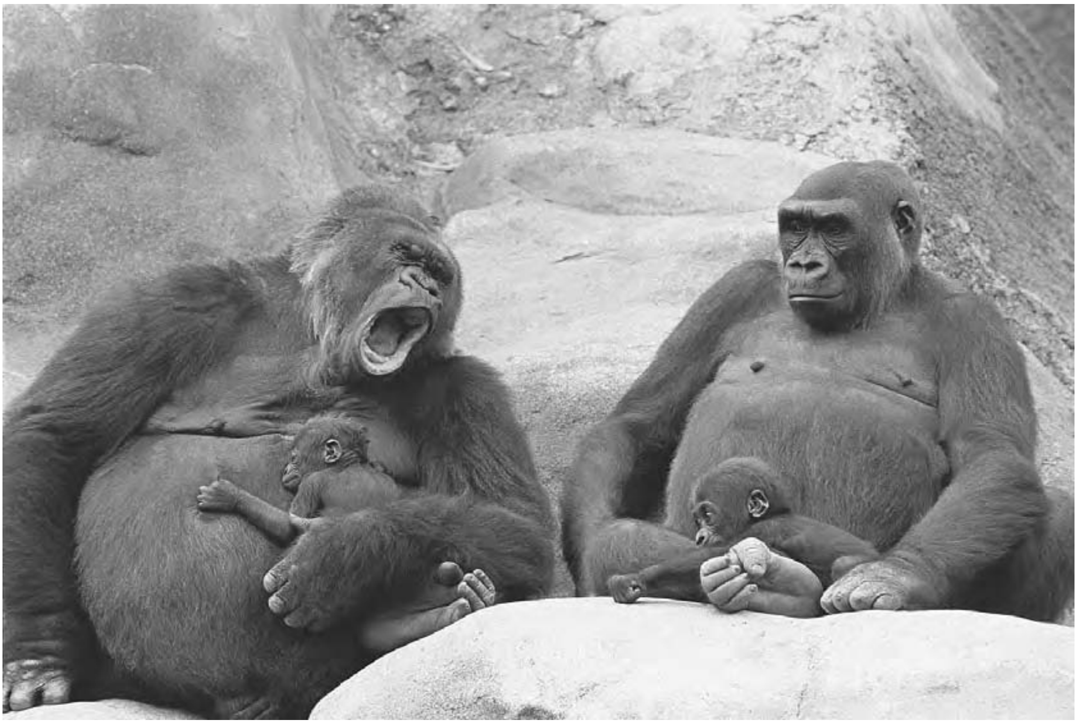
Mammalia

Mammals (Class Mammalia) are warm-blooded, fur-bearing tetrapods (vertebrates with four limbs) that lactate (produce milk) to nourish their young. Humans are especially interested in the biology and behavior of mammals because we are also members of Class Mammalia, and because mammals are aesthetically, economically, and ecologically important.

Mammals are differentiated from other tetrapods by a suite of unique characteristics that include: mammary glands providing milk to nourish offspring; skin that produces unique structures such as hair, nails, horns, and hooves; a diaphragm separating the thoracic and abdominal cavities; endothermy (warm-bloodedness); a lower jaw articulating directly with the cranium; a dentary (one side of the lower jaw) composed of a single bone; and a middle ear containing three ear ossicles. These and other unique shared characteristics support the widely accepted hypothesis that all living and extinct mammals are more closely related to each other (monophyletic) than to any other tetrapod group, such as birds or reptiles.

Class Mammalia is composed of Subclass Prototheria (Monotremata), which includes the two orders of egg-laying monotremes, platypuses and echidnas; and Subclass Theriiformes, which includes the remaining twenty-three orders exhibiting viviparity (live birth). Subclass Theriiformes is divided into two cohorts. Cohort Marsupiala includes the usually pouched mammals (most females possess a pouch, or marsupium) that give birth to altricial (relatively undeveloped) young. Marsupials have extended lactation with associated endocrine controls to nourish their altricial offspring. They also lack a complete placenta, the membranous structure that aids in the transfer of nutrients from the mother's circulation to the developing embryo. Cohort Placentalia is composed of the nonpouched mammals that give birth to precocious (relatively developed) young. Placentals have extended embryonic gestation (longer pregnancy), and a complete placenta that facilitates a more efficient transfer of nutrients from the mother's circulation to the developing embryo.

Mammals are amniotes. Amniota is a grouping of terrestrial tetrapods (mammals, reptiles, and birds) with watertight eggs. Amniote eggs have three membranes (including the amniotic membrane) that aid in protection, water retention, and gas exchange. These membranes, and a protective shell, surround the



Gorillas holding their babies (William Dow/Corbis)

embryo. Amphibian eggs lack extraembryonic membranes and a protective shell, and can be laid only in or near water, so the eggs do not dry out. The watertight egg is an important evolutionary novelty that reduced the necessity for proximity to standing water and allowed extensive land colonization and migration, otherwise impossible.

The first amniotes were small, insectivorous, terrestrial tetrapods and are known from the Early Pennsylvanian Period of the Paleozoic Era, around 310 million years ago. By around 300 million years ago, the reptilian ancestors of mammals had diverged from the evolutionary lineages leading to turtles, lepidosaurs (snakes and lizards), and archosaurs (crocodiles, dinosaurs [including birds], and pterosaurs). These early reptilian ancestors of mammals, Subclass Synapsida, are commonly referred to as "mammal-like reptiles." Although some synapsids exhibit mammalian characteristics, mammals are distinguished from synapsids by the suite of unique characteristics outlined above.

The earliest mammals (and the first dinosaurs) appear in the Late Triassic Period of the Mesozoic Era, approximately 200 million years ago. These first mammals were small and probably reminiscent of living shrews. Although dinosaurs dominated the land during the Jurassic and Cretaceous periods of the Mesozoic, mammals thrived and diversified into more than a dozen families during this era. Many Mesozoic mammal lineages became extinct, but the lineages leading to the three major groups of living mammals (monotremes, marsupials, and placentals) were successful. Marsupials and placentals are more closely related to each other than either is to monotremes, as they share several derived characteristics, including viviparity (live birth). Relationships among the fossil Mesozoic mammal groups, and their relationship to the lineages of extant mammals, are poorly understood.

At the end of the Mesozoic Era, the extinction of the dinosaurs and many other groups of animals and plants opened many previously occupied ecological niches, and also changed the parameters of those niches. In the Early Cenozoic Era (the era we live in, also known as "the age of mammals"), the theriiform mammals (marsupials and placentals) diversified and occupied these newly available and redefined niches. The monotremes apparently did not diversify, and were isolated on southern continents (former Gondwanaland), perhaps since the Early Jurassic. Although the fossil record from the earliest epoch (Paleocene) of the Cenozoic is fragmentary, most of the living orders and many extinct groups are represented by the Early Eocene Epoch (around 50 million years ago).

The nearly 5,000 species of living mammals are arranged into the following twenty-five living mammalian orders: Platypoda (platypuses); Tachyglossa (echidnas); Notoryctemorpha (marsupial carnivores, mice, and moles); Peramelia (bandicoots); Diprotodontia (wombats, kangaroos, koalas, and kin); Didelphimorphia (opossums and kin); Paucituberculata (rat opossums and kin); Cingulata (armadillos and kin); Pilosa (anteaters and sloths); Lagomorpha (pikas, hares, and rabbits); Rodentia (rodents); Cimolesta (pangolins); Carnivora (carnivores, including seals and walruses); Chrysochloridea (golden moles); Erinaceomorpha (hedgehogs and gymnures); Soricomorpha (shrews, moles, tenrecs, and kin); Chiroptera (bats); Primates (primates); Scandentia (tree shrews); Tubulidentata (aardvarks); Cete (whales and dolphins); Artiodactyla (pigs, camels, deer, giraffes, cattle, and kin); Perissodactyla (horses, rhinoceroses, and tapirs); Uranotheria (hyraxes, manatees, dugongs, elephants); and Macroscelidea (elephant shrews).

Many wild and domesticated mammals serve as significant food sources for humans. Some species, such as oxen, aid in vegetable crop production by pulling plows and other equipment; horses, camels, and llamas provide transportation. Hides and fur are used for clothing and adornment. Some species are important pollinators; others incidentally control insect populations. All mammals are integral links in the delicate ecological web; predators control prey populations, whose abundance in turn impacts predator populations, and both predator and prey are links in many other complex biological interactions. Humans value the beauty and intelligence of mammals and enjoy viewing, interacting with, and hunting certain species. Many species are kept as pets, and mammals are also utilized in medical and cosmetic research, the ethical and epidemiological ramifications of which are hotly debated.

—Mary Ellen Holden

See also: Artiodactyls; Carnivora; Cetacea (Whales, Dolphins, Porpoises); Chiroptera (Bats); Cretaceous-Tertiary Extinction; Great Apes; Lagomorpha; Lemurs and Other Lower Primates; Monkeys; Order Uranotheria; Perissodactyls; Permo-Triassic Extinction; Phylogeny; Primates; Rodents

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Marine Worms

See Annelida—
The Segmented Worms

Mass Extinction

A mass extinction is an event during which many kinds of organisms go extinct in a short time. These include species in different habitats and with a variety of modes of life, not only those that are related by evolution or that lived in similar habitats. Understanding mass extinction is important in the context of biological diversity, because knowledge of past mass extinctions puts into perspective today's changes in biodiversity going on all around us.

Mass extinction refers to extinctions occurring at a rate higher than background extinction. We all know that species vary in abundance. We see more starlings than whooping cranes and more mosquitoes than monarchs. Species evolve and, on average, become extinct after about 2 million years. A rare species may be on its way toward extinction as a result of natural causes, perhaps being poorly adapted to its environment, outcompeted by rival species, or more subject to disease or predation than other species in its environment. Background extinction has gone on for billions of years. It is deplorable, perhaps, but extinction is part of evolution. All species face the certainty of extinction, even our own.

The importance of mass extinction was apparent to geologists early in the nineteenth century. They noticed that the fossils in old rocks differ from those in younger rocks. Moreover, the changes in the kinds of fossils found are often rather abrupt. These early geologists defined the eras of the geological time scale on the basis of mass extinctions that resulted in major changes in the kinds of fossils found in the rock. The term *Paleozoic* means ancient life; *Mesozoic* means middle life; and *Cenozoic* means modern life. The boundaries between these three eras are the two most devastating mass extinctions our biota has ever faced.

In the past 545 million years since the beginning of the Cambrian, the earth's biota has been hammered by five major mass extinctions (Table 1). The first of these occurred at the end of the Ordovician. All the organisms that went extinct at that time were marine species, as plants and animals had not yet invaded terrestrial and freshwater environments. Table 2 lists these five extinctions and some of the groups of organisms that were hardest hit during each. The extinction late in the Devonian extended over 4 to 5 million years and was marked as much by the lack of evolution of new species as by the extinction of old ones. As during much of their history, the bivalves (clams) and gastropods (snails) were largely unaffected by the extinction.

The end of the Permian was the greatest crisis the biota has faced, exterminating per-

Table 1
Major Mass Extinctions

Era	*Period*	*Major Mass Extinctions*	*Age (Ma)*
Cenozoic	Quaternary		
	Tertiary		
Mesozoic	Cretaceous	Fifth	65
	Jurassic		
	Triassic	Fourth	206
Paleozoic	Permian	Third	245
	Carboniferous		
	Devonian	Second	364
	Silurian		
	Ordovician	First	443
	Cambrian		
Precambrian time			

Table 2
Organisms Most Affected by the Five Major Extinction Events

Mass Extinction	*Age (Ma)*	*Organisms Most Affected by Extinction*								
		Trilobites	Brachiopods	Corals	Bivalves	Gastropods	Cephalopods	Echinoderms	Fishes	Tetrapods
Cretaceous, K-T (end)	65						■			■
Triassic (end)	206		■		■	■	■			■
Permian (end)	245	■	■				■	■		■
Late Devonian	364	■	■	■			■		■	
Ordovician (end)	443	■	■	■				■		

haps 95 percent of the marine species and reducing the kinds of plants by half. (This extinction is covered in more detail elsewhere in this encyclopedia.) Note that it affected animals and plants on land as well as those in the marine world, as is true of later extinctions as well.

The extinction at the end of the Triassic impacted a wide variety of marine and terrestrial organisms. The clams and snails were affected, and the ammonoids were driven nearly to extinction. On land the tetrapods were decimated, clearing space for the expansion of the dinosaurs in the Jurassic.

The end of the Cretaceous is referred to as the K-T extinction (*K* being the symbol for Cretaceous, *T* for Tertiary). It is the most thoroughly studied extinction and is best known for the demise of the dinosaurs, clearing space for the evolution of mammals in the Tertiary. Besides the dinosaurs, important groups of marine reptiles, the ammonoids cephalopods, and a group of reef-building clams called rudists, also went extinct.

At least twenty-three other extinction events are known in which the number of organisms exterminated is greater than background extinction. With further study some of these may qualify as mass extinctions, and others may be of less importance than previously thought.

What causes mass extinctions? Terrestrial causes have been proposed—volcanic activity, changes of seawater chemistry, climate change, and tectonic uplift. Postulated extraterrestrial causes include impacts of bolides (meteorites and comets) or fluctuation of the sun's radiation. In spite of all the research of the past twenty years, however, the cause of no mass extinction has been tied down or universally agreed upon. Even the cause of the K-T extinction, which is widely believed to have been the impact of a comet or meteorite, is debated, some paleontologists preferring volcanic activity or climate change as the probable cause. Other extinctions are even less well understood, and we can expect that the next decade of research will produce tests of a great many hypotheses regarding the causes of these extinctions.

One intriguing idea is now under careful study. Extinctions may be periodic, occurring about every 26 million years. Such periodicity implies a common cause of all extinctions—for which, however, evidence is lacking.

Many species are adapted in ways that allow them to avoid extinction by coping with environmental changes. A species cannot, how-

Artist's conception showing a meteorite crashing into Earth in an event that some scientists believe caused the extinction of dinosaurs (Reuters NewMedia Inc./Corbis)

ever, evolve so as to be ready for a volcanic eruption or a bolide impact. Species that survived were typically widespread, had various kinds of long resting stages, lived in areas remote from the cause of the extinction, or were simply lucky.

In spite of our abhorrence of the modern mass extinction, the retrospective lesson from the fossil record is that mass extinction has been beneficial. Without it the modern fauna is unlikely to have evolved—including the mammals and, with them, humans.

—*Roger Kaesler*

See also: Extinction, Direct Causes of; Geological Time Scale; Permo-Triassic Extinction

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Mayflies, Stone Flies, etc.

See Arthropods, Terrestrial

Mayr, Ernst

See Evolution

Medicine, The Benefits of Biodiversity to

Biodiversity is essential to the maintenance of human health. Extracts from many species of plants and, to a lesser extent, animals are critical to treating infections, disease, and other illnesses. According to the World Health Organization, about 80 percent of people in the developing world still depend primarily on traditional medicine, and 85 percent of that medicine is derived from plants (Farnsworth et al. 1985). Biodiversity plays a central role in Western medicine also; 57 percent of the top 150 most prescribed prescription drugs are extracted from natural sources or are synthesized based on natural compounds (Grifo et al. 1997). Natural compounds are also a source of inspiration for the development of new drugs and treatments. Furthermore, biodiversity forms the basis of medical models that allow us to understand human physiology and disease.

Traditional healers use local plants and animals to treat a variety of illnesses, and their knowledge has been essential to the advance of medicine, pointing the way to many common drugs The precursors of modern antibiotics—molds—were used as medicine in ancient times and this usage likely originated more than 3,000 years ago. Chinese, Egyptian, Indian, Greek, and Roman healers used molds to treat wounds, inflammation, boils, and infections. The link between mold and antibacterial properties was later made by Sir Alexander Fleming in the 1920s when he found that a fungus (*Penicillium notatum*), a common bread mold, stopped the growth of *Stapholococcus* bacteria. Later another species, *Penicillium chrysogenum,* was discovered that has more powerful antibacterial activity and forms the basis of the antibiotic penicillin and its derivatives used today to treat many infections from pneumonia to tetanus. Microbes continue to be critical to the development of anti-infective agents.

Similarly, aspirin is derived from salicylic acids found in the bark of willow trees (*Salix sp.)* and in a European herb, Queen of the Meadow (*Filipendula ulmaria* or *Spiracea ulmaria* in the older literature*)*. Queen of the Meadow was long used in folk medicine to treat pain and fevers. In 1839, its active component, salicylic acid, was isolated from the plant's buds. Unfortunately, salicylic acid caused stomach upset. In 1899, the Bayer company created a synthetic derivative, acetylsalicylic acid, and called it aspirin, *a* for acetyl and *spirin* for the plant, *Spiracea,* that it was derived from.

A list of some common drugs derived from biodiversity, many of which were originally used as traditional medicine, is given in Table 1. However, most traditional medicines have not been tapped for use as a drug. Ginseng, for example, is one of the most important traditional medicines and has been used to maintain health and treat a range of illnesses across China, the world's most populous country, for over 5,000 years. The principal species used as medicine are Chinese and Siberian ginseng. Studies of ginseng's properties indicate that it is a general stimulant of the immune and nervous systems, and it is often touted for its ability to help the

Table 1
Common Drugs Derived from Biodiversity

Drug	*Source*	*Use*
Atropine	Belladonna* *(Atropa belladonna)*	Relaxant; sedative
Barbaloin, aloe-emodin	Aloe* (*Aloe* spp.)	Antibacterial; purgative; treatment of skin conditions
Codeine	Opium poppy* *(Papaver somniferum)*	Painkiller
Colchicine	Autumn crocus* *(Colchicum autumnale)*	Anticancer agent
Digitoxin	Common foxglove* *(Digitalis purpurea)*	Cardiac stimulant
Ephedrine, Pseudoephedrine	Joint fir* *(Ephedra sinica)*	Bronchiodilator: treatment of asthma; emphysema; hay fever
L-dopa	Velvet bean *(Mucuna deeringiana)*	Treatment of Parkinson's disease
Menthol	Mint* (Menta spcs.)	Nasal decongestant
Morphine	Opium poppy* *(Papaver somniferum)*	Painkiller
Quinine	Yellow cinchona* *(Cinchona ledgeriana)*	Antimalarial
Reserpine	Indian snakeroot* *(Rauvolfia serpentina)*	Treatment of hypertension
Scopolamine	Thorn apple* *(Datura metel)*	Sedative
Taxol	Pacific Yew *(Taxus brevifolia)*	Anticancer agent
Vinblastine, vincristine	Rosy periwinkle *(Catharanthus roseus)*	Treatment of leukemia

*Used in traditional medicine

Sources: Balick, Michael J., and Paul Alan Cox. 1997. *Plants, People and Culture: The Science of Ethnobotany.* New York: W. H. Freeman, pp. 34–35; Grifo, Francesa et al. 1997. "The Origins of Prescription Drugs." In Grifo, Francesa and Joshua Rosenthal, eds. *Biodiversity and Human Health.* Washington, DC: Island Press, pp. 131–163; Oldfield, Margery L. 1984. *The Value of Conserving Genetic Resources.* Washington, D.C.: U.S. Department of the Interior, National Park Service, pp.96–103; Wilson, Edward O. 1992. "Unmined Riches." In Wilson, Edward O. *The Diversity of Life.* Cambridge: Belknap Press of Harvard University Press, pp. 286–287.

body cope with stress. Although studies of ginseng have had mixed results, recent clinical trials with elderly patients indicated that those who took ginseng were less susceptible to respiratory infection. Along with garlic, ginseng is the most popular herbal supplement used in the United States, where alternative therapies are becoming increasingly popular. Renewed interest in everything from herbal supplements to teas stems in part from the rising cost of Western medicine and from new studies that show the health benefits of herbs. Garlic extracts, for example, were found to be better than many penicillins in fighting some bacteria.

A review of plants used as medicines from fifteen countries around the world found that traditional medicines tended to treat four main categories of illness: gastrointestinal, inflammation, skin ailments, and obstetric/gynecological diseases (Balick and Cox 1997). In contrast, most Western drugs are designed to treat cardiovascular and nervous system disorders, cancer, and microbial ailments. There are several possible explanations for these differences. Western drugs are typically targeted at the major illnesses in Western cultures—heart disease and cancer; the drugs are also created by market demands with economic incentives in mind. Also, it is more difficult to diagnose cancer and cardiovascular disease with traditional methods; because the drugs that treat these diseases can be toxic at low levels, it is difficult for a traditional healer to create appropriate doses.

A Matses shaman collects medicinal plants from the rain forest in the Amazon basin, Peru (Alison Wright/Corbis)

Unfortunately, as cultures disappear around the world, the knowledge of traditional medicine disappears. According to studies of language, of the 6,000 spoken languages, most are spoken by indigenous people and about half of their cultures are threatened with extinction (Maffi 2001). Since 1900, more than 90 different indigenous cultures in the Amazon region have disappeared. Indigenous peoples often have extensive knowledge of their local environment. For example, studies of the Chácabo Indians of the Bolivian Amazon found that they could identify 360 species of plants in the forests around them and had uses for 305 of them. Knowledge about plant uses is often passed on through oral traditions, but younger generations are rapidly losing this knowledge.

Sources of New Drugs—Terrestrial

Over millions of years, plants and animals have evolved unique compounds that enable them to combat pests or immobilize prey. Yet only a small fraction of these compounds has ever been tested for medical potential; the chemical composition of less than 1 percent of the estimated 250,000 species of flowering plants has been studied. These chemical structures are a source of inspiration in the quest to create new drugs.

The path to discovering new drugs is long, complex, and expensive. Initially, it begins with either a random or targeted approach. In random screening, a large number of plants or animals are collected and preserved. Alternatively, plants or animals are selected from families that are already known to produce useful compounds or chosen based on their use as traditional medicines. Scientists, known as ethnobotanists or ethnozoologists, spend many months or years working with traditional healers to understand the plants or animals that are used as medicines and to select species for testing. The success rate for random collections is relatively low compared to other methods, though it did lead to the discovery of Taxol, an extract from yew bark, which is used to treat ovarian and breast cancers.

For either approach, once plants have been collected, extracts are prepared from them and screened for different biological properties, such as anticancer or antibacterial activity. This testing, known as a bioassay, formerly required injecting animals with extracts and observing their responses, which was a relatively expensive and time-consuming process. Now the tests are highly automated, and the sensitivity of extracts is examined in petri dishes or tubes. Typically, additional plant or animal material is collected from those extracts that seem most promising. These extracts are further isolated and purified, and compounds that are already known are removed. The molecular structure of novel compounds is then determined. At this point, it is possible to determine if a compound can be synthesized in whole or in part in the lab, or if it must be harvested or cultivated. The compound must go through a series of clinical trials to determine whether it is safe for humans and to evaluate its effectiveness in treating the illness.

With new bioassay methods, it has become feasible to test a large number of extracts from nature relatively easily. Some species are of particular interest, for example, venomous animals are an important source of useful compounds because they produce very powerful chemicals that act against the nervous, muscular, and circulatory systems of their prey. The Fer-de-lance (*Bothrops jararaca*), a deadly, tropical snake, kills its prey by injecting it with venom that causes a fatal drop in blood pressure. Realizing that this property may aid people who suffer from high blood pressure, researchers analyzed it for its potential as a drug. The venom became the basis for two drugs, enalapril (Vasotec) and lisinopril (Zestril), to treat hypertension. These two drugs have reduced the number of deaths from strokes and heart attacks.

Poison Dart Frogs found in much of Central and South America secrete poisons from their skin to immobilize their prey. One species endemic to Ecuadorian lowland rainforests, *Epipedobates tricolor,* has been central to the development of the pain killer, epibatidine. Epibatidine is 200 times more powerful than morphine, but the frog seems to produce it only in its natural habitat not in the lab. Though epibatidine was found to be too toxic to use on humans, it served as a model to create a similar compound, ABT-594, that is nontoxic and lacks the side effects of morphine. It is currently being tested in clinical trials.

Anticancer drugs have been developed from a range of sources including fungus and mouse urine. One drug, called combretastatin, derived from the African bush willow (*Combretum caffrum*), is highly effective against several cancers that produce solid tumors. It functions by cutting off the blood to tumors killing about 85 percent of the cancerous cells. Unlike many cancer therapies, combretastatin does not affect normal blood vessels. In initial clinical trials, it appeared to be highly effective in combination with radiation treatment.

Sources of New Drugs—Marine

Even fewer marine organisms have been analyzed for medical potential. Marine organisms produce many novel compounds, including some of the most powerful toxins on earth. Currently, the aquatic realm is leading the next wave of medical discoveries. In particular, marine invertebrates (such as mollusks, tunicates, sponges, shrimp, and squid) have been found to contain novel, pharmacologically active compounds (National Research Council 1999). Unfortunately, many of these compounds are highly complex, making them difficult to synthesize in the lab and thus not as viable as a drug source.

Cone shells are mollusks that use a special harpoon loaded with a potent venom that paralyzes its prey almost instantly. Some species are so poisonous they can kill humans with small doses of venom. Ziconotide (SNX-111), a painkiller, was created from a peptide in cone shell venom. Ziconotide is hundreds of times more powerful than morphine; what is unique about this painkiller is its targeted action. Injected at the spinal cord, it blocks the channels where pain signals normally travel, basically blocking the pain without causing numbness. There are over 500 species of cone shell and each has 50 to 200 active peptides in their venom, which hold promise for developing very specified drugs without side effects.

Dideminm B, an extract from sea squirts, or tunicates (Family Didemnidae), shows strong antitumor activity. It is the first compound derived from a marine organism to be tested on several cancers in clinical trials. The compound was first isolated from tunicates living in mangroves on Puerto Rico. Related compounds are being extracted from Mediterranean tunicate species. Another anticancer compound is being developed from the spiny dogfish, a species related to sharks.

Of the more than 5,000 compounds derived from marine organisms, about 30 percent were found in sponges. Research is ongoing to study the effects of compounds derived from sponges in preventing and treating tumors. A successful antiviral drug, acyclovir (Zovirax), was created based on structures of cytosine arabionside that were isolated from a Florida sponge (*Tethya crypta*).

Medical models

Biodiversity also provides medical models that allow researchers to understand human physiology and disease. For example hibernating black bears may provide solutions to the treatment of trauma, osteoporosis, or kidney failure. When bears hibernate during the winter, they stop most normal functions (such as eating, drinking, urinating, or defecating) for 150 days (Nelson 1987). But unlike some hibernating animals, bears only lower their temperature slightly (about 5°C) to accomplish this feat.

Researchers are trying to understand the physiological changes that allow bears to survive hibernation. One discovery is a blood protein called Hibernation Induction Trigger (HIT), which slows organ metabolism and reduces blood coagulation. This protein could minimize blood loss for patients being rushed to the hospital after a severe accident. When HIT is injected into nonhibernating mammals, like monkeys, they enter a hibernating state, with a reduced heart rate and temperature.

Bears recycle urea when they hibernate. In humans a toxic buildup of urine is fatal in a matter of days, but bears seem able to break down urea and reuse it to build tissue. Most animals that don't exercise, including people, lose bone mass. But bears survive hibernation with little to no bone loss (Harlow et al. 2001). Understanding these mechanisms could help people who suffer from kidney failure or osteoporosis.

Although sharks have primitive immune systems, they are particularly resistant to cancerous tumors. Early studies found that even when sharks were exposed to cancer-causing agents, they did not develop tumors. Unlike mammals, which produce many different immunoglobulins, sharks only have one type and it resembles the one found in human fetuses. Sharks also appear to have natural antibodies to HIV (the virus that cause AIDs in humans). Understanding how a shark's immune system functions may provide clues to improving the human immune response to cancer or autoimmune diseases (Marchalonis et al. 1998).

Many organisms are ideal for the study of certain organs or diseases. The horseshoe crab (*Limulus polyphemus*) has one of the largest and most accessible optic nerves of any animal. This has made it ideal for the study of animal vision and has provided new understanding of human vision. Blood from the horseshoe crab also provides the most sensitive test for gram negative bacteria. The sea squirt or tunicate is the only animal other than humans to develop stones in its kidney-like organ. This animal as been used as a test case to develop strategies to prevent kidney stones in humans (Chivian 1997).

—*Melina F. Laverty*

See also: Bacteria; Economics; Valuing Biodiversity; Why Is Biodiversity Important?

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Meteorology

Meteorology has been defined as the science of the earth's atmosphere; it deals with its continuously occurring global changes and the daily variations in the conditions of the air and their effects on the earth. The analyses and prediction of weather is probably the most important aspect of meteorology.

Variations in weather are caused by the uneven heating of the earth's surface; the result is that the atmosphere is in a constant state of imbalance. As a result, the weather elements that vary are temperature, humidity, visibility, clouds, kind and amount of precipitation, atmospheric pressure, and winds. Heat from the sun and the gravitation pull of the sun and moon combined with the earth's rotation keep the atmosphere in constant motion.

Weather conditions are a result of the atmosphere's attempt to gain equilibrium, which never occurs as heat is continuously redistributed within the atmosphere-earth system. The movement of cold and warm air masses, cloud formations, and storms serves to counter heat balances. Meteorologists use a continuous flow of weather reports or mathematical models (based on the physics of the atmosphere) to predict the future conditions of the atmosphere. Individual air masses have their own uniform temperature and humidity characteristics, and when they meet they often clash along the narrow boundary between them, the front, producing severe weather conditions.

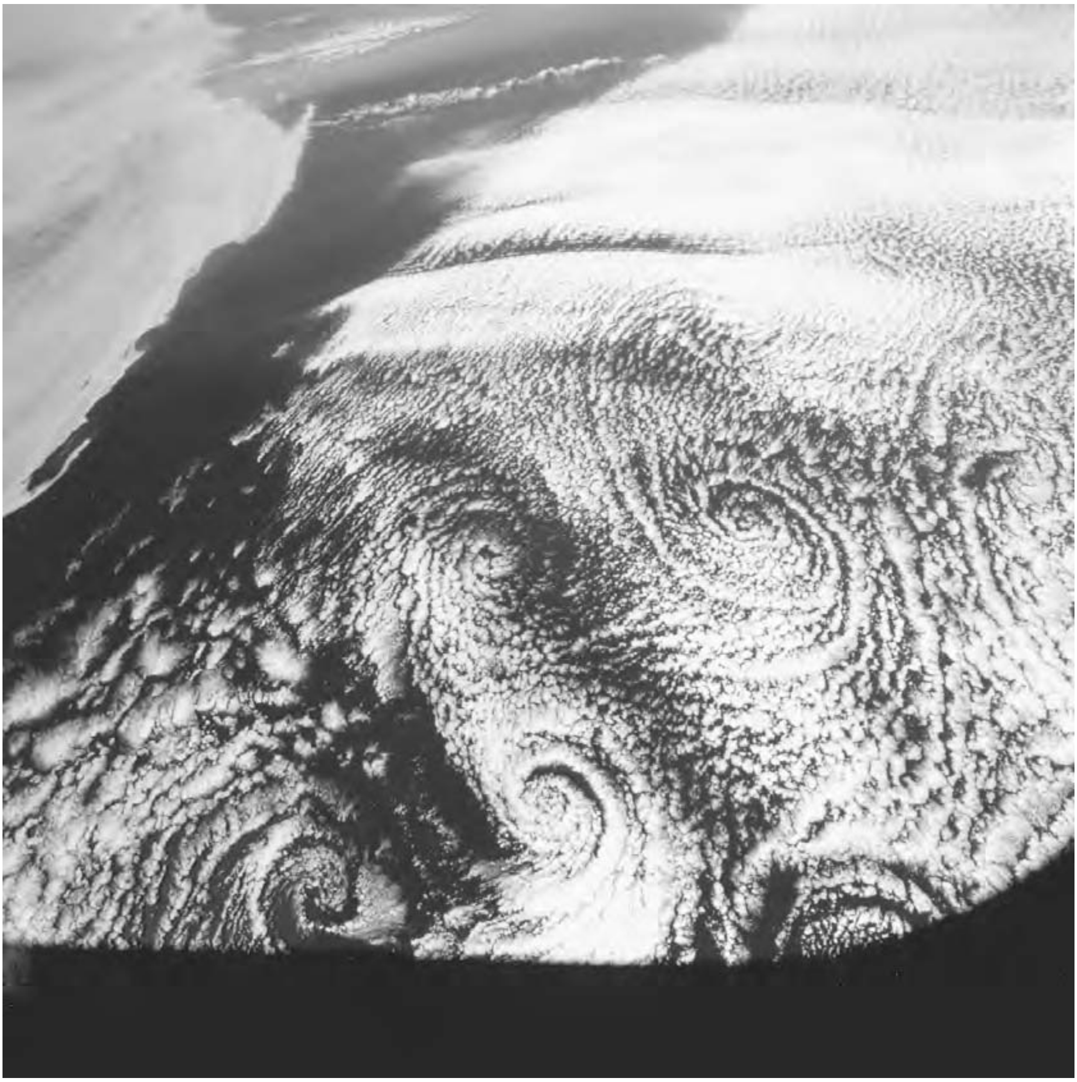
Changes in temperature and pressure are important parameters. A change in pressure usually means that a change in the weather is approaching; rising pressure indicates fair weather, falling pressure a storm. Rising temperature usually indicates that winds are approaching from the south and dropping temperature from the north. In the Northern Hemisphere rising clouds signal that the weather is clearing, and clouds that get thicker and lower usually forecast precipitation. People learn these characteristics by observing the weather patterns where they live, and they usually can predict the daily weather—as probably did ancient people.

However, there are weather patterns and phenomena, such as tornadoes and severe storms, that are hard to predict locally and yet are important to people's security and their property. Today, people who are threatened by severe weather rely on reports from the National Weather Service or from television and radio broadcasts. Beyond the standard instruments—such as the barometer, which measures pressure; the thermometer, which measures temperature; and the hygrometer, which measures moisture—there are modern instruments such as Doppler radar that continuously measure wind, moisture, and temperature in the upper atmosphere. Other radar systems detect and track hurricanes. Many weather stations are fully automated, transmitting data to a central office; several earth-orbiting satellite systems as well as weather balloons also continuously sense the world's weather systems.

In addition, meteorologists are concerned with the changing quality of the air. Although rain is naturally mildly acidic, the term *acid rain* refers to the production of sulfuric acid in the atmosphere from gaseous sulfur compounds emitted by industrial processes. Acidic precipitation often alters the chemistry of water supplies as well as natural lakes; it can kill plants and animals, and it damage structures by corrosion. In places where limestone bedrock occurs, however, the effect of acid rain is reduced, as the acids react with limestone and are neutralized. But in areas such as the Adirondacks in New York state, where the bedrock is granitic and the water already acidic, acid rain increases the acidity.

Thermal inversions occur where warm air overlies cold air. Under these conditions pollutants become trapped and continue to accumulate, creating potential health hazards for people with respiratory ailments. Aside from reducing the sources of air pollution, there is not much to be done but wait until the inversion disappears. In Germany, along the industrial Ruhr Valley one episode of an inversion was so severe and prolonged that schools were closed and private automobile use was banned.

Since weather plays such an important role in our daily lives, everyone is interested in forecasts: about conditions at sea, flood warnings, hail damage to crops, driving conditions, and deciding whether or not to take an umbrella to work. Although there were many



Meteorologists use satellites to study weather events such as this von Karman vortex, a turbulent atmospheric flow pattern, that formed around the Canary Islands. (NASA)

attempts in the past to predict the weather, it was not until the seventeenth century, when the thermometer and barometer were perfected, that accurate measurements could begin. But people were not able to communicate their observations quickly over long distances until the telegraph was invented and first used in 1849 by Joseph Henry of the Smithsonian Institution to make weather maps.

"Everybody complains about the weather, but no one does anything about it" is a common statement. But people have tried to control the weather. Orchard owners and farmers use smudge pots to prevent frosts from killing their crops. People seed supercooled clouds with dry ice pellets or silver iodide dust to produce rain during drought. Seeding has been used to prevent rain, to control flooding, and to disperse fog. In reality, however, it is difficult to tell what the net effects of these attempts are, because it is difficult to compare what would have happened it there had been no seeding.

—*Sidney Horenstein*

See also: Atmosphere; Atmospheric Cycles; Climatology; Global Climate Change; Hydrologic Cycle

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Microbiology

Scope of Microbiology

Microbiology is the study of microscopic organisms (microbes). Since all life, including visible forms, is composed of cells, however, microbiology is a broad and diverse topic that overlaps with many other disciplines. Microscopic cells, whether prokaryotic (bacteria) or eukaryotic (with nuclei), are the evolutionary and physiological basis of all protoctists, plants, fungi, and animals.

Modern microbiology has become increasingly focused on molecular biology, because the unifying role of DNA and its expression in proteins, most often studied in microbes, cuts across major taxa. Thus microbiology is studied not only explicitly by microbiologists but also in cell biology, genetics (whose use of cell culture mirrors the techniques of microbiology), physiology, pathology, ecology, medicine, forensics, marine sciences, agriculture, forestry, and so on. Many of the academic departments in which microbiology is studied, however, have burgeoned only secondarily from a pure curiosity: this is because of the immense practical uses of many areas of microbiology, from the development of new antibiotics in medicine to more effective techniques for crop improvement, medicine, and human hormone production in genetic engineering.

The financial resources devoted to microbiology have tended to bloat its development in certain directions, notably medicine and soil science, and atrophy it in others. But because medicine focuses on the health of humans and animals, and because microbes are considered causal in many diseases (although not all), microbiology has tended to promote an "us-them" mentality regarding microbes that obscures a more in-depth understanding. Without the financial focus, microbiology might also be considered a science of healthy relations among diverse organisms, including those that oversee the flow of biologically important chemicals on a global scale. In this article, then, we will look at microbiology from a nonmedical perspective that emphasizes the connections of microorganisms and their study to underlying ecological health as well as the disruptions we attend to in sickness.

History of Microbiology

Ironically, the huge interdisciplinary enterprise of microbiology was unknown prior to the seventeenth century. The discovery of the subvisible world had to await the invention of powerful enough microscopes. Although there is no clear date for the origin of the microscope, crude high-magnification lenses (the earliest "microscopes") seem to have been around in Holland by 1590. The Italian scientist Galileo Galilei, known for his astronomical studies, had heard by 1609 of the Dutch tube for magnifying objects and, within six months, had invented his own version—actually a reverse telescope with 32X magnifying power. Although this was good enough for observing insects, Galileo's friend Johannes Kepler, who studied lenses, described how a more powerful, compound microscope could be built. Such microscopes were used in 1660, notably by the Englishman Robert Hooke, who described the small compartments in cork, the elastic outer tissue of European oak trees, pieces of which he stuck to the head of a pin beneath his magnifier. Because these cubicles reminded him of the living quarters of a monastery, he called them "cells."

Antony van Leeuwenhoek, a Dutch draper, used another microscope design in the 1660s, and found subvisible beings swimming in pond water, feces, human gums, and semen. The latter were, of course, not microbes but wriggling sperm, similar in appearance to microbes and with an evolutionary connection to microbes. It would be two centuries before Charles Darwin's theory of evolution by natural selection would hint that microbes were our evolutionary ancestors—"hint" is the right word, because it was contentious enough to suggest that we had descended from apes, let alone microbes. Microbes, organisms visible only with the microscope, were considered natural curiosities—an interesting sideshow of freakish beings that could be observed in drawing rooms. Like bird-watching, the microbes attracted spectators, but the activity at first had no practical significance outside of pure intellectual curiosity. (That is true of much science that comes to have practical implications, such as Einstein's relativity theories, which led to nuclear power and nuclear bombs.) Calling them "animalcules," Leeuwenhoek described their number as "so extraordinarily great . . . that [it would] take a thousand million of some of [them] to make up the bulk of a coarse sand-grain."

Since they wriggle and move, and every being not a plant was classified as an animal, these microbes were called "animalcules." Although microbes are really not animals but the evolutionary precursors to all visible life forms, microbiology was ushered in with the discovery by Leeuwenhoek, Hooke, and others of this vast, previously unseen world.

Then, when observation gave way to experiment, further major discoveries were made, some with immense practical consequences. Prior to the evolutionary theory or the evidence of microscopes, it was often thought that life "spontaneously generates": mice arose from rags, flies from veal. In the mid-seventeenth century, however, the British physiologist William Harvey, studying the reproduction and development of the king's deer, showed that every animal comes from an egg. In the seventeenth century the Italian biologist Francesco Redi proved that the maggots in meat came from flies' eggs laid on the meat; and in the eighteenth century, the Italian priest Lazzaro Spallanzani established that sperm were necessary for animal reproduction. Although meat did not give rise to maggots when it was covered by a fly-proof net, grape juice, however, still fermented no matter what was put over it. Yet even though it was proved that the larger animals always come from eggs, it seemed obvious that, because of their prevalence, microbes must be generated continually from inorganic matter. Then, by constructing an ingenious piece of glass apparatus with a long curved neck to keep out bacteria and yeasts, French chemist Louis Pasteur proved that microbes arise only from other microbes. His sterile flask remains on exhibit today in Paris at the Institut Pasteur. Today we know that microbes all come from previous microbes, with the major probable exception of the first cell or cells, thought by most scientists to have evolved from cyclical chemical precursors on an energized but not yet living environment.

Modern Microbiology

Pasteur's experiments in the 1850s combined with Charles Darwin's *Origin of Species* in 1859 set the stage for the development of modern microbiology. The realization of the microbial basis of fermentation, spoiling food, and the associated involvement of microbes in diseased tissues pointed nascent microbiology in the directions of medicine, agriculture, and farming. Microbes were considered germs to be gotten rid of. Today our understanding has become more evolutionary and ecological. Much of the dry weight of our bodies is microbes; our "animal" cells themselves are the result of symbiotic mergers among bacteria. As such, "we" ourselves are microbiological: we require bacteria in our gut, for example, to metabolize vitamin B_{12}. Moreover, one can argue that disease is caused not so much by microscopic germs as by microbial overgrowth, a symptom of a complex ecological body that has come out of balance. Just as we would never ascribe death to the worms in a corpse, we may be too quick to describe disease to the organisms that thrive in its wake. *Candida albicans*, yeast normally found on human skin, are kept in check by bacteria, also normally found in the human body: yet such microbes can overgrow, appearing to be the sole cause of disease.

More than a thousand antibiotics—substances that prevent the growth of most walled bacteria—have been isolated from bacteria and fungi. Penicillin, a fungal (green mold) exudate from *Penicillium crysogenum* or *P. notstatum*, a substance that prevents the cell walls of bacteria from forming, is the most famous example. And microbes, of course, are not confined to the human or animal worlds. They also help lay down mineral deposits such as those of iron and manganese. Tiny ocean shelled protists (forams) and algae can be used to find and date oil-bearing sediments. One of the most significant recent developments in microbiology has been the discovery of a "deep hot biosphere." Microbes (so far only bacteria) have been found to thrive inside rocks on chemical transformations in the absence of light. The existence of these subsurface beings increases the chances that life may also exist on, or rather in, other planets. Metabolically diverse bacteria and fungi, breaking down decaying bodies, returning limited elements to the biosphere and its global circulation, and thriving everywhere on the earth's surface from the poles to the equator, the ocean abyss to the guts of astronauts, are the basis of all health as well as sickness.

—*Lynn Margulis and Dorion Sagan*

See also: Archaebacteria; Arthropods, Terrestrial; Bacteria; Ecology; Evolution; Evolutionary Genetics; Fungi; Medicine, The Benefits of Biodiversity to; Molecular Biology and Biodiversity; Oxygen, History of Presence in the Atmosphere; Paleontology; Protoctists; Soil

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Millipedes and Centipedes

See Arthropods, Terrestrial

Mining

Mining is the removal of materials from the earth's surface or underground that are useful and economically valuable. Strip mining

Surface mines, such as this uranium mine, cause more than just visual scars to the surrounding environment—waters flowing from mines contain substances that are harmful to plants and animals. Additionally, the chemicals used in processing at mines are toxic and can produce gases that are released into the atmosphere. (UN photo)

occurs where the material occurs in long bands and is near the surface. Coal, a fossil fuel, is an example of a commodity that occurs in extensive, relatively thin layers that are usually strip mined.

Open pit mines are somewhat circular, and occur where large amounts of the mined material are removed. Sand and gravel deposits and some types of copper deposits are examples of materials that are removed in that way. Placer mining is the removal of valuable minerals that are enclosed in loose sediments, such as beach and stream deposits. Quarrying refers to surface mining of solid rock that is used for building purposes. Surface mining leaves visual scars on the land by permanently altering the topography and, usually, by piling up large amounts of unwanted materials associated with the mining operation. Normally, the impact can be reduced substantially by putting the materials back into the excavation, covering them with topsoil, and using the surface for agriculture and home building. In some cases, for example sand and gravel pits, most of the material is removed, and all one can do is regrade the surface to its new configuration.

Underground mining does not usually leave a very large scar on the surface. In this kind of mining, the deposits are usually in bands or veins, and as little extraneous material is removed as possible. However, where the operations are extensive, there usually are large piles of unwanted debris. One way to get rid of this material is to backfill the mine, seal it, and restore the hillside where the opening had been. This process also prevents the mine, especially if it is not too far below the surface, from collapsing and leaving large depressions on the surface. Very often the timbers of old mines rot away, causing such collapses in long-forgotten mines.

There are other environmental effects of mining that are more important than the creation of visual eyesores. One has to do with water that accumulates in the mine as groundwater seeps into the opening. Depending on the nature of the ores, the water can become acidified as it dissolves some of the minerals in the mine. For example, many metallic ores are associated with sulfides that oxidize to form sulfuric acid. When these acidified waters flow out of the mine into the surrounding countryside, they can harm forests and animals. There are large numbers of old and abandoned mines that still drain acid waters, and little is done about them. In a few places in the world, where stricter laws are in effect, mine operators must capture this water and put it in holding tanks or lined reservoirs, where it is neutralized.

Often the dumps contain materials that upon weathering are released and wash into the environment. These harmful elements include mercury, arsenic, and cadmium, which contaminate both surface water and groundwater. Very often chemicals used for the processing of minerals are toxic and also produce unwanted gases that are released into the atmosphere.

Materials that are mined are usually divided into two groups, metallic and nonmetallic. We are familiar with the basic metals such as iron, copper, aluminum, lead, zinc, silver, gold, and chromium. Most of these are mined on or below the surface. Nonmetallic resources include sand and gravel, building and crushed stone, limestone for building and making cement, phosphates for fertilizer, salt, and gypsum for making plaster and gemstones. Except for salt, these are usually all removed from surface excavations.

—*Sidney Horenstein*

See also: Erosion; Geology, Geomorphology, and Geography; Pollution

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Mites, Ticks

See Arthropods, Terrestrial

Molecular Biology and Biodiversity

Molecular biology is primarily concerned with the study of the structure, function, and comparative composition of the molecules of inheritance DNA (deoxyribonucleic acid) and RNA (ribonucleic acid). All organisms have RNA in some form, while only some bacteria lack DNA. In general, the information stored in DNA is "translated" by RNA to govern the construction of protein molecules vital to the differentiation, growth, and maintenance of an organism's body. In eukaryotic organisms (those with a cell nucleus—which includes all organisms except bacteria), DNA is found in the chromosomes of the cell nucleus and also in the cellular organelles outside the nucleus that are concerned with energy production—for example, the mitochondria of animals and the plastids of plants.

Molecular data are being used to identify patterns of genetic diversity among endangered and threatened species. Moreover, very little is known about the genealogical (that is, evolutionary) relationships of a large number of species. Researchers use DNA sequence data to unravel the evolutionary relationships of species. Analyses of this tremendous amount

A researcher works in a molecular biology lab at the California Institute of Technology. Molecular data can be used to identify patterns of genetic diversity among endangered and threatened species, which could lead to a better understanding of evolution, geographic distribution, and other life characteristics. *(Vince Streano/Corbis)*

of data will allow us to better understand evolution, ecology, behavior, geographic distribution, and other life characteristics.

Research performed in the molecular biology laboratories has shown that a large number of species have low genetic variation caused by a reduced population size. Thus they are very prone to succumb to global climatic change and environmental degradation. To optimize the chances of species conservation, population size must be maximized, because a large number of individuals have a greater diversity of phenotypes, on account of their genetic variability, than does a smaller group. Thus the most important parameter is the inheritable variation within and between populations of organisms that resides in the variations of the sequence of the four base-pairs (adenine, thymine, guanine, and cytosine in DNA, and adenine, uracil, guanine, and cytosine in RNA), which, as components of the nucleic acids, constitute the genetic material. It is important to determine to what extent reduction of these populations has affected variability.

To understand how such changes could influence the origin of species, researchers are using protein electrophoresis and DNA sequencing to discover and catalogue existing species and to elucidate their evolutionary relationships. Only a small fraction (often less than 1 percent) of the genetic material of higher organisms is phenotypically expressed in the form and function of each cell of an organism; the purpose of the remaining DNA and the significance of any variation within it is still unclear. Genes that control fundamental biochemical processes are strongly conserved across different taxa and generally show little variation, although such variation that does exist may exert a strong effect on the viability of the organism. The opposite is true for other genes, An interesting example is the astonishing amount of molecular variation in the mammalian immune system, which is based on a small number of inherited genes.

New genetic variation arises in individuals by mutations (base substitution, deletion, duplication) in their genes and chromosomes. In organisms with sexual reproduction, mutations can spread through the population by recombination. Other kinds of genetic diversity can be identified at all levels of organization, including the amount of DNA per cell, and chromosome structure and number.

This pool of genetic variation present within an interbreeding population is constrained by selection. The ability to survive results in changes of the frequency of genes among this pool, and this is equivalent to evolution of the population. The significance of genetic variation is thus clear: it enables both natural evolutionary change and artificial selective breeding to occur.

With the aid of mitochondrial DNA (the DNA found outside the cell nucleus in the organelles called mitochondria), polymerase chain reaction techniques, and microsatellite DNA analysis, molecular geneticists and biologists try to determine what characterizes a species and to quantify how close or distant, genetically, species are. Furthermore, these techniques will help to determine whether the DNA within individuals of the same species is adequately diverse to survive drastic environmental changes.

—*Amalia Porta*

See also: Conservation Biology; Evolution; Evolutionary Genetics; Five Kingdoms of Nature; Natural Selection

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Mollusca

The animal Phylum Mollusca (mollusks) is the second largest animal group on earth, after insects. It is also the most numerically dominant taxon in the sea, where the vast majority of molluscan species live. The mollusks include a wide variety of forms, most of which are generally recognized by a hard external shell. Snails (Class Gastropoda) are the largest group, with an estimated 80,000 living species, ranging from periwinkles and cowries, to garden snails and slugs, and to the shell-less nudibranchs or sea-slugs. Clams (Class Bivalvia, formerly Lamellibranchia or Pelecypoda) are the second largest, with about 20,000 living species of scallops, freshwater mussels, giant clams, oysters, and their relatives. Next in terms of living species is Cephalopoda (squids, octopuses, nautilus, and cuttlefish), with approximately 650 species; Polyplacophora or chitons (600 species); Scaphopoda or tusk-shells (350 species); and two smaller groups—vermiform aplacophorans (divided into Caudofoveata and Aplacophora, with a total of 300 species); and the primitive, serially organized limpets called Monoplacophora (11 species).

Mollusks occupy most of the recognized ecological niches, spanning marine, freshwater, and terrestrial biomes, at nearly all elevations and ocean depths. Most mollusks are

Closeup of a sectioned chambered nautilus shell (Bettmann/Corbis)

dependent upon aqueous environments; aplacophorans, monoplacophorans, chitons, scaphopods, and cephalopods are all exclusively marine dwellers. Even land-adapted terrestrial snails largely require moist environments, and they have developed elaborate methods of preventing the desiccation of their bodies and spawn. Most mollusks are free-living, but numerous examples of commensal and parasitic species also exist. Some have antipredator toxins in their bodies (often signaled by bright colors), while others use toxins to subdue their prey. The feeding modes of mollusks include all of the major invertebrate types (herbivores, carnivores, detritivores, and filter feeders), but dietary specialization is common, with representatives that, for example, feed on a single type of algae or cast mucus nets into the water to trap planktonic particles. Although mollusks are famous for slow "creeping," some are modified for more unique modes of locomotion, such as active swimming, passive drifting, or boring into wood or coral. Reproductively, mollusks show examples of dioecity (separate sexes), hermaphroditism (both sexes in the same individual), broadcast spawning, copulation, brooding, and the construction of spermatophores (packets of sperm exchanged between partners) and elaborate egg cases. Mollusks range in size from microscopic to massive: the adults of many snails barely exceed 1 mm, while the giant squid

(*Architeuthis*) is the largest living invertebrate, attaining 20 m in length. Because the hard external of shell of mollusks fossilizes so well, the paleontological record of mollusks is extensive, with nearly 100,000 extinct species recorded from as far back as the Cambrian Era (530 million years ago). This remarkable diversity of form and function, plus a nearly continuous geographical and temporal record, makes the Phylum Mollusca an ideal group for studying almost any aspect of biological diversity.

Although mollusks are best recognized by their calcified external shells, the shell itself is not the synapomorphy (shared derived character) of the phylum. It is rather the shell-forming tissue, called the mantle, that is recognized in that role. The mantle forms a sheath around the body, enclosing a pallial cavity that houses the gills (or, in the case of land snails, lungs); the openings of the reproductive, excretory, and digestive systems; as well as a variety of chemosensory organs. When a shell is present, it is the cells of the mantle epithelium that extract calcium from the environment and secrete new shell material along a growing edge. A shell is absent (lost) in some members of nearly every class, most notably so in octopuses, garden slugs, and sea-slugs.

Other mollusks, such as squids and various close relatives of the sea slugs, have rudimentary or internalized shells that may not be fully calcified. Most molluscan shells (of gastropods, cephalopods, scaphopods, and monoplacophorans) are univalved. Gastropod shells are characteristically coiled, a form retained in the larvae even in those taxa whose adult shell is secondarily uncoiled. The shells of clams two usually subequal valves, held together with hinge teeth, an elastic ligament, and a pair of adductor muscles. The cephalopod shell is typically an internal, chitinous or lightly calcified rod, but the chambered nautilus has a coiled external shell equipped with gas-filled chambers used to control buoyancy. The shell of a chiton consists of eight (rarely seven) plates surrounded by a muscular girdle impregnated with chitinous scales or spines. The aplacophoran shell is represented solely by calcareous scales or spicules embedded in the integument. Monoplacophoran shells resemble those of gastropod limpets but are distinguished by a series of muscle scars on the inner surface. All molluscan shells retain a record of their growth, in the form of the larval shell and a series of growth lines.

Other primitive molluscan characteristics include bilateral symmetry; protostomous, schizocoelous embryonic development (with spiral cleavage, then splitting the mesoderm to form the body cavity, or coelom); reduction of the coelom; cephalization of the nervous and sensory systems into a well-developed head; a muscular foot for locomotion; a chitinous toothed ribbon (radula) for rasping and transporting food particles; an open circulatory system of haemocoels supplied by a three-chambered heart and blood vessels; kidneys (metanephridia) for waste excretion; a sophisticated nervous system of ganglia, nerves, and sense organs; and dioecious reproduction with free-swimming aquatic larval stages (trochophore and veliger). Almost all of these characteristics have been lost or radically modified in at least one major lineage. Cilia and mucus secreted from numerous glands are used for a wide variety of physiological functions, including locomotion; water circulation; gathering, sorting, and transport of food particles; egg formation and deposition; and chemosensation.

The anatomical modifications associated with feeding and reproduction are particularly character-rich and have proven especially useful in molluscan taxonomy and phylogenetic analyses. The molluscan radula provides an excellent example in this regard: impregnated with iron in chitons to facilitate scraping algae from rock surfaces; developed into a hollow dart in cone shells to deliver a dose of toxin to prey; or into a stylet in some shell-less gastropods for piercing individual algal cells and suck the liquid sap. Cephalopods have elaborate nervous systems, including the most complex brain of any invertebrate; eyes that are astonishingly similar (but not homologous) to vertebrate eyes; and chromatophores that make possible rapid color changes and complex behaviors. Several mollusks, notably the squid (*Loligo*) and sea-hare (*Aplysia*), are useful models for neurological research because of the simplicity yet accessibility of their nervous systems.

Gastropods and bivalves are the two most successful molluscan classes, in terms of extant species and ecological diversity. Gastropods are characterized by torsion, a 180-degree twist in the internal anatomy relative to the foot that occurs during larval development. Although the coiled shell might seem to reflect torsion, it does not: the coil is a strategy for increasing body size, while maintaining stability. The characteristics most illustrative of torsion are the anteriorly placed mantle cavity, the U-shaped digestive system (with anus adjacent to mouth), and the figure-eight-shaped nerve cords crossing at midbody (streptoneurous). Many derived gastropods are "detorted" or untwisted (euthyneurous), achieved through concentration of the nervous system or differential growth of the mantle. Part of the success of gastropods is measured by their escape from the aquatic environment, made possible by development of a "lung" from the mantle cavity, along with the ability to avoid desiccation through aestivation (sealing the shell during hibernation) and through development of air-tight egg cases.

Bivalves have entirely lost the head during the course of evolution, and along with it, the characteristically molluscan radular feeding apparatus and the cephalic sense organs (eyes, tentacles). In its place functionally, the bivalve gill has become a filter-feeding organ, complete with ciliated fields to sort particle sizes plus a food groove leading particles to the mouth. Bivalves have most successfully invaded soft sediments, with shell ridges and processes presumably to stabilize their position in the sediment. Another uniquely bivalve characteristic is the byssus, a bundle of elastic protein fibers secreted by the foot that can attach to hard objects as an "anchor." Some bivalves, such as mussels, form extensive beds of individuals attached to rocks and to each other using byssal threads. Other bivalves, such as oysters, cement their shells to hard surfaces and to each other. These assemblages frequently serve as crevice-rich substrata for a myriad of other invertebrates.

Many species of mollusks have had an economic impact on human populations, either beneficially as food sources, laboratory research animals, and ornamentals, or detrimentally as disease vectors, agricultural pests, and biofoulers. Alien molluscan species have played a significant role in the latter regard. In U.S. freshwaters, the Asian clam (*Corbicula manilensis*) spread quickly across the continent in the 1960s, establishing itself as a permanent resident. Then in the 1980s, two species of zebra mussels (*Dreissena polymorpha* and *D. bugensis*) entered North America through the Great Lakes and spread cross-continent even faster. Much has been made of the water-cleansing abilities of zebra mussels. Nevertheless, they create severe economic problems and seriously impact native freshwater mussels (Unionoidea), whose center of worldwide biodiversity lies in eastern North America.

In addition to competing for physical space and particulate food in the water column, zebra mussels physically attach to unionoids, effectively suffocating them. As a result of these impacts, coupled with the adverse effects of human development (damming, dredging/filling, chemical pollution, eutrophication, overcollecting, and so forth), thirty-five species of freshwater mussels are now extinct in North America. Another sixty-nine are formally listed as endangered or threatened, leading one knowledgeable source to estimate that 67 percent of all freshwater mussels are at risk of extinction. In recent years, alien species in marine localities have become more common; examples in the United States are green mussels (*Perna* spp.) in Texas and Florida, and Rapa whelks (*Rapana venosa*) in Chesapeake Bay. The impacts to both human populations and local ecology in these areas are comparable to those experienced in freshwaters, and control measures are proving equally difficult.

Conservation efforts are prominent in the field of malacology, usually by promoting reserve areas of critical habitat, regulating live collecting, and tracking critically endangered species. Organizations with active conservation groups include the American Malacological Society and the World Conservation Union. Marine species are comparatively unaffected by human activities (although there are a few recently extinct marine species, and local extirpations are common). However, freshwater and terrestrial species, whose home ranges are often extremely limited, have been strongly influenced by anthropogenic factors. The two most severely affected groups of mollusks are the unionoid freshwater mussels discussed above, and the landsnails (especially *Achatinella* spp.) of Hawaii. Unionoids have a specialized larval form, called a glochidium, which must attach to a fish before metamorphosing into a benthic juvenile. For that reason, their survival relies upon suitable ecological conditions for fish as well as for mollusks. Hawaiian landsnails have experienced the additional problem of unsuccessful biological control. In the 1950s, the carnivorous rosy wolfsnail (*Euglandina rosea*) was intentionally introduced to Hawaii to combat the alien giant African snail (*Achatina fulica*). Regrettably, *Euglandina* found the native landsnails more palatable than the intended *Achatina*, and contributed significantly toward eradicating fifteen to twenty endemic *Achatinella* species.

Molluscan systematics is far from well resolved, with new species and revised classifications appearing regularly in the published literature. Several important groups have been described only recently: for example, living monoplacophorans were discovered in 1952, although their shells had long been recognized as Paleozoic fossils. In the past twenty years, a resurgence of anatomical studies, plus the application of molecular and phylogenetic (cladistic) methods, has significantly advanced our understanding of natural groups and dramatically changed molluscan classification. One of the best examples is in Gastropoda, where the traditional classification of Prosobranchia (familiar snails such as conchs, whelks, limpets, periwinkles, and cowries), Opisthobranchia (sea-slugs and relatives), and Pulmonata (landsnails and slugs) has been transformed into a large series of equally ranked clades. Likewise, the traditional prosobranch classification of Archaeo-, Meso-, and Neogastropoda has been replaced by a newer, cladistically based taxonomy. Similar changes are occurring throughout Mollusca, as current research reworks long-held dogmatic ideas.

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See also: Alien Species; Phylogeny

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Monkeys

A garden-variety term commonly applied to an evolutionary grade of primates, excluding the prosimians (lemurlike and tarsierlike forms), the apes, and humans. This array of monkeys are typically divided into two main groups—the New World monkeys and the Old World monkeys—that reflect not only their current geographic distributions but also, more important, their independent evolutionary histories. These two main divisions can be technically divided into two infraorders called Platyrrhini (which contains only the New World monkeys) and Catarrhini (which contains the Old World monkeys, apes, and humans) within the Hyporder Anthropoidea. These infraorders were established in 1812 by the French zoologist E. G. Saint-Hilaire and chosen simply in reference to the external structure of the nose. Although not all monkeys exhibit these features, Saint-Hilaire felt that the Catarrhines are characterized by nostrils that are close together and tend to open downward, whereas Platyrrhines have widely separated nostrils that tend to open toward the sides. In addition, these infraorders are further characterized by differences in the bony parts of the ear and in their dentition.

Platyrrhines have an eardrum (tympanum) that is encased in a bony ring called the tympanic ring, and both are located at the surface of the skull. New World monkeys also have three premolar teeth on both sides of the upper and lower jaws, giving them thirty-six teeth. Catarrhines, on the other hand, are characterized by a tympanum that is situated well inside the skull and is connected to the outside by a bony tube called the external auditory meatus. Old World monkeys also have only two premolars in each quadrant of the mouth, giving them thirty-two teeth. Despite these general differences, the more important distinction between Platyrrhines and Catarrhines is their evolutionary trajectories. It is thought that both groups arose from a common primitive lemurlike primate at a time when landmasses representative of present-day North America and Europe were still connected. However, by the end of the Paleocene Epoch (55 million years ago), these landmasses had separated, thereby sparking the evolutionary divergence of the two main monkey groups, with Platyrrhines moving toward modern-day Central America continuing into South America, and Catarrhines moving into modern-day Europe continuing into Africa.

New World Monkeys

There are approximately sixteen genera and fifty species of living New World monkeys recognized today distributed throughout the tropical regions of Central and South America. Although new species of monkeys are being discovered as more research is undertaken in the New World, these same environments are fast becoming overdeveloped and destroyed because of human encroachment. This destructive activity has put many more species on the brink of extinction. Primatologists consider New World monkeys to be the most diverse in terms of diet, locomotor habits, and overall morphology, but more research is needed. On account of the little that is known about New World monkeys, taxonomic ranking seems always to be in constant revision. Currently, New World monkeys are recognized to constitute a single superfamily called Ateloidea. Within Ateloidea, New World monkeys constitute two families: (1) Atelidae, which contains two subfamilies: Atelinae, containing the spider monkeys, the Muriqui, the howler monkeys, and the wooly monkeys; and Pitheciinae, containing the night monkey, the titi monkeys, the bearded sakis monkeys, and the uakaris monkeys; (2) Cebidae, which also contains two subfamilies: Cebinae, containing the capuchin monkeys and the squirrel monkeys; and Callitrichinae, containing the marmosets and the tamarins.

New World monkeys are characterized by all members being arboreal; no living species of New World monkeys has adopted a terrestrial way of life. They inhabit tropical forests from sea level to forested regions approximately 2,500 m (8,500 ft) in altitude. Most New World monkeys are slender-bodied animals with lean limbs and long tails. In a few species of New World monkeys, the tail is prehensile and is generally used as a “fifth hand” to aid in grasping branches when traveling from one treetop to another, or when foraging for food. New World monkeys lack the buttock pads, known as ischial callosities, typical of the Old World monkeys. Females generally lack the sexual skin around the genitals that enlarges and changes color during estrus (when females are sexually receptive). However, many females have external genitalia that may become enlarged and swollen in appearance during estrus.

New World monkeys also lack a true opposable thumb (pollex), or they are very limited in the degree of opposability—the pollex is set apart from the other digits and can be moved to bring its fleshy lower portion into contact with the fleshy lower portions of one or more of the other digits. This pseudo-opposability reflects the lack of rotation at the wrist-thumb joint (metacarpotrapezium joint complex), but there is a downward movement of the pollex and the bending of the hand, which results in the meeting of the pollex and one or more digits for a functionally opposable grip. Marmosets generally lack even this pseudo-opposability, because their pollices are relatively shorter and their hands are not long enough to bend and meet the pollices—which explains why marmosets never eat with only one hand. Spider monkeys have either a vestigial pollex or lack one altogether, yet these larger New World primates are equipped with prehensile tails. Moreover, all New World monkeys have opposable greater toes (hallices) that aid in grasping branches during locomotion. New World monkeys range in size from the pygmy marmoset, *Cebuella pygmaea*, which typically weighs as little as 70 gm (2.5 oz), to the large spider monkey, *Ateles*, which weighs in at 10 kg (22 lb). Overall, we know less about Platyrrhines than all other primates, including the prosimians.

Members of Callitrichinae are generally small, weighing no more than 500 gm (1 lb), and are distinct from other New World monkeys by having laterally compressed nails (which are clawlike) on all digits except their hallices. Marmosets and tamarins also lack a third molar, giving them a tooth count of thirty-two, making them similar in number to Old World primates but not in tooth types. Marmosets inhabit moist and dry forests along the Amazon River basin and are the smallest of this group. Living in monogamous pairs, they typically feed on insects and fruit. Females generally give birth to twins, after which it is the job of the male parent to care for the young.

Members of Cebinae, known as squirrel monkeys (*Saimiri*), are somewhat larger than the callitrichs (up to 100 gm) and generally live in polygamous groups of up to fifty individuals. Squirrel monkeys have a thigh that is shorter than their shin, which aids in generating more force when leaping. They feed on fruit and insects but can survive by consuming only insects. The larger Cebid (*Cebus*) weighs up to 4 kg (8 lb), is skilled in leaping, and has developed a partially prehensile tail to aid during its acrobatic leaping. Their tails are unlike those of the Atelinids, in that only the tip of the tail has grasping capabilities. They too live in polygamous groups of up to thirty individuals.

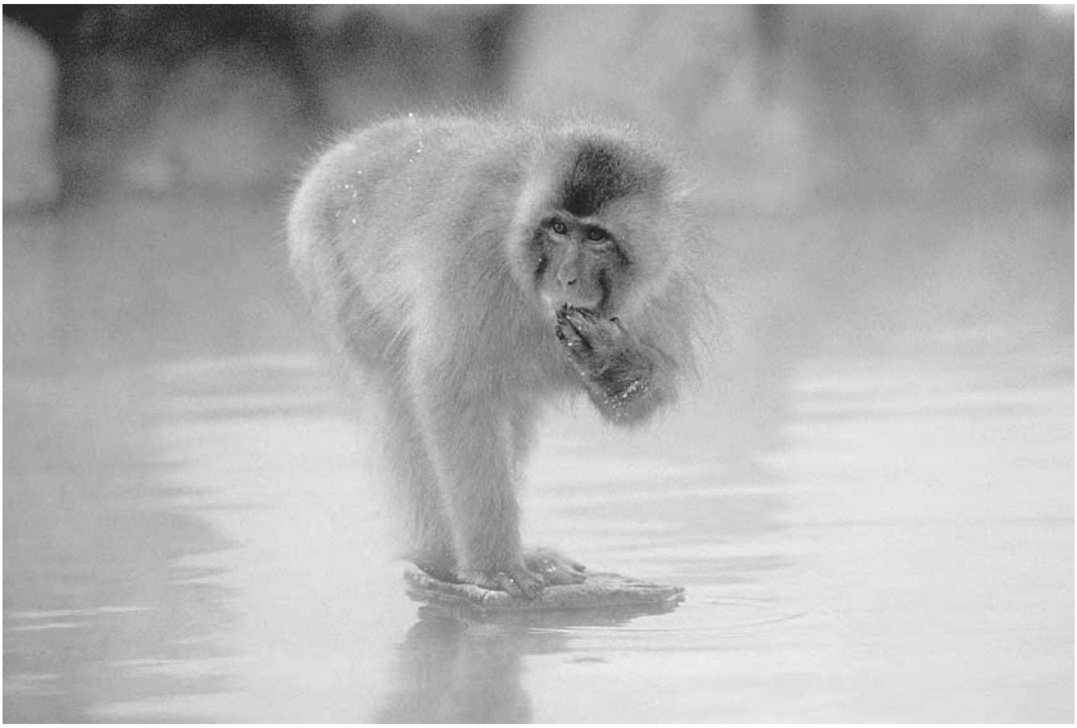
Members of the Atelinae subfamily are the largest of all Platyrrhines and live in polygamous groups of twenty individuals; however, roaming groups more often typically contain only four to eight individuals. Spider monkeys tend to live in mature moist forests and eat fruit and leaves, enjoying a higher percentage of ripe to unripe fruit . Howlers, on the other hand, prefer undisturbed dry to wet forests and woodland savannas and tend to eat more unripe fruit than spider monkeys. Members of Pitheciinae include the colorful nocturnal owl monkey that lives in pair-bonded social groups, and the diurnal titi monkeys that also live in small, monogamous groups of no more than six individuals. Both eat fruit, leaves, and insects. The owl monkey occasionally feasts on small vertebrates and eggs.

Old World Monkeys

There are approximately fifteen genera and eighty-two species of living Old World monkeys recognized today, distributed throughout Africa and Asia from dry grasslands and savannas to rain forests and snowy mountains. Unlike the New World monkeys, a wealth of knowledge is available for Old World monkeys, because of their distribution in areas of high human population. That being the case, seldom are new monkey species discovered, but dozens are flagged for extinction if something isn't done to alleviate the pressure caused by competition with humans. Despite their wide geographic distribution, Old World monkeys are a relatively similar group that constitutes one superfamily called Cercopithecoidea. Within Cercopithecoidea, Old World monkeys constitute only one family, the Cercopithecidae, which is further divided into two subfamilies: (1) Cercopithecinae, containing the guenons, macaques, and baboons; and (2) Colobinae, containing the leaf monkeys and colobines.

Old World monkeys are characterized by many species having adopted a terrestrial manner of life. They inhabit most of Africa in a variety of environments, but water seems to be a common limiting factor for those living in drier grasslands and savannas. They also inhabit higher latitudes, with some macaque species keeping warm during snowy days by sitting in naturally heated rock-filled pools of water.

Unlike their cousins, the New World monkeys, Old World monkeys do not have prehensile tails. In fact, many species have either flimsy, uncontrollable tails or extremely reduced tails. Old World monkeys have ischial callosities—thick, rugged calluses that cover the ischial bone (the bony portion of the buttocks); they are used for sitting for long periods of time with little discomfort, such as sleeping in trees or on rock ledges. In almost all species of Old World monkey, forelimbs are similar in size to the hind limbs, which may



Japanese Macaque (Michael Freeman/CORBIS)

reflect their quadrupedal locomotor skills. All species except the colobus monkey have feet and hands of moderate length, and opposable thumbs and great toes. The colobus typically has a reduced pollex almost to the point of being just a nub. The opposable pollex in Old World monkeys allows for finer manipulation of objects and eating with one hand. Cercopithecinae are distinct from Colobinae on account of their cheek pouches (muscular cavities that extend below the jaw), which are used to store food for consumption at a later time. Colobinae are distinguished from other Old World monkeys by their complex stomach, which is partitioned into several chambers and equipped to break down usable nutrients from their cellulose-rich diet. Old World monkeys have bilophodont cheek teeth (molars with two pairs of cusps evenly distributed on the tooth surface, and each pair connected by a cross ridge or loph). Some species of Cercopithecinae are highly sexually dimorphic (that is, the males are much larger than the females). Old World monkeys vary in size, ranging from 2 kg (5 lb) in adult talapoins to adult male mandrills, which may weigh up to 45 kg (100 lb).

Members of Cercopithecinae known as mangabeys are medium-size monkeys generally restricted to forest dwelling. Mangabeys have large incisor teeth that allow them to exploit hard seeds that are not accessible to other species. Guenons are the African long-tailed monkeys that are typically brightly colored and generally live in forest or scrub savanna. Males are much larger than females. Male vervets are easily recognized by their bright blue scrotum and red penis and perineal patch.

All species are typically omnivorous, with eclectic diets that include fruit, insects, eggs, rodents, shoots, flowers, leaves, and buds. Macaques are to some extent terrestrial monkeys that live in large groups with multiple males. Baboons are the largest members of the Cercopithecinae and are terrestrial. They live in extremely large close-knit groups of up to 300 individuals, moving across the landscape like regimented soldiers. When an outside male tries to enter the group, he is faced with several family-oriented subgroups that must be penetrated if he is to be accepted.

Members of Colobinae include the proboscis monkey, which lives in Borneo tidal mangrove swamps. This monkey, *Nasalis*, is the largest of the Asian colobines (weighing up to 22 kg [52 lb]) and is distinct from all other primates with its large, protruding, fleshy nose. The langurs (*Semnopithecus*) reach weights similar to that of *Nasalis* and are highly adapted to living in mountainous regions, such as the troops living in the Himalayas. The true colobines (genus *Colobus*) live in the equatorial regions of Africa. Population densities vary greatly, with some species (*Presbytis*) congregating in groups of up to 125 individuals per square mile, while much larger groups are found in the Hanuman langurs, whose groups have up to 2,000 individuals per square mile. Smaller groups are typical in less forested regions.

Fossil Monkeys

The oldest-known New World monkeys are rare. *Branisella* consists of several jaw fragments recovered from Oligocene deposits in present-day Bolivia that date to 27 million years ago. Other fossils—*Dolichocebus* and *Tremacebus*—are of Oligocene age but found in Argentina; absolute geological dates are not available. *Tremacebus* is represented by an almost complete skull and jaw fragment, exhibiting both lower and higher primate characteristics, and is thought to be ancestral to *Aotus* (the owl monkey). *Dolichocebus* is represented by a highly distorted skull and a few isolated teeth, and is thought to be ancestral to the squirrel monkey. These phylogenetic associations should be considered tenuous at best.

Perhaps the earliest occurrence of an Old World monkey in the fossil record includes *Parapithecus* and *Apidium*, discovered in Oligocene deposits in the Fayum region of present-day Egypt and dated at 30 million years ago. Authorities still argue over their evolutionary relationship to other catarrhines. However, a frontal bone and tooth recovered from 19-million-year-old deposits in Uganda show that a common ancestor to both subfamilies (ceropithecinae and colobinae) was already present in the fossil record. This is further supported by the presence of *Victoriapithecus*, a member of cercopithecinae, recovered in 18-million-year-old deposits on Rusinga Island in East Africa.

—*Ken Mowbray*

See also: Great Apes; *Homo Sapiens;* Primates

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Mountains

Simply defined, mountains are large landforms that rise more or less abruptly from the surrounding low places. In general, mountains

Mountains near Asheville, North Carolina (From the collections of the Library of Congress)

are parts of the earth's crust that have been raised above their surroundings by upwarping, folding, buckling, faulting, or volcanic eruptions. These deformations and resulting uplifts are directly or indirectly the consequence of plate tectonics.

When a continental plate collides with an oceanic plate, the oceanic plate is subducted below the much thicker continental plate, and sediments from the seafloor are scraped off and pushed, folded, and pasted onto the adjacent continent—often forming a series of parallel mountain belts. Associated with the folded and faulted rocks are volcanoes whose magma is derived from the melting of the subducted ocean plate, which intrudes and erupts within and on the sediments. A good example of this type of mountain is the Andes Mountains on the western side of South America.

When continental plates collide they crush against each other, resulting in massive folded belts, and remain towering features as long as the tectonic zone remains active. The Himalayan Mountains, driven up by the collision between the Indian and Eurasian plates, are a classic example. Uplift rates of about 1 cm per year are great enough to create very high and steep topography. Mountains such as these are high enough to alter atmospheric circulation and present a barrier to the migration of plants and animals. They, like lower mountains, produce a feature termed the *rain shadow*, by means of which moist air currents forced up the windward sides of mountains cool and drop their moisture as rain or snow. Once over the mountain the dried-out air moves across a parched terrain because it supplies little if any precipitation. The Rocky Mountains of Colorado are a good example and illustrate how mountains can control the types of plants and dependent animals in a region.

Once mountain-building activity has shifted elsewhere, erosion becomes the dominant process, and the mountains wear away. However, the worn down mountains—such as the Appalachians of the eastern United States—mark the place of former plate interaction. They are an example of one of the most striking features on the earth's surface, the long mountain belts that are found on all continents, composed of numerous parallel ridges that resulted from plate collision.

Where the accumulative stresses are tensional rather than compressional, a series of fault block mountains can result. In the Basin and Range of Nevada and adjacent states, tension has pulled the earth apart as a result of arching and subsequent downward movement of segments of the earth's crust caused by collapse. The consequence is a series of more or less parallel high mountains interspersed with the down-dropped basins. Fault block mountains such as the Sierra Nevada occur where the eastern side has dropped downward along a fault and the mountain mass has rotated upward.

Volcanic mountains, cone-shaped edifices resulting from the extrusion of magma from a vent, may occur singly or, usually, in a series. Once volcanism ceases the volcano erodes rapidly and may eventually leave a feature called a neck—the material that solidified within the vent. Eventually the neck will disappear also. In the western United States, Mt. Saint Helens and Mt. Rainer are examples of active volcanoes, ones that have erupted in historical times.

Calderas are volcanic mountains that have collapsed as a result of the rapid extrusion of magma, leaving a large circular basin that is usually filled with water. Calderas form during an eruptive phase when large amounts of magma are extruded, leaving behind a partially empty magma chamber into which the overlying volcanic edifice collapsed.

The major mountain system in the world is the midocean rift, built along divergent plate boundaries; it is about 60,000 km long and 2,000 km wide. Iceland, like all oceanic mountains, is volcanic and is one of the few places where the midocean ridge is above sea level. Rates of spreading movement along the rift are 2 to 6 cm per year.

Many oceanic mountains result from "hot spots" that bring large volumes of magma to the surface, and frequently form high volcanic islands aligned in a row. Iceland stands above sea level because it is located where a hot spot coincides with the midocean ridge. Hot spots also produce massive volcanoes on the land; none have been active recently, however, so they have eroded forms and do not form imposing features. Examples of this type of volcano are found in Yellowstone National Park in Wyoming, and Lake Toba in Sumatra.

Island arc mountains are created where an oceanic plate dives downward, underthrusting the adjacent oceanic plate and creating a series of volcanoes. The Aleutian Islands and the Japanese Islands in the Pacific Ocean are examples. The rate of decent is 5 to 12 cm per year.

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See also: Glaciation; Volcanoes

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Museums and Biodiversity

Museums of natural history have recently come to the forefront in society's efforts to understand the nature of biodiversity, why biodiversity is valuable, how and why biodiversity is rapidly being lost in the natural world, and what can be done to stem the tide of the current Sixth Extinction—the rapid loss of biodiversity that some biologists think is occurring at the rate of 30,000 species a year, or three species every hour.

Although some small museums devoted to the display of biological, geological, and anthropological specimens were founded several centuries ago, the real beginnings of modern natural history museums took place in the mid–nineteenth century—the same time at which art museums, symphony orchestras, operas, public parks, zoos, and many other institutions came to be seen as vital to the cultural life of major cities. This was the era, for example, when the British Museum and its sister institution, the Natural History Museum, were established in London; in the United States, the Metropolitan Museum of Art and the American Museum of Natural History, as well as the Smithsonian Institution in Washington, D.C., were founded. Today there are important natural history museums in every major city in Europe and the United States. In addition to the American Museum of Natural History (in New York City) and the Natural History Museum of the Smithsonian complex on the Mall in Washington, D.C., the Field Museum of Natural History (Chicago), the Academy of Natural Sciences in Philadelphia, as well as major natural history museums in San Francisco, Los Angeles, San Diego, Denver, and elsewhere in the United States are all world-class institutions.

Natural history museums are often the main source of information about the natural world available to city dwellers. Natural history museums serve as a source of both entertainment and education to people of all ages, and of the 3 million visitors annually to New York's American Museum of Natural History, some 2 million are children; most visit the museum on field trips from their schools in the city or surrounding suburbs.

Natural history museums have several different roles and functions—all devoted to the development and dissemination of knowledge about the natural world. Most obvious to the general public are the exhibitions, often utilized in conjunction with educational activities designed by professional educators on the museum's staff or in the school system. Behind the scenes, however, museums are repositories of natural history collections—rocks, fossils, archaeological and other cultural artifacts, and specimens of the entire spectrum of life's diversity. Finally, most major museums are also scientific research institutions, dedicated to finding, describing, and analyzing the natural world, chiefly through the study of specimens in its collections and those of its sister institutions. As members of research institutions, the scientific staff are often directly engaged in the task of training young scientists to ensure that the research effort continues.

This entry will discuss all three aspects of the work of natural history museums, with a special emphasis on the role museums have recently come to play in dealing with the challenging issues posed by the current biodiversity crisis.

Exhibitions. Originally, natural history exhibitions consisted of endless rows of specimens and artifacts; in some instances, nearly the entire collection of, for example, birds, Devonian brachiopods, or arrowheads would be lined up in cases, usually with little or no written material ("label copy") beyond simple identification of where and when the object was collected. Those days are now gone—superseded by advances in exhibition concepts and technology, and the desire to educate.

One major advance was the invention and perfection of the techniques of constructing dioramas. Museums rarely keep living animals, so they cannot compete with zoos in displaying the living world in terms of live specimens. But museums can go to the necessary time and expense to construct accurate reconstructions of habitats in the natural world—and beginning especially in the 1920s, expeditions to collect specimens and to photograph and paint places all over the globe led to the creation of many stunning diorama displays. Usually, dioramas have curved plywood back walls that are painted (often by well-known artists) to depict the background with meticulous accuracy, and to blend that background into the three-dimensional foreground, which is filled with soils and rocks, vegetation, and (quite often) the reptiles, mammals, and birds of that particular setting. If you want to know what it is like to visit a water hole on the savannas of Kenya, or to encounter a group of mountain gorillas in the rain forests of Rwanda, the dioramas of the Akeley Hall of African mammals at the American Museum of Natural History are the next best thing to being there (and sometimes better—it is extremely difficult to observe gorillas in the wild!). Zoos cannot capture the details of environment nearly so well (the animals tend to destroy it), and televised nature shows, while often entertaining and informative, do not convey the vivid sense of actually being there that a good diorama does.

Recently, natural history museums such as the American Museum have begun to take on serious modern issues, such as the biodiversity crisis (see Sixth Extinction). Dioramas historically have portrayed nature in a pristine, unspoiled state. When the Hall of Biodiversity was being constructed in the 1990s at the American Museum of Natural History, it was difficult to come up with a natural history scene suitable for a diorama that hadn't already been built somewhere in the museum. But it was also soon realized that virtually none of the scenes depicted in these older dioramas still exist in their native, wild state. For example, the mountain gorilla scene had been recently photographed by a museum staff member, whose photo revealed that the forests on the distant volcanoes had all been cut down and turned into terraced farmland.

Thus the scientists responsible for planning the contents of the Hall of Biodiversity realized that there was both an opportunity and even an obligation to depict the natural world, not in its largely gone pristine state, but as it now is: severely changed by the hand of humanity as population pressures and the exploitation of natural resources put relentless pressure on all environments.

The hall features a single 100-foot-long diorama, with many innovations made possible by modern technology. It portrays the rain forest in its present condition in Dzanga-Sangha National Park of the Central African Republic—portraying the forest in its wild, pristine state in the opening section—but showing how elephants, first, and then people have encroached upon the forest and damaged it. The museum mounted several expeditions to collect specimens and to photograph the environment in high-definition still and motion pictures. Instead of the traditional paintings, the background is photographic, including four motion picture segments. The sounds and smells of the forest are also included, to impart a sense of realism. Exhibition specialists made rubber casts of trees, which were then used to construct facsimiles of the trees for the diorama. More than sixty species of plants and over 600,000 leaves were cast in plastic, then painted. The overall effect is extremely realistic.

In the first scene—the rain forest at dawn—the visitor sees (and hears and smells) the rain forest in its primal state. Periodically, on the background film, a band of Ba-Aka people walk into view, conducting a search for medicinal plants; the middle scene, showing forest elephants in the background at the daily mud bath in the open "saline," also shows the effects that elephants have on the trunks of trees. In the final scene, the effects of slash-and-burn agriculture and logging are depicted: Even on the edges of this protected natural park, inroads are constantly being made into the integrity of the forest. Burned and cut tree stumps, adjacent to a field of grain, are all that is left of the forest in this scene.

The Hall of Biodiversity is neither a hall of ecology nor a hall of evolution, but rather an exhibition that says, at its core, that biodiversity consists of all the species of the world ("evolutionary biodiversity") in all the ecosystems of the world ("ecological biodiversity"). To understand biodiversity, one must understand both aspects simultaneously. The exhibit deals with the rest of the world's ecosystems—and the problems they face—through a sixty-foot-wide slide-and-film show, showing different environments in both pristine and degraded form.

Evolutionary biodiversity, on the other hand, is depicted in a 100-foot-long "wall of life," upon which hundreds of specimens from each of twenty-seven subdivisions of life depict the entire spectrum, from bacteria to horseshoe crabs. A "crisis center" deals in greater detail with habitat destruction, human population growth, and solutions that have been proposed for the biodiversity crisis. There is also an introductory film outlining the major themes of the hall, and a film presentation of three or four current issues in biodiversity loss and conservation that is changed every two months. Visitors can also use kiosks to get on the Internet and explore biodiversity issues in even greater depth.

The Grande Galerie d'Évolution of the Museum Nationale d'Histoire Naturelle (National Museum of Natural History) at the Jardin des Plantes in Paris is another spectacular example of an exhibition devoted to biodiversity. Originally opened in the nineteenth century and featuring the great collections arranged by the famed scientist Baron Georges Cuvier, this building had been closed for nearly a century. Architecturally renovated and newly reopened in the mid-1990s, the Grande Galerie features a dramatic parade of African mammals in the center of the main floor—with periodic dimming of the lights to simulate a storm crossing the savanna to the sound of thunder.

Three additional floors, constructed as balconies ringing the walls of the building, discuss topics as diverse as DNA and garbage disposal in present-day Paris. A set of three relief maps show the growth of Paris from a primordial settlement along the banks of the River Seine, graphically illustrating how the growth of cities is at the expense of the natural world. A particularly poignant part of the exhibition is a side room, very dark and quiet, lined with the mounted specimens of extinct, or highly endangered, species. It is like walking through a graveyard.

Other museums have mounted smaller exhibitions on environmental issues, and more programs are constantly in the works. Museums are beginning to respond to this very real crisis faced by life on earth, and through their exhibitions they are beginning to educate the public on biodiversity: what biodiversity is, why it is important, how it is being destroyed, and what can be done about its destruction.

Collections. Natural history museums are literally "libraries" of biodiversity. Because many museums had their origins in the early days of scientific and commercial exploration during the nineteenth century, collections were made in depth of every conceivable sort of paleontological, geological, archaeological, and cultural specimen or artifact—including, of course, specimens of the living world. Indeed, one way to tell how much we have lost is by consulting this enormous treasure-trove of specimens.

The specimens on exhibit in any museum at any one time are just the tip of the iceberg compared with the often vast collections that are stored away out of public view. The American Museum of Natural History, for example, has 32,000,000 specimens, ranging from Northwest coast Indian war canoes, elephants, whales, and dinosaurs to tiny hummingbirds, formaniniferans (microfossils), beads, and even DNA samples. Each type of specimen poses its own difficulties in terms of proper storage and preservation: DNA needs to be frozen; archaeological woven materials need to be stabilized; skeletons need to be cleaned (usually by dermestid beetles, which pick the bones clean); fossils need to be removed from their rocky tombs; worms, fishes, snakes, and clams need to be "fixed" in the chemical formalin (formaldehyde), then preserved in jars filled with alcohol, which need to be topped off periodically and changed at longer intervals.

These objects are all treasures. Some, like rare gemstones or archaeological artifacts, command enormous prices on the open market (forcing museums to keep under lock and key in vaults their most valuable items while not on display). But every item is a treasure in a deeper, intellectual sense. Most cannot be replaced. And each has something important to tell us about the natural world and how it is changing. And that brings us to the scientific study of these specimens.

Museum science. Most of the larger natural history museums have a tradition of maintaining a staff of research scientists. Usually called curators, these scientists hold a Ph.D. from a major university. Although the duties of curators are many and varied, their basic job is to perform and publish original scientific research (but they also add to and maintain the collections under their care; cooperate in the planning and building of exhibitions; teach and lecture; and sponsor Ph.D. candidates and postdoctoral researchers). And, because of their intimate association with collections of natural history objects, most of the scientific research at natural history museums is in those branches of science pertaining to natural history specimens and artifacts. Counting research associates, Ph.D. students, and visiting scientists, major museums often have a hundred or more scientists associated with them.

The major traditional areas of research in natural history museums include the following:

Anthropology. Anthropology, the science of mankind, includes ethnology (the study of modern cultures), archaeology (the study of ancient, buried cultures), physical anthropology (the study of the biology of humanity, including the human fossil record; also includes primate paleontology and studies of other living primates), and linguistics (the study of languages). Of these four fields, the first three are usually well represented at natural history museums. Human behavior, ecology, and evolutionary history are absolutely central to understanding the current biodiversity crisis.

Geology. Geology is the study of the earth. Most geological research at natural history museums centers around the rocks and minerals that can be collected and housed at the institution. Geological processes (erosion, mountain building, volcanism, plate tectonics, and so forth) have combined to shape the earth the way we find it today. Together with climate, they constitute the physical forces that have provided the context—and a lot of the stimulus—for extinction events in the geological past, as well as the evolutionary events that have followed these extinction events. Biodiversity cannot be understood without reference to the physical world.

Paleontology. The outlines of the history of life on earth are preserved in the fossil record. Extinction has profoundly affected life in the deep geological past, and the patterns and processes of both extinction and evolution as learned from the fossil record have much to tell us about the very nature of the present-day Sixth Extinction.

Systematic Biology. Modern biology has many different subdisciplines. That branch of biology pertaining to the naming and classifying of species of plants, animals, fungi, and microbes, is known as systematics. Nowadays, most (though by no means all) of research in systematic biology is performed in natural history museums—because that's where the specimens are. Along with ecology, systematics is the central scientific area pertaining to biodiversity, for it is only through knowing what species are out there—and which have already succumbed to extinction—that we can establish the very existence of, and measure the severity of, the Sixth Extinction.

Biodiversity Studies. In addition to the traditional fields listed above, some natural history museums (and zoos and universities as well) have established programs especially focused on biodiversity issues. Programs such as the Center for Biodiversity and Conservation at the American Museum of Natural History conceive and help fund field studies, help elaborate conservation policies, train students, and cooperate in exhibition and educational endeavors pertaining to biodiversity.

—Niles Eldredge

If possible, visit one of the natural history exhibitions mentioned in this article. The following Web sites contain information about three natural history museums, the exhibitions, collections, and research: American Museum of Natural History (New York City) http://www.amnh.org. Grande Galerie d'Évolution, Museum Nationale d'Histoire Naturelle (Paris) http://cimnts.mnhn.fr/Evolution/GGE.NSF. Natural History Museum, Smithsonian Institution http://www.mnh.si.edu.

See also: Anthropology; Ecology; Evolutionary Biodiversity; Geology, Geomorphology, and Geography; Paleontology; Sixth Extinction; Systematics

Mushrooms

See Fungi

Mycology

See Fungi

N

Natural Selection

Natural selection is treated as the primary—and by some scientists the sole—mechanism producing evolutionary change. In essence it involves the process whereby some aspect of an organism's environment (either climate, competition, predation, or parasitism) interacts with one or more traits of the organism, such that the survival or reproduction of that organism is enhanced (or diminished) relative to organisms that lack those traits. Natural selection is intimately tied to the phenomenon of adaptation: adaptations are honed by natural selection; over time the proportion of organisms with these adaptations will increase in a population because of natural selection.

Natural selection is associated with the idea that nature is red in tooth and claw, the implication being that there is a fierce competitive struggle among all organisms, with natural selection weeding out those less fit organisms while favoring those that are more fit. Charles Darwin is usually credited with developing the concept of natural selection, but this viewpoint is, however, incomplete. For instance, Augustin de Candolle wrote in the early 1820s that all nature is at war with itself—implying an intuitive grasp of the principle of natural selection; Darwin was familiar with de Candolle's work. The philosopher Herbert Spencer also anticipated aspects of Darwinian natural selection in 1852, particularly through his use of the term "survival of the fittest." Darwin later championed this term as a synonym for natural selection.

More important, Alfred Russel Wallace, while recovering from a tropical fever in the Malay Archipelago in 1858, discovered the principle of natural selection, which he described in his manuscript "On the Tendency of Varieties to Depart from the Original Type." In this manuscript Wallace discussed how in nature there is a struggle for existence such that organisms become adapted. He also emphasized how human manipulation of domesticated crop and animals—specifically, the artificial selection of desired types and the removal of other types by humans—was prima facie evidence for the importance of natural selection to evolution in the wild. This was a theme that Darwin also emphasized.

Wallace subsequently mailed his manuscript to Darwin, along with a letter asking him to present it to the Linnean Society in London. Darwin did present the paper, but he added his name as first author and changed the title, and it was published in 1858 in the *Jour-*

nal of the Proceedings of the Linnean Society. Darwin subsequently published his book *On the Origin of Species* in 1859. It is true that Darwin had been thinking about issues relating to natural selection prior to 1858, but these thoughts were only mentioned to a few close friends or transcribed in his private diaries or notebooks. Thus, based on the principle of priority, Wallace deserves significant credit for his theoretical contributions and insight.

It has been asserted by some that natural selection is a mechanism that over time will produce organisms that are more complex and progressive. That is not certain, though, and Darwin was ambivalent on this point. At times Darwin (1859) argued that organisms only become adapted to local environments, and that this need not lead to advances toward what he referred to as a higher type of organism (one more complex or progressive). Furthermore, Darwin articulated the point that supposedly simple, parasitic organisms actually have very complex life cycles, such that it is often difficult to determine how complex and advanced organisms are. Still, Darwin (1859) also argued that on the whole organisms do become more fit as they evolve, and he predicted that modern organisms would be able to outcompete extinct organisms. More recently, scientists, especially Stephen Jay Gould, have convincingly argued that there is little if anything about natural selection or evolution that is progressive. This can be partly attributed to the fact that environments oscillate through time, such that traits that were once adapted may not be for long. Moreover, there are major mass extinction events in the history of life that seem to play little favorites among organisms that prior to extinction were well adapted.

Although Darwin may not have unequivocally pioneered thoughts on natural selection, he can likely be credited with developing and pioneering ideas on sexual selection. This idea differs in an important way from natural selection, because sexual selection is a mechanism that involves competition for mates, yet those structures that may aid in getting mates may reduce the probability that an organism survives. Thus natural and sexual selection are different mechanisms that can at times act against each other.

One thing that is potentially confusing to those working outside of evolutionary biology is that some scientists have incorrectly equated natural selection and evolution. As mentioned above, natural selection is a mechanism that produces evolution or descent from a common ancestor. The synonymy between natural selection and evolution is valid only if natural selection is the sole mechanism that produces evolutionary change. It is clear, however, that there are many other factors that have caused life to descend or evolve from a common ancestor. Thus, challenges to aspects of the theory of natural selection do not represent challenges to evolution per se, just as a change from Newtonian to Einsteinian mechanics did not obviate the significance of gravity. Our understanding of evolution has changed much from the time of Darwin. For example, we now know that chance factors contribute in an important way to evolutionary divergence. These factors include mass extinction events as well as effects associated with how evolution occurs in small populations. Other important challenges to the relative role of natural selection include the neutral theory of evolution, developed by Kimura, which suggests that many or even most genetic and evolutionary changes that occur are neither adaptive nor inadaptive but merely selectively neutral.

Another challenge to the exclusive dominance of the mechanism of natural selection involves the recognition that although natural selection was defined in relation to the dynamics of survival and the reproduction of organisms within populations, other types of entities can be selected. For example, populations or groups can be selected. This occurs when there are traits emergent at the group level that make groups more likely to survive or give rise to new groups. Genes can also be selected. The best example of this involves selfish DNA. Some genes have been found consisting of thousands of copies. These genes have no effect on an organism's adaptedness, but the number of copies of these genes appears to have increased over time, simply because these genes are more likely to undergo duplication events than other genes. Thus these genes are better adapted than other genes because, in effect, their ability to produce similar descendants is enhanced. Species are other units that potentially may be selected, though the existence of species selection has neither been refuted nor corroborated. Species selection is a mechanism which requires that certain species have species-level characteristics that would make them more likely to speciate (or less likely to go extinct). If species selection is a valid mechanism, it could have an important effect on evolution, because certain groups might become more diverse over time—not because they were more adapted through the action of natural selection but because they were more likely to speciate. Thus traditional, organism-based natural selection is not the only selection process that occurs and influences evolutionary dynamics. In the elaboration of ideas on group and species selection, Elisabeth Vrba and other scientists have recognized that it is important to distinguish between evolution produced by group or species selection and evolution that is just an effect of selection acting at the level of organisms.

Natural selection has also been challenged by some on philosophical grounds. These arguments have been based on the premise that natural selection is tautologous and therefore not scientific. In particular, it has been argued by some that with survival of the fittest only the fittest survive—and the only way to determine the fittest organisms is to see who survives. This reasoning is in fact fallacious. Natural selection is best thought of as a statistical law. On average, those organisms that are most fit are the most likely to survive or give rise to more offspring. Organisms may die for many reasons, including chance. Fitness is not equivalent to survival or the number of offspring an organism produces, but in the long run individuals that are more fit are more likely to survive and produce more offspring.

In spite of challenges to the idea of natural selection, it is clear that it is a potent evolutionary force. Studies conducted in the lab and in the wild on time scales ranging from weeks to decades indicate that selection can lead to evolutionary divergence that, when extrapolated over time, is sufficient to produce new species in a few hundred years. In fact, the ability of natural selection to produce evolutionary divergence stands at odds with much of the data from the fossil record, which shows that species often change little over many millions of years. Moreover, the minor changes that occurred typically require that natural selection have operated at only an almost infinitesimal level.

Some of the best examples of the power of natural selection involve activities related to our own species. Humans have become powerful agents of selection, both purposely and inadvertently; the development of antibiotic resistance by bacteria is a frequently cited and unfortunate example.

—Bruce S. Lieberman

See also: Adaptation; Darwin, Charles; Evolution

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Nearctic

See Biogeography

Neotropics

See Biogeography

Nitrogen Cycle

The term *nitrogen cycle* refers to biologists' attempts to locate and quantify the movement of the chemical element nitrogen, crucial (along with other elements in limited biological supply) to the survival of organisms, whose reproductive systems require nitrogen to function. Nitrogen, coming up through volcanoes and produced by life, and forming compounds with hydrogen and oxygen and other elements under the influence of light, is needed by cells to make proteins as well as the DNA and RNA molecules central to cell reproduction. But unlike, say, carbon, nitrogen is not readily assimilable by organisms. Although our atmosphere is mostly (79 percent) nitrogen, it cannot be directly accessed by most organisms. Intermediaries are thus necessary.

Some high-energy phenomena (ionizing cosmic radiation, lightning, and meteor trails) can combine nitrogen atoms with hydrogen or oxygen to make biologically assimilable molecules, but the lion's share of such work (collectively called nitrogen fixation) is done by marine organisms and soil bacteria, alone and as nodules in the roots of plants. The result is that fixed nitrogen is a valuable commodity, exploited by organisms that incorporate it into their bodies, releasing some (for example, in urea) as wastes that wend in complex biospheric cycles involving ammonium, nitrites, nitrates, nitrous oxides, and other compounds. Indeed, such a valuable commodity is nitrogen that human activity has significantly added to global nitrogen fixation—first by the planting of legumes (which contain nitrogen-fixing bacteria in their roots) and then by industrial methods. It is a rather astonishing statistic, but human, factory-based fixation of nitrogen means that, for a person living in Europe or the United States today, some 40 percent of the nitrogen atoms in your body have seen, at some point, the inside of a factory; if you live in China, an estimated 75 percent of the nitrogen atoms in your body come from a factory.

—Lynn Margulis and Dorion Sagan

See also: Agriculture and Biodiversity Loss: Genetic Engineering and the Second Agricultural Revolution; Agriculture and Biodiversity Loss: Industrial Agriculture; Atmosphere; Atmospheric Cycles; Carbon Cycle; Evolution; Five Kingdoms of Nature; Food Webs and Food Pyramids; Lichens; Microbiology; Nutrient/Energy Cycling; Pollution; Protoctists; Soil; Topsoil Formation

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Number of Species on Earth

See Evolutionary Biodiversity

Nurseries

In aquatic and especially marine environments, certain estuarine habitat types are commonly thought to serve as nurseries for particular species. Although they are rarely defined explicitly, by labeling a habitat a nursery, one implies that this habitat may be disproportionately important (relative to other habitats) in supporting juveniles that eventually enhance the adult population of a given species. The nursery concept also implies that organisms move among different habitats during the course of their life cycles, starting in nurseries and perhaps other suboptimal habitats before differentially moving on to subadult and adult habitats. In other words, only species with developmental (or ontogenetic) shifts in their habitat usage have nursery habitats. Habitats that are traditionally considered to be nursery zones for many species, including seagrass meadows, mangroves, algal beds, and marshes, typically provide important three-dimensional structure as well as good ecosystem productivity for juveniles to exploit. Mangroves and healthy seagrass meadows, for example, are frequently cited as providing nursery habitats for various coral reef fishes, while certain types of algal beds are important for other reef fishes and spiny lobsters (*Panulirus* spp.). Lemon sharks (*Negaprion brevirostris*) also use certain lagoons with seagrass beds as nurseries before dispersing as adults. Other species are thought to take advantage of the

Mangroves, such as this one on Lizard Island near Queensland, Australia, provide nursery habitats for various coral reef fishes. (Mark A. Johnson/CORBIS)

structure and productivity of oyster reefs as well as rocky reefs with algae.

For adult population enhancement to occur via nursery habitats, some combination of factors is necessary. These nursery habitats should, relative to the average for all habitats, (1) support higher juvenile population densities, (2) produce increased juvenile growth rates, (3) promote increased juvenile survivorship, and (4) facilitate greater movement from juvenile to adult habitats. Since gathering data across all these areas would be difficult, and management decisions regarding the fate of potentially important nursery habitat areas usually need to be made quickly, scientists must frequently use the best data available to make assessments about the importance of specific areas for fisheries populations. Since there is often general evidence supporting the importance of certain habitat types (for example, seagrass meadows) for a given species, but all expanses or patches of this habitat are probably not equally important, the next step involves estimating which specific habitat patches are likely to be of greatest value for conservation. Issues such as habitat patch quality or health, size, likelihood of disturbance, and proximity to subadult and adult habitats (to maximize movement between habitats) are critical for this determination.

—Daniel R. Brumbaugh

See also: Arthropods, Marine; Bony Fishes; Chondrichthyes; Coastal Wetlands; Coral Reefs; Estuaries; Lagoons; Preservation of Habitats

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Nutrient/Energy Cycling

Nutrient/energy cycling refers to the way in which the limited materials, atoms, compounds, and ions, are reused at the earth’s surface. The main systems of life—cells, organisms made of cells, and ecosystems made of populations of species—join the biosphere as a whole as functioning energy-driven systems. Thermodynamically, these systems are not closed but open—that is, they admit of material and energetic flow across their boundaries. All complex systems in the cosmos, including those of life, are energy-driven systems. (Whereas organisms take in some materials and produce others, ecosystems can be fully recycling, using energy to turn wastes into food.) What has been nominated the fourth law of thermodynamics, Morowitz’s cycling law (after U.S. biophysicist Harold Morowitz), states that the flow of energy from a source to a sink through a steady-state system will lead to at least one cycle in the system. Just as the materials of life are not special, nor is its tendency to become cyclical and complex. The second law of thermodynamics, which says that systems become less organized when isolated (that is, when they are left alone, not fed with new energy or materials), was based on a study of energy in artificially closed conditions. A more complete, extended version, which applies to life and other open systems, says that gradients, differences across a distance, are reduced. Cycle formation occurs and even gives rise to physical and nonliving chemical systems with nascent identity. In the presence of gradients—differences of temperature, pressure, and chemical concentration (electron potential)—cycles are generated. Thermodynamically, the gradient represents a previous improbability. The cycling system functions to dissipate a pre-existing improbable state in accord with the second law. Just as life’s carbon, nitrogen, sulfur, hydrogen, oxygen, and phosphorus are elements that make up nonliving matter, so living matter—in which cyclical chemistry and growing complexity appear in regions of energy flow—is not unique.

It is in the context of thermodynamics and ecology that we can best appreciate the cycling of nutrients and wastes, for each does sometimes transform into the other on the earth's surface. The main elements of life are found in the environment because life is an open thermodynamic system that has, over evolutionary time, progressively integrated more of the earth's surface, more chemical elements and compounds into its cyclical processes. Biomineralization, in which minerals can be laid down under precise genetic control, includes crystals of magnetite and calcium phosphate (apatite), made in bacteria and in our inner ear's balance organs, respectively. Life orchestrates, beyond the body of its flesh proper, an expanding mineral house including bony infrastructure and shelly walls. Trace metals, inorganic phosphorus, nitrate, carbonate, and silica in seawater are scavenged for functional uses in and around cells. Technology—for example, the extraction and processing of silicates to make silicon computer chips for the information industry—is part of an ancient process of recycling materials. Indeed, long before man, diatoms (a kind of alga) that need silica to make their frustules, and sponges (a kind of animal) making spicules, depleted the ocean of silica for their own biotechnological purposes.

Seen from space, the earth is a system far from equilibrium that would never be predicted under the standard mixing rules for chemicals in an isolated system. That is because life has found a very elaborate way to capture and degrade, in ever more complex chemical material cycles, the energy of the sun. Unlike nonliving energy-driven systems that cycle and become more complex (for example, chemical patterns or a tornado until it dissipates a barometric pressure gradient), cyclical chemistry on earth has spawned reproduction—a process for making, more or less faithfully, finely tuned "vehicles" of energy degradation. But earth's locally complex organisms and cells are not only excellent energy degraders, producing wastes and even using energy to turn wastes back into food; in addition, the lack of perfect fidelity leads naturally to new systems able to recognize and use new gradients, and thus in turn producing new wastes.

The nutrients that organisms need are ultimately the atoms that cyclically compose their bodies. Although many complex models exist showing chemical changes in and out of cells as atoms circumnavigate the planet, all are provisional in detail. The interactions of cycles such as the carbon, nitrogen, and sulfur cycles are even more complex; investigation into their details is underway by biogeochemists. Seemingly minor sulfur compounds formed by microbes over the ocean, for example, can react to form the nuclei of raindrops that fall, feeding algae eaten by other organisms that carry the compounds of their bodies to new places, producing still other changes. But something is known about the main cycles and their major players. Phosphorus, for example, which is needed as the "backbone" of DNA and RNA, is unlike the other elements of organisms because it is not available in a gaseous form. Thus, from a global cycling perspective, the phosphorus-rich feces of sea birds (such guano is known to create entire islands) is a means of distributing this biologically limiting element. Beginning more than 3 billion years ago, carbon dioxide has been taken from the atmosphere and used to construct cells and their cyclical aggregations.

The oldest and most prodigious cyclers of materials on the planet are the bacteria, whose cells provided the site for the evolution of all the major modes of metabolism by which energy is used to produce cell chemistry and its waste products. These waste products, in an ancient and more efficient version of the recycling efforts instituted by humanity, are incorporated again as nutrients. Bacteria, for example, produce carbon dioxide in methanogenesis, fermentation, and respiration, and incorporate it into bodies by using light or chemical reactions. Organisms that use light for energy are known as phototrophs; those that use chemical gradients are chemotrophs. Cells that eat other cells tend to be chemo-organotrophs, using the energy stored in the organic compounds of other bodies. Some organisms, such as the newly discovered abundant denizens deeper in the rocks of the biosphere, are chemolithotrophs; they tap into inorganic chemical reactions to metabolically maintain and reproduce themselves.

Bacteria are about 50 percent dry weight carbon, and 12 percent nitrogen; apart from the other elements mentioned, potassium, magnesium, sodium, calcium, and iron are required by cells for functions such as building enzymes and cell walls. Bacteria get these elements as salt ions in solution, or from solid rocks or minerals in rocks. On a cell level gradients, such as the oxidation/reduction gradient between the hydrogen-rich organic compounds of eukaryotic cells (cells with nuclei) and the oxygen from the atmosphere, run complex metabolic cycles. Whether eaten alive or exposed to decay after death by fungi and bacteria, organisms take from the environment and each other as they propagate increasingly energy-seeking systems in a swirl of thermodynamic cyclical activity beyond any single life form. Fermentation, photosynthesis, sugar metabolism (including glycolysis and the citric acid cycle), and production of nucleic acids (genes) are all part of the overarching sun-driven energy cycle by which the limited atoms of earth's surface are co-opted, used up, and reused, in the evolving systems of life.

—Lynn Margulis and Dorion Sagan

See also: Agricultural Ecology; Agriculture and Biodiversity Loss: Genetic Engineering and the Second Agricultural Revolution; Atmosphere; Atmospheric Cycles; Carbon Cycle; Evolution; Five Kingdoms of Nature; Food Webs and Food Pyramids; Lichens; Microbiology; Nitrogen Cycle; Pollution; Protoctists; Soil; Topsoil Formation

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Oceanic Trenches

Oceanic trenches are narrow (up to 100 km wide), elongate depressions on the seafloor that are adjacent to active continent margins and island arc systems. Although most of them are found in the Pacific Ocean, there are a few in the Caribbean Sea and the Atlantic and Indian oceans. The Challenger Deep in the Marianas Trench adjacent to the Philippines is the deepest place on earth, reaching 10.7 km below the surface, a vertical relief greater than that of Mount Everest. The Puerto Rican Trench reaches a depth of 8.4 km. The 5,900-km Peru-Chile Trench is the longest; it is bordered by volcanoes on South America.

It was not until the modern concept of plate tectonics was developed that an understanding of how oceanic trenches form was established. These trenches are associated with both earthquakes and volcanic activity and are the result of the interaction of two crustal plates, one sliding under the other and descending. As the underlying plate moves downward at a steep angle into hotter regions of the earth (a process known as subduction), pulled by convection currents and gravity, a trench is formed where one plate slides below the other. Subduction produces additional heat by friction. Heat causes the plate to melt, and the resulting molten material (magma) rises to the surface, erupts, and builds volcanoes. The downward movement also causes earthquakes. Where two oceanic plates converge, a volcanic island arc system of basaltic rock develops in the direction of the downward-dipping plate, such as occurs in the Aleutian Islands. An oceanic-continental interaction creates mountains as sea sediments are squeezed and raised upward, and volcanoes as a result of the melting of the inclined plate. In this situation the molten material rises through the mountains, is contaminated by the surrounding rocks, and erupts high on the mountains to form andesite volcanoes.

Trenches are relatively steeper on the landward side and gentler on the ocean basin side. Sediments accumulating in the trench derived from the erosion of the adjacent continent tend to be thicker on the landward side.

The oceanic trenches are home to famous hydrothermal vent faunas.

—*Sidney Horenstein*

See also: Deep-Sea Hydrothermal Vent Faunas; Oceans; Plate Tectonics

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Oceans

The oceans cover 71 percent of the earth's surface and contain all of the saltwater found on earth. Oceanography, the study of the oceans, includes many sciences whose goal is to understand the oceans and the life within them. From the oceanographer's point of view, the planet Earth should be called the water planet, because only 29 percent of its surface is land and the rest is water. It is estimated that the volume of water in the oceans is 1.37 billion cubic kilometers—an amount that is difficult to comprehend. If the Earth were a smooth sphere, the water depth around the globe would be 2,686 meters (8,800 feet) deep or 1.7 miles. Adding water from the land, the level would rise another 56 meters (200 feet).

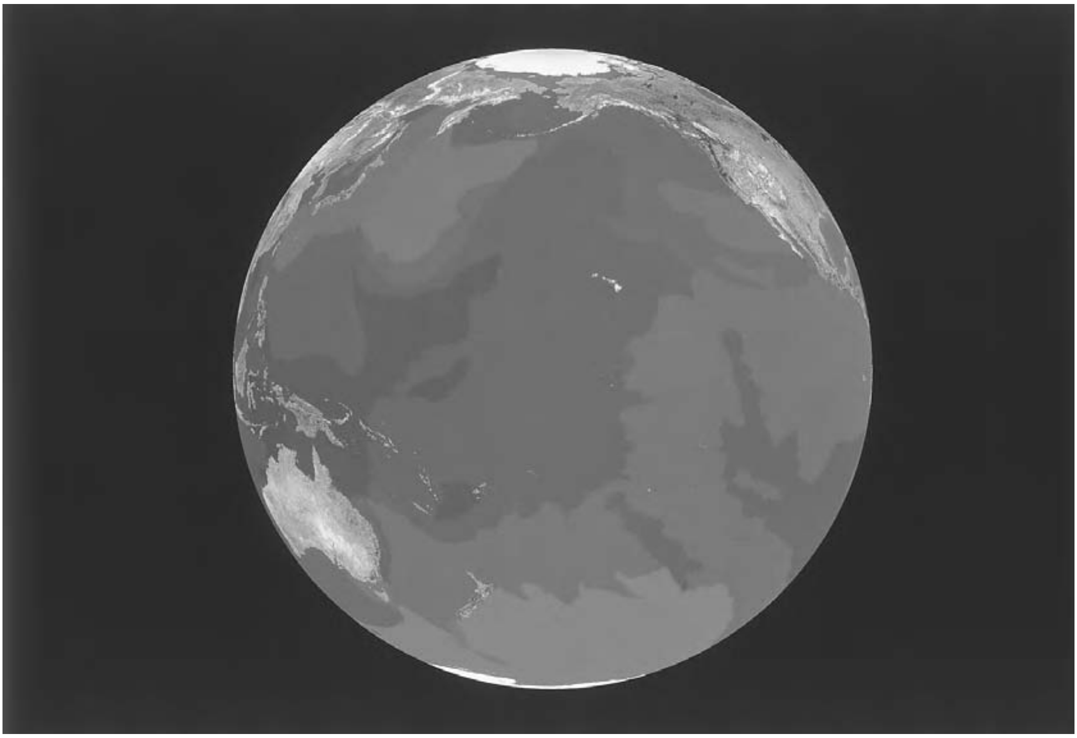
The average depth of the oceans as they exist today is 3,795 m; 75 percent of the ocean basins are between 3,000 and 6,000 m deep. The Pacific Ocean is the deepest, with an average depth of 4,188 m and contains 50.1 percent of the world's oceanic water; the Pacific covers one-third of the earth's surface.

The Southern Hemisphere contains 80.9 percent water and 19.1 percent land, while the Northern Hemisphere is 60.7 percent water and 39.3 percent land. The land is not as high as the oceans are deep—84 percent of the ocean floor exceeds 2,000 m in depth, while only 11 percent of the land surface is greater than 2,000 m above sea level. The Marianas Trench adjacent to the Philippines is 11,035 m deep while Mount Everest is 8,848 m high.

The uneven distribution of the land and sea affects wind and ocean circulation systems. The most important force that drives the circulation of the oceans at the surface is the wind. Friction between the wind and the sea surface creates waves on the surface of the water that help move the water. Differences in atmospheric pressure produce wind patterns of easterly and westerly belts and, with the addition of the earth's rotation, produce water movements. As the water circulates, opposing currents bring water together from different directions causing the water to build several meters high. These convergence zones are located, for the most part, at 30° north and south of the equator. Water flowing away from these highs and influenced by the rotation of the earth forms a nearly closed circulation system called a gyre. Most of the currents move predominantly in east-west directions in the open sea and as a result remain approximately in the same climatic belt.

In the Northern Hemisphere the gyres circulate clockwise and in the Southern Hemisphere they circulate counterclockwise. This circulation pattern is obstructed by the imposition of continents, which interfere with the free movement of water.

Deflection by continents causes the currents to move in a north-south direction across climatic zones, with the result that cold or warm currents move through water of different surface temperatures. The Gulf Stream, for example, formed by the northward movement of a warm, low-latitude current into northern areas, moderates the temperatures along the Atlantic Coast of North America and Europe. Temperatures in the Gulf Stream may be more than 5°C higher than the surrounding water it is moving through. Currents transport large volumes of water, and in the case of the Gulf



The Pacific Ocean is the deepest and largest of the oceans, covering one-third of the earth's surface. (Tom Van Sant/Corbis)

Stream as much as 150 million cubic meters per second flow past Nova Scotia.

The average temperature of the ocean surface layer down to 200 m is about 15°C. Below the surface layer is the thermocline, a zone of rapidly decreasing temperature that extends from 200 to 1,000 m. Below 1,000 m the temperature decline is not as steep, but the bottom water at the seafloor can be close to freezing. This cold, deep layer originates largely in the polar regions where dense, cold water sinks and migrates toward the equator very slowly, taking up to 600 years to get there. Winds parallel to coasts cause warm surface waters to be blown offshore, creating a region of low pressure that causes upwelling of cold, deep water that replaces the surface water that has moved offshore. Containing dissolved nutrients, the water reaching the photic zone supports abundant plant life and the animals that feed on them. Many of the world's fishing grounds are located in zones of coastal upwelling.

Life on the seafloor is classified into zones; benthic plants and animals live on the seafloor and pelagic forms live in the water column as either swimmers or floaters. The neritic zone refers to water overlying the continental shelf, and oceanic water is located from the edge of the continental shelf seaward.

Where did all this water come from? Oceanographers turn to astronomy and geology for the answer. Ultimately, everything on earth came from the gaseous nebula that condensed to form the solar system. But as the earth began to evolve, it was too hot to contain water on its surface; huge volumes of water expelled by the large numbers of volcanoes remained as vapor. It was only after the earth cooled that vapor was able to condense and form liquid water. As early earth evolved, the differentiation between high granitic continents and lower basaltic ocean basins occurred, providing a place for liquid water to accumulate in large volumes in low places on the surface of the earth. In the traditional view it is thought that from the end of earth's formative period, about 3.9 billion years ago, the amount of water has remained the same—but its distribution between land and sea has been variable dependent on the hydrologic cycle, tectonic activity, and the changing shapes of the ocean basins and the subsequent rise and fall of the sea. However, all of this water might not have come only from within the earth; some scientists now believe that a large amount of water was added by impact of ice comets, which were much more numerous in the early days of the solar system

Modern technology utilizing satellites, sonar, and radar has allowed extensive mapping and sampling of the seafloor since the 1950s. Prior to that time, the shape of the seafloor remained largely unknown. Information came from activities such as dropping heavily weighted ropes to the bottom of the sea to determine depths. There were also tantalizing suggestions that the ocean floor had some relief as scientists contemplated the shapes of volcanic islands rising out of the sea. Today we know that the seafloor contains some of the most magnificent features of the earth's surface: continental shelves, continental slopes and rises that drop down to the abyss, and the very deep oceanic trenches. There are volcanic mountain ranges, and huge, solitary volcanoes, many of which form the underlying structure of atolls and others that are tall enough to break the ocean's surface and form oceanic islands.

A variety of sediments, either derived from land or from the accumulated remains of skeletons of plants and animals, cover vast areas of the seafloor. These sediments provide oceanographers with the records about the rate of accumulation and the history recorded in their layers.

In addition to drawing academic interest, the oceans contain resources that are needed and removed by mining and drilling. Sand and gravel are pumped from shallow seas for construction, beach replenishment, and landfill. Many sands from the ocean contain large amounts of gold, diamonds, and tin. Phosphorite, for fertilizer, and sulfur and manganese nodules are removed from the seafloor. In addition, coal, oil, and gas are found below the seafloor where the continents are covered by water.

Salt is the resource with the longest history of being harvested from the oceans. On average, 1,000 g of seawater will contain up to 35 g of salt. The salinity at any given location is determined by the rate of evaporation, the amount of precipitation, freezing and thawing that may occur, and the amount of freshwater that enters the sea from the land. The original saltiness of the oceans came from the weathering of rocks and from the release of chemicals from volcanic eruptions.

Salt in seawater is more than sodium chloride; it is a complex mixture of inorganic salts, atmospheric gases, traces of organic matter, and a small amount of particulate matter. The most abundant dissolved ions by weight are chloride (55.04), sodium (30.61), sulfate (7.68), and magnesium (3.69).

Although the oceans have been receptacles for material created by natural processes, people have used them as dumping grounds. Most of the products of civilization have made their way to the oceans. Huge quantities of industrial wastes, sewage sludge, and garbage, not only from land-based communities but also from ships, have been dumped in the oceans. Studies are underway to determine the feasibility of placing toxic and radioactive materials in the seafloor, where they can remain for hundreds of thousands of years undisturbed, eventually becoming harmless. The containers for such wastes will consist of corrosion-proof material, and the burial in sediment will exert enough pressure to prevent leakage. The containers would be placed within plates, not along plate boundaries where volcanism and earthquakes could disturb them. Critics say that the dangers of leakage are real; that tectonic activity on the ocean floor cannot be predicted, and that there is great uncertainty that all nations would follow the proposed safety procedures.

—Sidney Horenstein

See also: Abyssal Floor; Continental Shelf; Continental Slope and Rise; Deep-Sea Hydrothermal Vent Faunas; Oceanic Trenches

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Order Uranotheria

Order Uranotheria, proposed in 1997, contains hyraxes (which resemble rabbits or large rodents); the aquatic sirenians (manatees, dugongs, and the extinct Steller's sea cow—sea cows), and elephants, the largest living land mammal. Traditionally each group has been recognized as a distinct order (Hyracoidea, Sirenia, and Proboscidea), but their evolutionary histories can be traced back to a common ancestral stock of condylarths (primitive herbivorous placentals) living in Africa during Paleocene times, and researchers have combined them into a single order to reflect their evolutionary origin.

Human interactions with these remarkable mammals has ranged from positive to disastrous. Hyraxes are appreciated as a part of the African ecosystem, especially as part of African nature safaris, but they are incidentally exterminated when their habitat is destroyed for agricultural activities. Sirenians have been persistently hunted and abused in other ways, reducing population size and geographic range, and forcing one species to extinction. Elephants have been tamed for transportation and work, but many have been killed for their ivory; they have been eliminated from great expanses of their former range to make way for farms and towns, a reflection of expanding human population in Africa and Asia.

Living hyraxes (Suborder Hyracoidea) are in Family Procaviidae and consist of three genera and seven species found throughout Africa (except the very arid northwest) and in southwestern Asia (from Turkey to the Arabian Peninsula). They are either grazing or browsing herbivores. Their evolutionary history extends back to the Early Eocene of Africa, from which point they spread to Asia and Europe. There are eighteen extinct genera containing species ranging in size from modern hyraxes to a small rhinoceros. They were the dominant members of African herbivore communities during the Oligocene and eventually expanded into Asia and Europe during Miocene-Pliocene times.

All hyraxes have a compact body (30 to 60 cm long); inconspicuous tail (1 to 3 cm long); short, sturdy legs; and small ears. The forefoot has four digits, the hind foot three. The inner digit on each foot bears a curved claw, all other digits ending in flattened nails resembling tiny hooves. Soles of the hind feet have specialized pads kept continually moist by glandular skin secretions. Muscles retract the center of the sole to form a hollow that acts as a powerful suction cup. Teeth consist of two pairs of lower incisors, a single pair of upper incisors, a premolar in each quadrant of the jaw, and three molars; canines are absent. The pointed, widely separated upper incisors are triangular in cross-section, ever-growing, with enamel front surfaces and softer dentine behind, so that wear produces pointed cutting edges; lower incisors are chisel-shaped with bicuspid tips. The chewing surface of the molars resembles that seen in rhinoceroses. The skull is short and stocky with a large and deep mandible. The three species of *Dendrohyrax* live in forests, are arboreal and nocturnal, foraging in trees and on the ground. They form small family groups. The single species of *Procavia* and three of *Heterohyrax* are diurnal, and, although capable of climbing, are generally terrestrial; they inhabit cliffs, rock ledges, and lava beds in grasslands. Terrestrial species are gregarious, forming colonies of up to fifty individuals among rocky outcrops that bask in the sun when not feeding or avoiding predators. Hyraxes run, jump, or climb over rocks, cliff faces, and tree branches, and have acute hearing and excellent vision.

The four species of living and one of recently extinct sirenians are in families Dugongidae (extinct Steller sea cow, *Hydromalis gigas;* and living dugong, *Dugong dugon*) and Trichechidae (Amazon manatee, *Trichechus inunguis;* West Indian manatee, *T. manatus;* and West African manatee, *T. senegalensis*). The dugong is found only in coastal waters of the Old World tropics. The Amazon manatee inhabits the Amazon River basin of northern South America; the West Indian manatee occurs in coastal waters and rivers from the southeastern United States, around the Gulf of Mexico and the Caribbean Sea to eastern Brazil; and the West African manatee lives in coastal waters and larger rivers from Senegal to Angola. Steller's sea cow, the largest sirenian (reaching 8 m in length and weighing up to 10,000 kg) was first encountered in the shallow western Bering Sea during the 1700s; it was hunted to extinction by about 1768, twenty-seven years after its discovery. It is the only sirenian known in historical times to occur in cold ocean coastal habitats, and may have been the largest noncetacean aquatic mammal.

The evolutionary history of the group extends back to Eocene times, as documented by fossils found in Europe, Africa, Asia, and North America in tropical marine sediments. Weighing up to 1,500 kg, living sirenians have a massive, spindle-shaped body (2.5 to 4 m long), flipper-shaped front limbs, a horizontally flattened tail, and lack hind limbs and a dorsal fin. The nearly hairless, wrinkled skin is thick and tough. The rounded head has a stubby muzzle; the mouth is small, and lips are surrounded by stiff tactile hairs (vibrissae). Nostrils are separate, located on top of the muzzle, and can be closed. Eyes are small and external ear flaps are absent. The skeleton is composed of dense, heavy bone. Long, unlobed lungs lie horizontally in the body and are separated from the capacious gut by a long and horizontal diaphragm. The orientation of the lungs combined with the dense bone allows the sirenian to adjust its lung volume and maintain a horizontal position while feeding at different depths. Dugongs have large, columnar, ever-growing teeth without enamel but covered with cementum. The teeth of manatees are covered with enamel and rooted; as the front teeth wear out they are replaced by rear teeth pushing forward, so that at any one time five to eight teeth are functional in each quadrant of the jaw. All sirenians have horny plates covering the front of the palate and adjacent mandibular surfaces.

African elephants, Samburu Wildlife Reserve, Kenya (Darrell Gulin/Corbis)

Sirenians are heavy, slow-moving, and the only completely aquatic mammals that are also strictly herbivorous, consuming vast quantities of submerged vascular aquatic plants along with emergent and floating vegetation, sea grasses, and marine algae. Because their diet is low in nutrients, sirenians have a slow metabolism and generate meager body heat for their size. This physiology, combined with lack of a thick layer of blubber, promotes rapid loss of body heat in cool waters. They are thus restricted to tropical seas and rivers where water temperatures are warm and stable. Sirenians travel in small groups, or in pairs, or are solitary, and they live their entire life in the water. Even the young suckle while the mother is submerged in a horizontal attitude.

Indian (*Elephas maximus*) and African (*Loxodonta africana*) elephants are the only living representatives of Family Elephantidae. The Indian elephant inhabits tropical forests and savannas in continental Asia and some of the larger islands on the Sunda Shelf. The African elephant is now found only in sub-Saharan Africa. The woolly mammoth (*Mammuthus primigenius*), also a member of Elephantidae, apparently survived up to 3,700 years ago on Wrangel Island in the Arctic Ocean, off northeastern Siberia; elsewhere it became extinct about 10,000 years ago in Europe, and 8,000 years ago in North America. The evolutionary history of elephants is first documented by fossils in the Paleocene of North Africa. These were likely small animals similar to tapirs in size and body conformation. By the Late Eocene the species had evolved into forms more closely resembling elephants, with either a long proboscis or trunk and columnar limbs. Later, during Miocene times, proboscideans evolved into an array of species and genera and dispersed out of Africa into Europe, Asia, and North and South America, even making their way to numerous coastal islands along the major continents and in the Mediterranean and Indo-Australian regions. The Indian and African elephants are the living remnants of this spectacular evolutionary radiation.

Elephants are known to everyone by their great size (nearly 4 m tall and weighing up to 7,500 kg); huge head; short neck; massive body; thick, long, and columnar legs; expansive, fan-shaped ears; and the very long, muscular, and flexible trunk ending in nostrils and fingerlike projections. The feet are short and columnar, like the legs. The skin is thick and nearly hairless, and the moderately long tail bears a brush of wirelike hairs at the tip. Elephants do not have sebaceous glands, which are found in the hair follicles of most mammals and produce secretions to soften and lubricate the skin and hair. Limb bones are heavy and separate. The bones of the fingers and toes are short, spread out, and braced at the heel by a pad of dense connective tissue, which supports the elephant's weight. The animal actually walks on its digits (five fingers on the forefoot, three or four toes on the hind foot), supported by the heel cushion. The skull is short but high and contains large air chambers.

Dentition is highly specialized. Each tusk is actually the second upper incisor. There are six cheek teeth (three premolars and three molars) in each half of each jaw. The tooth replacement pattern is unusual among mammals. The cheek teeth erupt from front to rear so that only a single tooth and fragment of another is functional at any one time. As a tooth becomes worn, it is replaced by the tooth behind it. The first three teeth in each quadrant of the jaw erupt during the first four years, the fourth erupts at four to five years of age, the fifth when the elephant is twelve to thirteen, and the last tooth becomes functional at about age twenty-five and remains in the jaw until the animal dies (for about the next fifty years). The high (hypsodont) and wide tooth consists of a series of thin laminae formed of enamel surrounded by dentine with cementum between each lamina. The last molar has the most laminae. This complicated chewing surface and pattern of tooth replacement provides a dentition lasting the lifetime of the elephant, up to eighty years. Elephants need these wide grinding cheek teeth because they consume more than 200 kg of forage each day, consisting of trees, leaves, shrubs, grasses, fruits, and aquatic plants.

Asian elephants differ from the African species by having much smaller ears, a flatter forehead, a dome-shaped head that is the highest point of the animal, four nails on the hind foot, and a single, fingerlike projection at the tip of the trunk. The shoulders are the highest point for the African elephant, the hind foot has three nails, and the trunk has two processes at its tip. These differences can be seen in any zoo; what cannot be viewed is the difference in number of ribs: nineteen pairs in the Asian, twenty-one in the African.

During the last few years, analyses of protein and DNA sequences of African mammals have supported the close relationship among hyraxes, sirenians, and elephants, as reflected by aspects of their anatomy and fossil histories. Surprisingly, results of the molecular analyses also indicated that the aardvark (Order Tubulidentata), elephant shrews (Order Macroscelidea), and tenrecs and golden moles (Order Afrosoricida) are also closely related to hyraxes, sirenians, and elephants, and all have been combined into Superorder Afrotheria. Judged by the fossil record, the divergence and major part of the evolution of these six assemblages occurred in Africa, between 105 and 40 million years ago, when that continent was an island after separating from South America and before colliding with Eurasia. The origin of aardvarks and elephant shrews can be traced by fossils back to African condylarth ancestors, but tenrecs are represented only back to the Miocene and still look shrewlike and molelike. The concept of Afrotheria is one of the most remarkable current hypotheses dealing with mammalian evolution, and it is being tested by anatomists, paleontologists, and molecular systematists. In a child's alphabet of animals, A is for aardvark, E is for elephant, H is for hyrax, and S is for sea cow; different letters signaling animals wildly unalike in form, function, and habitat. But the letters are related in being part of a linguistic whole—an alphabet—and the mammals, along with elephant shrews, tenrecs, and golden moles, are linked by their evolutionary origin in Island Africa.

—*Mary Ellen Holden*

See also: Biogeography; Deserts and Semiarid Scrublands; Evolutionary Biodiversity; Extinction, Direct Causes of; Herbivory; Mammalia; Preservation of Species; Species; Systematics; Tropical Rain Forests

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Organizations in Biodiversity, The Role of

There are many types of organizations that are actively involved in biodiversity conservation. They fall into several categories based on their policies, expressed perspectives, or programs. Although many organizations are difficult to place in one particular category, this article discusses the following categories based on the primary purpose of the organization:

Religious organizations: based on a shared belief in and reverence for God, a deity, or a supernatural power; this belief is central to the attitudes and conduct of these organizations and their members.

Government and governmental agencies: formally represent local, regional, or national government interests, having jurisdiction over such issues as national parks, forest and wildlife management, and community development.

Academic and research institutions: primarily nonprofit, scientific institutions (including natural history museums, botanical gardens, aquaria, and zoological parks) and universities that conduct a range of biological, social, economic, and political studies.

Nongovernmental organizations: private, nongovernmental organizations (NGOs) that may pursue a range of strategies to achieve an institutional goal, including working in communities, conducting research, analyzing policy, and lobbying for legislative action.

Although these types of organizations may have different agendas, they are increasingly finding common ground in their shared concern for the environment and conserving biodiversity. These links are important for conservation. In addition to discussion of the distinctive roles of organizations, cases illustrating complementary efforts and alliances among organizations are included below.

Religious Organizations

The teachings and programs of religious organizations are critical for influencing the underlying values of human societies. Inasmuch as billions of people around the globe count themselves as members of the world's major faiths, religious organizations play a significant role in influencing attitudes, and in inspiring and mobilizing communities to action. Religions provide their faithful with the ethics, or codes, that serve as goals for human behavior and norms by which behavior is evaluated. They can also offer an organized view and powerful voice to influence policy, as well as what is taught in schools.

The role of religion in biodiversity conservation is controversial. The Judeo-Christian tradition, predominant in the United States, has been held responsible by some people for the current environmental crisis. Controversy has centered on the interpretation of the relationship between God, humans, and nature as set out in Genesis 1:26–28. Here, God created humans in his own image and gave them dominion over other creatures. Environmentally concerned Christians and Jews have emphasized that "dominion" does not give humans license to abuse or destroy God's creation. Rather, humans have responsibility to care for this creation that God declared to be very good. Organized religion in the United States is taking environmental stewardship seriously, preaching on the environment in churches and synagogues, and training seminarians about the interface between religion and the environment.

Other major world religions have examined the relationship between their faiths and the environment. Leaders of three of the world's major faiths—Buddhism, Hinduism, and Islam—joined with those from Christianity and Judaism in Assisi, Italy, in 1986 to discuss their religions in relationship to conservation. Religious leaders made declarations about the intrinsic relationship between faith and the environment, briefly summarized here:

- For Buddhists there is a natural relationship between a cause and its resulting consequences in the physical world. Buddhism is a religion of love, understanding, and compassion. It is committed to the ideal of nonviolence and attaches great importance to wildlife and protection of the environment upon which every being of this world depends for survival.
- In Hinduism, humanity, though at the top of the evolutionary pyramid, is not seen as something apart from the earth and all other life forms. The Hindu viewpoint on nature is permeated by reverence for life, awareness of the forces of nature, with the orders of life bound to each other. The divine is not exterior to creation, but expresses itself through natural phenomena.
- In Islam, the entire universe is God's creation and belongs to God. Humanity's role is to be God's stewards on earth, to oversee what God has entrusted to us, not to do with it as we wish. Allah is Unity; his trustees have responsibility for maintaining the unity and integrity of the earth, wildlife, and the environment.

Three more faiths—Baha'i, Jainism, and Sikhism—have since produced their own declarations to accompany those of the other religions.

- For the Baha'i, the grandeur and diversity of the natural world are reflections of the majesty and bounty of God. Thus nature is to be respected and protected; it is a divine trust for which we are answerable.
- Since the beginning of the Sikh religion in the late fifteenth century, the faith has been built on the message of "oneness of Creation." The universe was created by almighty God, who sustains, nourishes, and protects it.
- The term *jain* means "the follower of Jinas (spiritual victors)," human teachers who attained omniscience. Jains practice the

> principle of ahimsa (nonviolence) toward all humans and all nature. The Jain cosmology recognizes the natural phenomenon of mutual dependence; all aspects of nature belong together, bound in a physical as well as a metaphysical relationship.

Subsequently, representatives from these faiths have reconvened to evaluate their conservation record since Assisi and to develop plans for the future. They agreed to establish the Alliance of Religions and Conservation (ARC), an international organization that works with religious communities and environmental groups to improve the effectiveness of conservation activities. In November 2000, a joint effort of the Worldwide Fund for Nature (WWF) and ARC convened leaders of the previous eight faiths with Shintos, Taoists, and Zoroastrians in Katmandu, Nepal.

Indigenous peoples have been voicing concerns about maintaining their cultures and traditions—often intertwined with religion. Religious sanctions may be invoked to protect areas and species. For example, sacred groves throughout the world have cultural and religious significance, and also serve to protect the biodiversity within them. According to criteria adopted at the 1992 Earth Summit in Rio de Janeiro, indigenous peoples are: descendants of groups inhabiting an area prior to the arrival of other groups; politically not dominant; culturally different from the dominant population; and they identify themselves as indigenous. The worldview of many indigenous peoples includes the concept of a community-of-beings, including humans, animals, and plants. Traditional societies are highly varied; some have used the resources of their environments sustainably, and many have played an integral role in shaping the composition of their environments through selective hunting and gathering and agricultural practices. These relationships of indigenous peoples with their environment have shifted over time, and today traditional societies often face rapid changes as they come increasingly into contact with outside influences.

Joining the Forces of Faith and Science

In 1991, thirty-two scientists wrote an "Open Letter to the American Religious Community" expressing grave concern about humankind's understanding of its place and purpose in the web of life. They recognized that scientific data, laws, and economic incentives were not a sufficient response to the environmental crisis, and that a change in the values of society is a moral issue requiring an active role by the religious community. Religious leaders responded enthusiastically, and in 1993 they established the National Religious Partnership for the Environment (NRPE) across a broad spectrum of faith groups that collectively serve more than 100 million Americans. The NRPE's mission is to integrate care for creation throughout organized religion, contributing to moral perspective and breadth of constituency in efforts to protect the natural world and human well-being.

Government and Governmental Agencies

Governments make laws and policies, set regulations, and enforce them. Although the actions of private companies, landowners, fishermen, and farmers have the most direct effect on biodiversity, governments need to provide leadership in setting rules to guide natural resource use and protect biodiversity. This takes place at local, regional, national, and international (intergovernmental) levels.

One of the greatest challenges to political action at any level, however, is that governments are often compartmentalized with mandates covering education, environment, agriculture, energy, or health, while concerns such as biodiversity conservation are affected by, and affect, more than one of those areas. In many cases it appears that federal and state governments place more importance on protecting current economic growth and private property rights than on protecting biodiversity.

In addition, ecosystem concerns are measured in decades or generations, while the political agendas of particular agencies are measured in months or years leading up to the next election or budget cycle. Agencies may also work at cross purposes. For example, the U.S. Forest Service has a mandate to produce timber for harvest at the same time that the U.S. Fish and Wildlife Service works to protect biodiversity dependent upon the forests that are being cut.

Conservation action is typically carried out within national policy and legal systems (in some cases by state or provincial governments). With the exception of Antarctica, virtually all of the world's terrestrial biodiversity occurs within national boundaries, and thus measures taken by national governments are critical. Many countries set tolerance limits on environmental pollution, have legislation that regulates wildlife use, and are increasingly including the protection of endangered species in these laws.

In the United States, there are laws directly affecting biodiversity within the country's borders. The National Environmental Policy Act (NEPA), signed into law by President Nixon in 1970, requires thorough environmental impact assessments of all major programs, a cornerstone of environmental law today. In addition to NEPA, important legislation includes amendments made in 1970 to what came to be known as the Clean Air Act. Following that and the Clean Water Act, a number of laws were passed including: the Consumer Product Safety Act (1972), the Environmental Pesticide Control Act (1972), the Endangered Species Act (1973), the Safe Drinking Water Act (1974), the Toxic Substances Control Act (1976), the Superfund legislation to clean up hazardous waste sites (1980), and the Emergency Planning and Community Right-to-Know Act (1986). The Environmental Protection Agency (EPA), also created under the Nixon administration, was established to administer the new statutes.

The Endangered Species Act of 1973 is the principal conservation law protecting species in the United States. Although it has served as a model for other countries, its implementation has often been controversial.

There are also many fisheries laws, principal among them being the Magnuson Fishery Conservation and Management Act of 1976, which provides for a governing structure for fisheries management by establishing regional fisheries management councils throughout the coastal areas of the United States and its territories.

According to the U.S. Constitution, all powers that are not given to the federal government are retained by the states. State governments have an important role to play in protecting people's health, safety, and welfare—and have primary responsibility for stewardship of biological resources within their borders. Federal laws define the minimum standards for states to follow. States can then pass laws to protect plant and animal species, wetlands, forests, and other ecosystems within state lines. Local governments (for example, municipalities, towns, cities, and counties) can undertake comprehensive municipal planning to address specific human activities that affect biodiversity within their jurisdictions.

In addition to local, state, and federal laws, international treaties or agreements are important for conserving biodiversity because many species and ecosystems are not contained within political boundaries, and the increasing movements of people and globalization in trade have far-reaching impacts on biodiversity.

At the 1992 Summit in Rio, one of the key agreements adopted was the Convention on Biological Diversity (CBD). The CBD establishes three main goals: the conservation of biological diversity, the sustainable use of its components, and the fair and equitable sharing of the benefits from the use of genetic resources. Some 180 countries are now a party to the convention. Although it is international, however, the responsibility for achieving the goals of the agreement lies within the countries that signed the agreement. Governments are required to develop national biodiversity strategies and action plans, and integrate these into broader national plans for the environment and development. The success of the CBD depends upon the combined efforts of the world's nations. Ratification of a treaty by each country is voluntary, and enforcement can be difficult. The United States signed the CBD in 1993, but approval by two-thirds of the Senate, needed to ratify international agreements, has not yet occurred. Although the CBD is not recognized as law in U.S. federal and state courts, the policy actions of federal agencies conform to the treaty to the extent possible. However, U.S. influence on the actions and policies of the CBD are limited because it is not a party to the convention.

Other important international treaties concerning biodiversity conservation include:

- Convention on International Trade in Endangered Species of Wild Flora and Fauna (CITES). Drawn up to protect wildlife

Conservation Group Sets Precedent by Suing in the Public Interest

Precedent for environmental law in the United States was set in 1965, when a landmark decision was made in favor of a conservation group that sued to protect a natural area in New York state from the development of a power plant. Consolidated Edison, New York's utility company, announced plans to build a hydroelectric power plant on Storm King Mountain near the Hudson River. The plan was intended to meet the increasing demand for energy and was welcomed by many residents as a source of new jobs and a benefit to the local economy. Others saw the prospect of a new power plant as a threat to the mountain, the surrounding Hudson Highlands, and the entire Hudson Valley, a wilderness area that had figured prominently in U.S. literature and culture. The latter view had little support until Con Ed made the mistake of publishing a drawing that exaggerated the size of the power plant in relation to its surroundings. Opposition to the plant grew and organized as the "Scenic Hudson Preservation Conference." Hearings before the Federal Power Commission (FPC) focused on the technical questions of whether the plant was needed and whether Con Ed was capable of running it. Aesthetic questions were not considered. When the judge ruled in favor of Con Ed, Scenic Hudson appealed the case on the grounds that the FPC had failed to protect the public interest in accordance with its mandate. In circuit court, Scenic Hudson was granted "standing to sue" as an "injured party" in the case. Although litigation went on for many years afterward before Con Ed was forced to abandon plans for the plant, the ruling helped establish the legitimacy of environmental issues and opened the way for lawyers and the courts to play a role in conservation cases. (See http://www.nrdc.org)

Center for Biodiversity and Conservation

The American Museum of Natural History's Center for Biodiversity and Conservation is an example of an effort to bring the expertise and resources of natural history museums into conservation decisions and actions. The center's programs integrate research, training, and outreach so that people, a key force in the rapid loss of biodiversity, will become participants in its conservation. The center works with governmental agencies, universities, and NGOs to expand scientific knowledge about diverse species in critical ecosystems and apply this knowledge to conservation. Center projects are in the Bahamas, Bolivia, Madagascar, the Metropolitan New York City region, and Vietnam. In Bolivia, for example, Bolivian and U.S. museum scientists are conducting surveys of species found in selected protected areas to help advise the government in managing those areas. Working with nearby community groups, the project also aims to increase participation in conservation.

against overexploitation and to prevent international trade from threatening species with extinction, CITES entered into force on July 1, 1975, and now has a membership of 152 countries. These countries act by banning international commercial trade in an agreed list of endangered species ("Appendix I") and by regulating and monitoring trade in others to ensure their sustainable use and prevent them from becoming endangered ("Appendix II").

- Convention on Wetlands of International Importance (Ramsar). Signed in Ramsar, Iran, in 1971, this treaty provides the framework for national action and international cooperation for the conservation and wise use of wetlands and their resources. There are 123 parties to the convention, with 1,060 wetland sites, totaling 80.6 million hectares, designated for inclusion in the Ramsar List of Wetlands of International Importance.
- Convention Concerning the Protection of the World Cultural and Natural Heritage (World Heritage). Agreed to at the general conference of the UN Educational, Scientific and Cultural Organization meeting in Paris in 1972, this treaty is unusual for its emphasis on the cultural as well as biological significance of natural areas. There are 162 parties to the convention.
- Convention on Migratory Species. One of a small number of intergovernmental treaties concerned with the conservation of wildlife and wildlife habitats on a global scale, this treaty aims to conserve terrestrial, marine, and avian migratory species throughout their range. Since the convention's entry into force in 1983, membership has grown to include seventy parties from Africa, Central and South America, Asia, Europe, and Oceania.

Academic and Research Institutions

Academic and research institutions have an important role to play in increasing our understanding of biodiversity and how to conserve it. Natural history museums are the principal institutions through which past and present biodiversity is preserved, interpreted, and presented. The museum's role in gathering and maintaining collections is critical as biodiversity is lost from nature. Scientific collections provide primary evidence for the existence and identification of different species; offer reliable documentation of past extinctions; record approximations of past abundance and the distribution of extant species; document the responses of organisms to environmental stress; and provide researchers with a historical perspective on contemporary biological questions.

Long viewed as dusty storehouses of the past, natural history museums are now providing leadership in bringing the scientific knowledge derived from these collections to bear in biodiversity conservation issues. Museums as well as botanical gardens, aquaria, and zoological parks play an important role as scientific, educational, and social institutions. They sponsor expeditions to survey biodiversity; make recommendations for managing wildlife resources and habitats based on data collected; organize and communicate information; serve as a location for convening people for conferences, workshops, and discussions; and focus attention on issues through exhibitions.

Although universities cover a wide variety of disciplines that are relevant to understanding and conserving biodiversity, research has traditionally been based within a particular discipline, limiting communication across disciplines as well as limiting relevance to complex problems relating to conservation. Increasing emphasis on interdisciplinary work gives university faculty and students the tools and perspective to examine real world problems. Biology, economics, sociology, education, and communications are among the many disciplines that help us to understand biodiversity.

Many universities are research institutions, but they are first and foremost educational institutions, offering formal training to prepare students for jobs in which they will make decisions that affect biodiversity. Universities are increasingly offering interdisciplinary programs with practical experience. In many countries, university-level programs to train conservation biologists have grown rapidly. However, in developing countries—often among the richest in biological diversity—there is a critical need to expand and improve university-level training.

University extension programs address community issues, generally in the state in which they are located. These programs often utilize information that is derived from research conducted by university faculty and students and apply it (through educational activities, training, and demonstrations) to improve agricultural methods and yields, to assist community health programs, or in other endeavors to improve the quality of life.

Nongovernmental Organizations

Nongovernmental organizations (NGOs) are difficult to categorize as one organizational type. They come in many sizes and represent a wide variety of agendas, ranging from global concerns to a specific issue or community, and thus they play different roles in relation to biodiversity conservation. Some NGOs are affiliations of professionals, some plan and carry out programs, and others lobby for a particular policy. Some NGOs conduct research in much the same way as a university or museum, while others take the results of research and utilize them in analyzing policy; they then package information for various audiences, often working closely with the communities they serve. In many cases, NGOs provide a link between government and a particular segment of the population.

In the United States, NGOs play an important role in the success and evolution of regulation by lobbying for new or amended legislation, and overseeing how government agencies are interpreting and implementing legislation. Internationally, NGOs are active in conservation in many ways. They support various international treaties by providing data, training, financial resources, and publicity.

Specialist groups made up of scientists from research institutions and NGOs offer critical expertise and advice for CITES and the CBD.

—*Meg Domroese*

See also: Ethics of Conservation; International Trade and Biodiversity; Museums and Biodiversity; Sustainable Development

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Selected Directory of Organizations

Academic and Research Institutions

Academic Programs in Conservation Biology
http://www.conbio.net/SCB/Services/Programs
Lists more than 60 graduate programs in conservation biology

American Museum of Natural History's Center for Biodiversity and Conservation
http://research.amnh.org/biodiversity

Directory of Environmental Programs
http://ncseonline.org/dep
Lists more than 200 undergraduate and graduate environmental programs

Government and Governmental Agencies

Convention on Biological Diversity
http://www.biodiv.org

Convention on International Trade in Endangered Species of Wildlife Flora and Faun (CITES)
http://www.cites.org

Convention on Migratory Species
http://www.wcmc.org.uk

Convention on Wetlands of International Importance (Ramsar)
http://www.ramsar.org

World Heritage Convention
http://www.unesco.org

Nongovernmental Organizations

National Wildlife Federation
http://www.nwf.org
Conservation Directory: A Guide to Worldwide Environmental Organizations. Print and on-line versions published annually.

Religious Organizations

Alliance of Religions and Conservation
http://www.icorec.f9.co.uk

National Religious Partnership for the Environment
http://www.nrpe.org
With links to Evangelical Environmental Network, Coalition on the Environment and Jewish Life, United States Catholic Conference, and National Council of Churches of Christ in the U.S.A.

Religions of the World and Ecology, Harvard University Center for the Study of World Religions
http://www.hds.harvard.edu
Publications exploring specific religious traditions regarding their views of nature, ritual practice, and ethical constructs

Web of Creation
http://www.webofcreation.org
Information and links to resources relating to a variety of environmental topics, including an overview of major biodiversity concepts and a list of books and Web sites.

WWF International's Sacred Gifts for a Living Planet
http://www.panda.org

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Overharvesting

See Extinction, Direct Causes of

Oxygen, History of Presence in the Atmosphere

Earth’s atmosphere contains about 78 percent nitrogen and 20.9 percent oxygen—but it was not always that way. When the earth first formed some 4.65 billion years ago, it was surrounded by gases rich in hydrogen compounds, ammonia, methane, and water—a composition similar to that of the nebula from which it was born. How the earth got its oxygen has been a continuing controversy; it is now believed that it is not a remnant of the primitive atmosphere. Rather, it is now thought that gases, water vapor, and carbon dioxide, released from the interior of the earth about 4.65 billion years ago, heated up as a result of meteoric collisions and radioactive decay, replacing the primitive atmosphere.

In addition, two processes allowed oxygen-rich conditions to evolve: (1) the breakup of water molecules into hydrogen and oxygen in the upper atmosphere by ultraviolet radiation from the sun, and (2) photosynthesis, after green plants evolved. Sediments formed prior to 2.5 billion years ago were deposited under oxygen-poor conditions, but those deposited later indicate that oxygen molecules began to increase in concentration rapidly after about 2 billion years ago, to form an oxygen-rich atmosphere. Life and the atmosphere evolved together as oxygen molecules increased in number; small amounts high in the atmosphere were split into oxygen atoms by solar ultraviolet radiation, which then combined with oxygen molecules (O_2) to form ozone (O_3). The ozone layer itself absorbs ultraviolet radiation, which is lethal to life on earth. Apparently as a result of its formation, the ozone layer allowed more complex forms of life to evolve on earth. Oxygen content reached a critical level about 700 million years ago as life began to rapidly evolve into the great variety of life forms characteristic of the earth today.

—*Sidney Horenstein*

See also: Atmosphere; Atmospheric Cycles; Climatology

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P

Palearctic

See Biogeography

Paleontology

Paleontology is the branch of science that deals with the fossilized remains of life. Fossils may be the body parts or direct traces of activities left behind by animals, plants, fungi, and microorganisms. Thus they might include a mammalian tooth, a clam shell, a leaf, or the entire skeleton of a dinosaur, as well as dinosaur footprints, feces (coprolites), or clam burrows.

Neanderthals knew about fossils; they used, for example, the beadlike plates of the stems of ancient sea lilies to make necklaces and for exchange in trade. The ancient Greek historian Herodotus correctly deduced that the fossil shells he found in Egypt must be the remains of organisms that had once lived in a sea where now only desert stands. Many years later, the great Leonardo da Vinci saw sharks' teeth high in the mountains of Italy—and came to the same conclusion. But, for the most part, people had no idea of the true nature of fossils; one sage of the Middle Ages pronounced them to be "thunderbolts" frozen into the ground. And when the ideas of organic evolution came along, with the added possibility that fossils might actually be what they seem to be—the remains of ancient creatures, most of which no longer inhabit the earth—those who resisted the idea of evolution tended to see fossils as tricks of the devil, placed in rocks to deceive the minds of human beings. Another theory simply saw them as the remains of creatures that were excluded from Noah's Ark—and so perished in the Great Flood recounted in the Bible; indeed, some creationists still take that position.

But fossils are real, and truly are the remains of long-dead organisms. Some body parts—such as the woody tissues of plants, vertebrate teeth, or the calcareous shells of many marine invertebrates—are hard enough in life that they may be preserved for millions of years with little or no chemical alteration. Most fossils, however, are "permineralized": ground water bearing silica and other chemical compounds often perfuses the natural cavities and cracks in shells, bones, and teeth, hardening them considerably. For example, dinosaur bones from the Jurassic Morrison Formation in the western United States often have the natural cavities of the "spongy" part of their bones filled with carnotite and other uranium min-

A curator from the Division of Paleontology, United States National Museum, Smithsonian Institution, preparing the skeleton of a dinosaur for exhibition in 1921 (From the collections of the Library of Congress)

erals—making them discoverable with Geiger counters! Silicon dioxide (quartz, in the form of chalcedony or other "crypto-crystalline" minerals) often fills the empty cells of fossilized tree trunks, as in the famous Triassic specimens that still litter the ground in Petrified Forest National Monument in Arizona.

In still other fossils, silica and minerals such as iron pyrite (iron sulphide, commonly known as "fool's gold") may replace the bone, shell, or wood completely. Sometimes this chemical replacement happens molecule-by-molecule, but in other instances, the shell or bone is dissolved, leaving a cavity in the sediments that is later filled by the replacement mineral—forming a natural "cast." Most often, however, when remains are dissolved to leave a "mold," the fossils can still be studied because the impressions of the inner and outer portions of, for example, a clam shell are often preserved in exquisite detail. Paleontologists can then pour liquid rubber or other compounds into the mold, producing an artificial cast that is an exact replica of the animal.

Fossils are most commonly found in sedimentary rocks, which are most often the hardened ("lithified") deposits of sand ("sandstone"), clay ("shale"), or particles of lime ("limestone")—or mixtures of two or all three. Metamorphic rocks—which are formed from other rocks by intense pressures and heat, may also reveal traces of fossils, if the metamorphic rock had been formed from a fossiliferous sedimentary rock; but fossils in metamorphic rocks are comparatively rare and most often highly distorted. Igneous rocks, which are formed from a liquid melt (such as lava), almost never have fossils, though there are rare exceptions: a cavity in a lava flow in Washington state preserves the outline of a wooly rhinoceros that had become trapped and died during the eruption.

Fossils usually form as dead organisms become buried by layers of sediment. Most dead organisms, of course, are completely consumed by bacteria and fungi in the normal decay process, which still goes on even after burial in muds or sands. But the harder tissues, such as wood, shells, teeth, and bones, are the last to decay, and they often escape full decomposition until they are buried so deeply that decay stops. Sometimes, though, the decay process stops before it has really begun, especially when organisms are buried suddenly in environments with little or no free oxygen (anaerobic environments); truly remarkable preservation of soft tissues such as skin and internal organs in such rare instances sheds amazing insight into long-dead worlds—such as the famous Burgess Shale deposits of the Middle Cambrian of British Columbia, where soft-bodied worms and arthropods are fossilized in intricate detail alongside the trilobites and other marine invertebrates that normally are the only kinds of fossils to be found in rocks of that age.

If at least some parts of the dead organism survive decay, then the potential fossil must be spared further destruction by chemicals and pressures in the earth's crust. To be discovered, the fossil must be uplifted as part of a rock mass exposed to the air (except for the case of deep-sea marine microfossils, which are discovered through drilling on ocean floors). As soon as rocks are exposed, they begin to erode, and many fossils that have survived millions of years are destroyed as they weather and crumble apart at the foot of some isolated cliff. With luck, though, they will be discovered by paleontologists (or knowledgeable amateurs), brought back to homes or laboratories in universities and museums, studied, and eventually named and described in the scientific literature. The study of all the processes from death to complete fossilization forms a branch of paleontology known as taphonomy.

Historically, people have studied fossils for two separate though related reasons: they have been interested, of course, in the history of life. But fossils also help geologists to "tell time": geologists discovered nearly 200 years ago that fossils occur in a definite sequence through the rock record (a sequence now known to have been produced by the evolutionary process). The same fossils found in different places are roughly the same age—a discovery that allowed geologists to unravel the pages of earth history and to divide up geological time and produce the "geological time scale." This geological side of paleontology has proven indispensable in the search for oil reserves, as oil occurs in traps in sedimentary rocks that must be studied in detail—in terms of age, as well as understanding ancient environments crucial to oil formation. The study of ancient environments through fossils is known as paleoecology.

But paleontology is perhaps best known as our only direct means of understanding the history of life. And though the fossil record is incomplete—as the remains of soft-bodied organisms only rarely are fossilized—the record is good enough for many groups not only to give us an outline of the sequential events of life's evolutionary history but also to help us understand how the evolutionary process works. Perhaps most important, the fossil record is our only means of knowing about organisms that have become extinct—thus filling in huge gaps of our knowledge of life's evolutionary diversity.

Within the past thirty years, there has been a veritable explosion of knowledge about the fossil record of the most ancient forms of life on earth. We now know that the oldest fossils are of bacteria—simple rod shapes discovered in sediments in Australia that are approximately 3.5 billion years old. The oldest eukaryotic cells (micro-organisms with complex cell structures, including a nucleus housing most of the cell's DNA) are now known as far back as some 2.2 billion years.

But it is the diversity of complex, multicellular, macroscopic animal and plant life, beginning some 540 million years ago, that forms the bulk of the known fossil record, and houses some truly remarkable, extinct kinds of organisms that have been very well studied by paleontologists over the past two centuries. Two examples of important, entirely extinct groups of animals are given below.

Trilobites, for example, are among the most primitive and oldest known arthropods. They first appeared in the Lower Cambrian Period—and lasted until the very end of the Paleozoic Era, nearly 300 million years later. The term *trilobite* refers to the three-lobe cross-sectional profile of these animals: a central, prominent axis seen on the middle region (the glabella) of the head (the cephalon), and running down the body's midsection (the thorax) and into the tail piece (the pygidium). The three front-to-back divisions of a trilobite's body (that is, cephalon, thorax, and pygidium) are unlike the anatomy of any modern arthropod; the head housed a pair of eyes. Although usually not preserved, there was a pair of antennae protruding forward from under the cephalon, as well as three pairs of legs that served the multipurposes of walking, eating, and breathing (through an upper gill branch). The central region of the body consisted of from two to more than forty separate segments, each with a pair of legs underneath; these thoracic segments were attached to one another along a joint system, allowing trilobites to roll up into a ball.

Trilobites are among the most common fossils in the remains of Cambrian oceans. After a major extinction episode wiped out many of the Cambrian families, trilobites rediversified and were major elements of Middle Paleozoic marine communities. The phacopid trilobites were prominent among them, possessing large eyes that are typically so well preserved that one paleontologist was able to take photographs through them. Study of the evolution, over an interval of approximately 7 million years, of the eye in one species, *Phacops rana* of the Middle Devonian of North America, led to development of the evolutionary theory of "punctuated equilibria."

Ammonoids if anything had an even longer history than trilobites. Ammonoids are coiled, shelled molluscan relatives of modern-day squid and octopi—and of the similarly coiled pearly nautilus of the southeastern Pacific Ocean. Like these other cephalopods, ammonoids swam by means of a form of jet propulsion, whereby water is taken into a body chamber (the mantle cavity) and then forcefully expelled through a nozzle (the siphon), propelling the animal in the opposite direction. With their fast speeds, cephalopods are very efficient predators.

Like the nautilus, ammonoids have partitions (septa) that are formed behind the body; as the animal grows, the body moves forward and a new partition is formed. The line where the partition meets the outer shell is called the suture—and it is the evolution of this suture pattern that is most distinctive about ammonoid history.

Evolving from nautilid ancestors in the Devonian Period, ammonoids diversified into so many species that geologists have long used them to correlate rocks and subdivide geological time. These earliest ammonites (goniatites) had very simple, wavy suture patterns. They were cut back by the great mass extinction in the Late Permian some 245 million years ago, and only a few species survived. But the ammonoids soon bounced back and proliferated once again—this time with crinkles in some parts of their sutures (the ceratites). Then the mass extinction at the end of the Triassic once again drove all but a very few of these ceratite ammonoids extinct. The few that survived managed once again to spring back, into the last great flowering of ammonoids—the "ammonites proper." These last ammonoids were abundant in the seaways of the Jurassic and Cretaceous, during the heyday of the dinosaurs. Theirs were the most complex sutures of all—a dense array of crinkles all over the suture. To geologists, the ammonites are the most important fossils for subdividing marine Mesozoic rocks.

Thus ammonoid history has much to tell us about the evolutionary process—including how important extinction is in eliminating some groups and spurring evolutionary bursts among surviving lineages. And ammonoid suture patterns also show that complexity sometimes increases during evolutionary history.

—*Niles Eldredge*

See also: Arthropods, Marine; Evolution; Evolutionary Biodiversity; Geological Time Scale; Mass Extinction; Mollusca; Punctuated Equilibria

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Paleotropics

See Biogeography

Palestinian Painted Frog

The Palestinian painted frog (*Discoglossus nigriventer*) formerly inhabited Lake Huleh (Lake Hula) in Israel and has not been recorded since the lake was drained in the 1950s. This species is known only from two adult and two tadpole specimens collected in 1940 on the lake's eastern shore in what was then Palestine (Mendelssohn and Steinitz, 1943) and a single adult specimen reported by Steinitz in 1955 (Werner, 1988). This species was the first of its genus to be reported on the eastern shore of the Mediterranean (Mendelssohn and Steinitz, 1943).

D. nigriventer was a small frog (4 cm in length) colored in shades of brown and gray with many white dots on its underside, marking the glandular openings in its skin. Nothing is known of its habits, food preferences, or life cycle. Of the two specimens collected by Mendelssohn and Steinitz, the smaller was eaten by the larger while they were housed in a terrarium for study.

Lake Huleh, the northernmost lake in the Jordan valley, was formerly one of the few large freshwater habitats in the Near East. The shallow pear-shaped lake extended over 12 square kilometers, with swampy meadows and dense stands of papyrus at its borders. In total, the lake and swamps covered up to 60 square kilometers, with significant seasonal and interannual variations caused by changes in water level. These wetlands provided vital wintering grounds and stops along migration routes for many bird species. Prior to the lake's drainage, surveys found several species of endemic fish and invertebrates. The primary source of the water in the lake was the Jordan River, and beyond Lake Huleh this water flowed onward to Lake Kinneret (the Sea of Galilee).

In an attempt to tame the environment and make it more hospitable and profitable for its human inhabitants, plans were proposed to drain Lake Huleh with the goals of eradicating malaria, creating land suitable for agriculture, and safeguarding the water for human use. Although the plans were proposed in the 1930s, World War II, the Israeli War of Independence, and other pressing domestic concerns delayed action until the 1950s. The scientific community pleaded for more extensive study of the lake and the impacts of the proposed drainage, but difficult working conditions and political instability impeded their efforts. The drainage plans went forward in 1951 and were completed in 1958 (Dimentman, Bromley, and Por, 1992).

Public and scientific concern prompted the government to set aside a portion (3.1 square kilometers) of the Huleh swamp and lake as the Huleh Nature Reserve, which was formally established in 1964 (Ashkenazi and Yom-Tov, 1997). The actual area that remained as a wetland following the drainage turned out to be significantly smaller than had been planned because of unanticipated drainage, evapotranspirational losses, and seasonal drying. In addition, the water that fed the reserve was primarily the effluent from neighboring fish farms. This water contained high levels of nitrogen and suspended organic matter that promoted eutrophication (the proliferation of algae and associated decreased oxygenation). Settling ponds were incorporated in the 1970s to improve the quality of the water entering the reserve (Dimentman, Bromley, and Por, 1992).

In retrospect, the drainage project was a limited success. The incidence of malaria was reduced, and more water was made available for human use. Initially the land was fertile, but soil subsidence and erosion led to diminished productivity within a few years (ibid.). In addition, decomposition of the peat soils in the Huleh lakebed released large amounts of nitrates and sulfates, which were washed by the rains into Lake Kinneret, leading to eutrophication and reduced water quality in that lake.

The Hula Restoration Project, overseen by a scientific advisory committee, was initiated in the 1980s. Rather than trying to achieve the impossible goal of restoring Lake Huleh to its pristine state, the committee formulated a plan to create a carefully engineered system of wetlands, lake, and agricultural areas. The plan aimed to restore wildlife habitat, control erosion, maintain the security of the water supply, provide alternative income for displaced farmers, and create ecotourism-oriented economic opportunities. The original course of the Jordan River was reopened, and a new, smaller lake, named Lake Agmon, was established in 1994.

Although it was hoped that many native plant and animal species would gradually recolonize the area by migration from adjoining remnants of the native habitat, intentional reintroductions were also performed. Migrating birds and other wildlife were attracted to the area by the re-established plant community. Nesting colonies of some bird species have been established. Following the draining of Lake Huleh, many birds discovered the commercial fishponds as an alternate source of food, causing extensive economic losses for farmers. To reduce this problem with the newly increased bird population, natural fish populations are being supplemented by artificial stocking (Zohary and Hambright, 2001).

The main water source for the new lake is the relatively pure water of the Jordan River, but the nitrogen and other nutrients that continue to be leached from the peat have contributed to the growth of plant matter that provides the basis for the food chain in the lake. In the drainage canals, however, the dense stands of plant growth impede water movement and make it more difficult to manage the water table elevation. The stagnant water in these canals may encourage the return of malaria-transmitting mosquitoes.

The results of the hurriedly conducted surveys of the 1950s, which attempted to document the biota of Lake Huleh, were not collated and published for more than forty years. Using these data, Dimentman, Bromley, and Por (1992) compiled a list of more than 100 species that have not been recorded in the Huleh valley since the drainage. Some of these species have never again been recorded anywhere in Israel. Several species that were endemic to Lake Huleh are now extinct. The Palestinian painted frog, not reported since 1955, was one of the inhabitants of Lake Huleh that did not survive to populate Lake Agmon (Werner, 1988).

—*Julie Pomerantz*

See also: Amphibians; Draining of Wetlands; Interior Wetlands; Lakes

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Peregrine Falcon

See Endangered Species

Perissodactyls

Order Perissodactyla (odd-toed ungulates) contains herbivorous grazing or browsing ungulates (hoofed mammals) that walk and run entirely on their hooves or digits; the sole of the foot and heel never touch the ground. Domestic horses and donkeys have been part of the human experience for thousands of years. Domestication of horses began about 3100 B.C.E., and of asses approximately 6,000 years ago. Both have accompanied human dispersal over the planet's land surfaces, functioning as sources of transportation, leather, and food. The mule is the sterile offspring of a male donkey (*Equus assinus*) and female horse (*Equus caballus*) and has been bred for more than 3,000 years for heavy pulling, as a pack animal, or for riding. Perissodactyls evolved from the Family Phenacodontidae (Late Paleocene to Eocene), member of the extinct Order Condylarthra, a group of ancient herbivorous ungulates from which several mammalian orders originated. The earliest perissodactyls, such as the dog-size *Hyracotherium*, are known from the Early Eocene of North America. The seventeen recent species are arrayed in six genera and three families: Equidae (*Equus*, eight species of horses, zebras, and ass); Tapiridae (*Tapirus*, four species); and Rhinocerotidae (*Dicerorhinus*, one species; *Rhinoceros*, two species; *Diceros*, one species; *Ceratotherium*, one species).

In all perissodactyls, body weight is borne by the central terminal digits (mesaxonic). All terminal digits are encased in hooves. Perissodactyls also have elongate skulls because

Two zebras neck-to-neck, Tanzania (Carl and Ann Purcell/Corbis)

the facial region is enlarged to accommodate a complete series of premolars and molars (cheek teeth) with expansive and complex chewing surfaces. Perissodactyls lack a clavicle and horns with bony cores. Unlike most artiodactyls, perissodactyls have a small, simple stomach. Cellulose from their herbivorous diet is broken down in the intestines by microbial action.

Wild populations of horses, zebras, and ass are now found only in Africa, the Middle East, and parts of Asia. This group has an extensive fossil record, providing a superb example of large-scale evolutionary change over a long time. Most of the evolutionary history of Equidae took place in North America, with the greatest diversity of species occurring in the Miocene. Wild equids became extinct at the end of the Pleistocene in North and South America but persist today in Eurasia and Africa. Domestic horses were brought to the New World during the 1600s.

Tapirs first appear in the Oligocene, and they retain many primitive traits shared with the common ancestors of all perissodactyls. Tapirs have a short proboscis, the front feet have four digits (with a vestigial fifth), and the hind feet have three digits. They inhabit tropical evergreen rain forests in the neotropics and Indomalayan region. Fruit and succulent vegetation constitute their diet.

Rhinoceroses first appear in the Middle Eocene. Recent species occur in Africa and the Indomalayan region, where they inhabit semideserts, grasslands, savannas, forests, and marshes. Rhinoceroses have been hunted for about 1,000 years to obtain the horn and other body parts that are valued for their supposed medicinal properties. All species are extremely endangered; the Asian rhinoceroses and African black rhinoceros face extinction.

—*Mary Ellen Holden*

See also: Black Rhinoceros; Endangered Species; Preservation of Species

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Permo-Triassic Extinction

The Permo-Triassic extinction occurred 245 million years ago at the end of the Permian Period. It marked the close of the Paleozoic Era and was a time when perhaps 95 percent of all species went extinct. The extinction was ecumenical in scope. Species that went extinct belonged to every phylum, lived in a variety of marine and nonmarine habitats, and had many modes of life. Understanding the Permo-Triassic extinction, the greatest crisis the biota has faced, is important if we are to put into perspective the biodiversity crisis facing our modern world.

Studying the Permo-Triassic extinction is not easy. In many areas the Permian-Triassic boundary is marked by an unconformity, a surface of erosion where uppermost Permian rock was eroded before the first Triassic rock was deposited. Because all evidence in geology comes from the rocks and their contained fossils, where Upper Permian rock is absent, evidence of the mass extinction is lost forever.

Douglas Erwin (1993, pp. 51–73), who specializes in the Permo-Triassic extinction, discussed places in which Permian rock is not separated from the Triassic by an unconformity. These include northeastern Greenland, the southern Alps, Transcaucasia and Iran, the Salt Range in Pakistan, Kashmir, the

Table 1

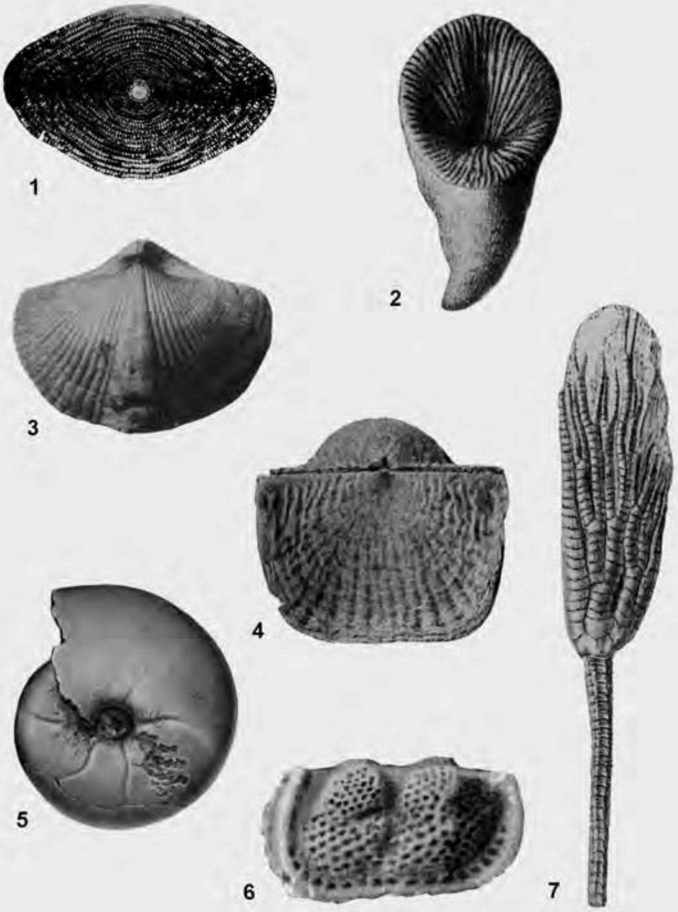
Major Groups of Invertebrates Affected by the Permo-Triassic Extinction

Period	*Protists*	*Corals*		*Brachiopods*		*Molluscs*		*Arthropods*		*Echinoderms*	
	Fusulinids	Tabulate	Rugose	Productids	Spiriferids	Gastropods	Ammonoids	Trilobites	Ostracodes	Crinoids	Blastoids
Cretaceous						░	E		░	▒	
Jurassic					E	░	░		░	▒	
Triassic					▒	░	░		░	▒	
Permian	E	E	E	E	■	▓	■	E	▓	■	E
Carboniferous	░	░	░	░	░	░	░	▒	░	░	░
Devonian		░	░	░	░	░	░	░	░	░	░

E Complete Extinction
■ Heavy losses
▓ Moderate losses
▒ Diminished importance
░ Abundant and diverse

Figure 1

Extinct Invertebrates at the End of the Permian Period



1. Fusulinid, a single-celled organism with a complex shell of calcium carbonate
2. Solitary rugose or horn coral
3. Spiriferid brachiopod
4. Productid brachiopod
5. Ammonoid
6. Palaeocopid ostracode
7. Crinoid

Sources: 1957, 1961, 1964, 1965, 1981. *Treatise on Invertebrate Paleontology.* Lawrence: University of Kansas in association with the Geological Society of America, Part L, fig. 65A, Part Q, fig. 102 *1b,* Part C, fig. 327 *2b,* Part H, fig. 370 *2c,* fig. 564 *2d,* Part F, fig. 162; Moore, Raymond C. 1962. “Article 29, Echinodermata 5.” *University of Kansas Paleontological Contributions*. Lawrence: University of Kansas Paleontological Institute. (Reprinted with permission).

Himalayas, and southern China. Most of these areas are remote from the centers of paleontological research, and in a few civil war is raging. Thus some have not been studied in detail, and evidence of an unconformity is stronger in some than others.

Table 1 lists the major groups of invertebrates that were strongly affected by the extinction. Some of these kinds of organisms had dominated marine ecosystems for 300 million years. Nevertheless, they were extinguished in a short time, although the length of time over which the extinction took place is not known.

The fusulinids (Figure 1,1) were single-celled, animal-like organisms that evolved in the Carboniferous and thrived to the end of the Permian. Their rapid evolution produced a high diversity, and in some rock units they are the most abundant fossils. Yet they went extinct at the end of the Permian, leaving no descendants. Two major groups of corals were abundant in the Paleozoic, the tabulate corals and the rugose or horn corals (Figure 1, 2). Both groups died out at the end of the Permian, leaving no descendants.

Brachiopods are present in the sea today, but during the Paleozoic they were a dominant element of the marine fauna. The spire-bearing brachiopods (Figure 1, 3) lost half of their families at the end of the Permian and went extinct in the Jurassic. The productid brachiopods were less successful (Figure 1, 4). Abundant and diverse during the late Paleozoic, none survived into the Triassic. In fact, following the extinction, brachiopods were never again dominant elements of the marine fauna.

Ammonoid cephalopods evolved in the Devonian and fluctuated in biodiversity for the rest of the Paleozoic and Mesozoic (Figure 1, 5). They were reduced in numbers at the end of the Permian but rebounded and became dominant predators until their extinction at the end of the Cretaceous.

Ostracodes—microscopic crustaceans related to lobsters—are abundant today, although they are often overlooked because of their small size (Figure 1, 6). Several groups survived the end-Permian extinction, but the major group of Paleozoic ostracodes went extinct, and post-Paleozoic ostracode faunas are quite different from those of the Paleozoic.

Many other groups of invertebrates were affected by the mass extinction. Two that are common in Paleozoic rocks are crinoids (Figure 1, 7) and trilobites. Crinoids live in the sea today, but they went almost extinct at the end of the Permian. Trilobites had been in decline for much of the Paleozoic, and the last species went extinct at the end of the Permian. Several groups of marine fishes were decimated by the extinction, but freshwater fishes and those tolerant of fluctuating salinity persisted.

Terrestrial tetrapods were affected as severely as marine forms of life. Nearly two-thirds of the tetrapod families went extinct. Many families of amphibians were exterminated at various times in the Permian, not only at the end of the period; and two-thirds of the remaining nine families of amphibians were lost in the extinction. The mammal-like reptiles were very hard hit; they rebounded in the Triassic but were never again the dominant tetrapod group, being displaced by the archosaurs, the ancestors of the dinosaurs.

The global turnover of plants from the Permian to the Triassic required some 25 million years and, thus, scarcely qualifies as a mass extinction. Nevertheless, the dominant groups of Permian plants, the seed ferns and primitive gymnosperms, were replaced by the more modern seed ferns and gymnosperms with which we are familiar today: conifers, ginkgoes, and cycads.

The cause of the Permo-Triassic extinction is unknown. Erwin suggested that it may have been the result of the coincidence of a regression of the sea and massive eruption of basalt in Siberia. The regression would have caused ecological instability and increased the concentration of carbon dioxide in the atmosphere, causing global warming and anoxic oceans. Eruption of basalt also would have contributed CO_2. We now know that the onset of extinction coincided with the first eruption of basalt. More recently, evidence of a bolide impact has been found, but work remains to be done to confirm the cause of the extinction.

The end of the Permian, marked by the extinction of many groups of organisms that had dominated marine and terrestrial environments for hundreds of millions of years, cleared the way for the expansion of the modern fauna of today.

—*Roger Kaesler*

See also: Geological Time Scale; Mass Extinction

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Phylogeny

A phylogeny results from evolutionary descent with modification. As such, a phylogeny is one kind of genealogy. At the level of biological organization of species and groups of species, a phylogeny results from a number of speciation events (new species evolving from ancestral species) that have happened over time. Biologists recognize that all living organisms are related to each other through this descent and that there is a single phylogeny, or Tree of Life, that exists objectively in nature and quite apart from our ability to discover it. In accepting this idea, biologists embrace the grand paradigm of evolution and reject both special creation and spontaneous generation.

Processes that generate the Tree of Life operate at several different levels. Reproduction, growth, and ontogeny (development of the individual) predominate at the level of individual organisms. Although natural processes operate on the level of individual organisms, processes such as natural selection, genetic drift, and migration, birth, and death, are best studied by considering entire populations. Speciation predominates at the level of lineages (species), which are composed of one to many populations.

Discovering the Tree of Life is one of the major preoccupations of systematic biologists. The origin of the term resides in the fact that early evolutionary biologists used the tree metaphor to characterize phylogeny. We should be careful to distinguish between the Tree of Life and our attempts to reconstruct the Tree of Life. The phylogenies presented by systematic biologists are hypotheses about the Tree of Life and not the thing itself. A useful metaphor is a roadmap. A roadmap may accurately present information on the location and intersections of roads, but it is a graphic representation, not the roads themselves. It represents many useful facts about roads using abstract symbols. Phylogenic hypotheses most frequently map the descent thought to have occurred between entire species or entire groups of species such as families, orders, or even phyla.

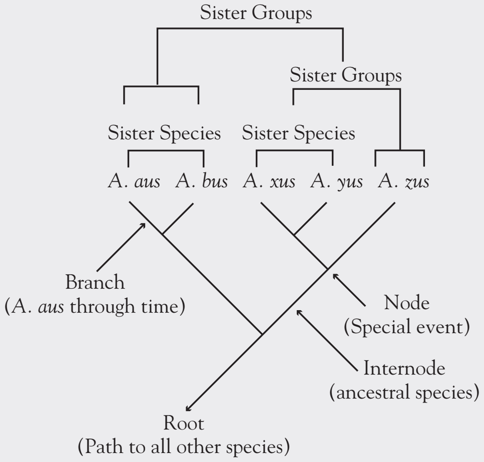
Phylogenetic tree hypotheses have very explicit meanings, and it is worth examining what is implied. Consider a tree hypothesis of some species. Like a real tree, tree hypotheses have branches, nodes, and internodes. In most cases branches and internodes are entire lineages (see below for the exception). Since species are the highest levels of individual organization on which forces of evolution can work (speciation), these branches and internodes are graphic representations of at least one species. In Figure 1 the branches are labeled with species names, forming a hypothesis of how they are related. Species who share a common ancestor not shared with any other species, such as the two in the hypothetical genus *Aus*, are termed sister species. Groups of species that share a common ancestor not shared with any other groups are termed sister groups. The branching events that separate the branches and internodes represent speciation events: cladogenesis. Cladogenesis is a term for a variety of modes of speciation that are characterized by a lineage being split to form two different lineages. Cladogenesis is probably the most common form of speciation. In parts of the tree where cladogenesis has occurred, the internodes are the symbolic representation of common ancestral species.

In some phylogenies, especially in higher plants, there can also be reticulations: individual organisms of different lineages interbreed, and the hydrids form a new, third, lineage. Although it is possible for two entire lineages to join to form a third, most of these kinds of events involve individual organisms from local populations. In these cases the internodes do not represent species but only parts of species. They are the graphic representation of the individual organisms that hybridize to produce the new species.

Systematic biologists reconstruct parts of the Tree of Life by studying the similarities and differences among organisms and attempting to sort out which of the similarities denote unique common ancestry. Traits may be the result of convergence, the independent origin of a similar trait. They may be homologous: traits that evolved in a common ancestor and were retained in descendants of that ancestor. For example, the body shape of sharks and dolphins are similar but convergent; the body shape of garter snakes and rattlesnakes are similar and homologous. Of course, the only reason we conclude that the body shapes of sharks and dolphins are convergent is that we already have a hypothesis of phylogeny: dolphins are more closely related to cows than to sharks.

Figure 1

A Hypothetical Phylogeny of Five Species of Organisms Classified in Two Genera, Aus and Xus



Note: This figure illustrates some of the implied meaning of the graphic representation of a phylogenetic hypothesis.

So, how do we reconstruct phylogeny in the first place? The answer lies in the methods of phylogenetic systematics, a set of methods that allow systematists to use agreement among many characters to test different hypotheses about phylogeny. Initially, it might be quite reasonable to think that the body shapes of sharks and dolphins are homologous and thus derived from the same body shape in their common ancestor. But many other traits argue otherwise. We conclude that dolphins are mammals, and thus their body shape has evolved independently from that of sharks. To complicate things even more, not all homologous characters are equally useful for any particular phylogenetic problem. For example, the coelacanth is a living fossil fish that, like most other fishes, has a caudal fin. No one doubts that this caudal fin is homologous with the caudal fin of tunas. Humans don't have a caudal fin. In fact, humans even lose their tails as embryos. Does this mean that coelacanths are more closely related to tunas? No, as it turns out, coelacanths are more closely related to humans. They are one of the early branches in that part of the Tree of Life leading to the legged vertebrates, and they bear the mark of that common descent in other homologous features shared with humans, such as the presence of the vena cava as a major artery of the circulatory system leading from the heart.

The basic methods for reconstructing phylogenies were formalized by the German entomologist Willi Hennig in the 1950s. The method consists of searching for patterns of potentially homologous characters and accepting only those phylogenetic tree hypotheses that contain the maximum number of homologies and the minimum number of convergences. For example, if we accept that dolphins and cows are more closely related to each other than dolphins and sharks, then we can accept such traits as being warm-blooded, having a placenta, and having bone as homologous while rejecting only body shape as being convergent. Conversely, if we accepted the idea that sharks and dolphins were more closely related, we would have to accept a whole suite of mammalian traits as convergent. Although that is certainly a possibility, it is not very likely.

—E. O. Wiley

See also: Classification, Biological; Linnaean Hierarchy; Systematics

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Physical Anthropology

An evolutionary science, physical anthropology is the anatomical and evolutionary study of humans as biological organisms. Physical anthropology, also referred to as biological anthropology, is one of several subfields within the anthropological discipline: cultural, linguistic, archaeological, ecological, and physical.

The field of physical anthropology is composed of many topical areas of interest. The more traditionally defined areas are: (1) primate studies, (2) paleoanthropology, and (3) human variation. Today's physical anthropology relies on a multidisciplinary approach, bringing with it a whole host of methodologies that will lend some clarity on the biological history of our human and nonhuman primate ancestors. Only then can we know what it means to be human. Only then will a clear picture emerge of how and when humanity took an evolutionary foothold that luckily for us has yet to loose its grip.

History

Its origin can be traced back to the eighteenth century, when Linnaeus included humans in his book *Systema Naturae* in 1735 with minimal descriptions at the species level. In the 1770s and 1780s, Johann Friedrich Blumenbach fathered this field, with his anatomical circumscription of modern human variability into five populations, or races: Caucasian, Mongolian, Ethiopian, American, and Malaysian. During the nineteenth century it continued to blossom, mainly out of concern among natural historians interested in delineating the mechanisms by which biological variation arises. Additionally, tremendous doubt was raised among natural historians whether dogma presented by biblical literalists provided tenable interpretations of how humans came to exist on earth, especially in light of the numerous fossil mammal (and human) discoveries in sediments beneath and alongside those containing evidence of ancient cultures. Fortunately, the more common Lamarckian paradigm of evolution would soon shift because of two events: (1) the 1859 announcement of Charles Darwin's—and to some extent Alfred Wallace's—proposal of natural selection as a mechanism for explaining how species gradually change over time; and (2) the 1864 naming of an extinct human ancestor. In 1856, miners discovered a fossil human inside the Feldhofer Grotto in the Neander Valley, Germany. This was a critical juncture for physical anthropology, because Darwin's research reintroduced earlier concepts proffered by the geologist Charles Lyell and others, concepts that conceptualized the idea of deep time and the similarity of processes at work then and now. It was also important because a friend of Darwin's, Thomas Huxely, would spend the rest of his life educating lay people about natural selection and its influence on all living creatures, especially humans. In effect, Huxely's research laid down the foundation for physical anthropology to grow and develop.

Discoveries of fossilized humans now meant that evolutionary concepts could be applied to modern humans. Lyell, who was once a firm believer that God was in some way responsible for life on earth, abandoned many of his theological notions and accepted Darwin's work. After examining what remained of the Feldhofer Grotto, Lyell would soon write a popular book on the geological antiquity of man. With deep time and evolution gaining acceptance, the only thing missing was a direct mechanism of inheritance.

At the turn of the twentieth century, the field of genetics would fill in the gaps and influence most of the evolutionary sciences, including the field of physical anthropology. However, the field's research interests clearly bifurcated in ideology at that time. Most physical anthropologists remained content with measuring head shapes, describing skin and hair types, blood types, and overall body shapes, but others were interested in the eugenics movement. Many years would pass and many decent people would be captured by the movement, earmarked as genetically challenged, and eventually sterilized. Although this was happening in many U.S. neighborhoods, physical anthropologists were concentrating on building comparative skeletal collections in order to get a handle on the range of morphological variation among human populations. Fortunately, the eugenics movement ended, and genetic studies in modern human and nonhuman primates are now used to address the origin and evolution of humanity and not to create a perfect race. Today the field of physical anthropology does not tolerate racist ideology, but we are left to sort out the legal and ethical ramifications generated by the turn-of-the-century collectors of human skeletal material.

Areas of Interest

The field of physical anthropology is composed of three main areas of interest: (1) primate studies, (2) paleoanthropology, and (3) human variation. Primate studies are concerned with defining humans in their naturally defined niche (earth) by examining living species of prosimians, monkeys, and apes (Order Primates). Primatologists primarily study and record the behavior, functional morphology, and anatomy of extant primates. Many physical anthropologists, such as A. Schultz (d. 1976) and Sherry Washburn (d. 2000) believed that primate studies held high promise for addressing questions of human origins, which in the early 1960s transformed the way in which physical anthropologists asked evolutionary questions. M. E. Morbeck, a physical anthropologist trained under Washburn at UC Berkeley, currently studies the skeletal remains of the famous Gombe chimpanzees to "read" from the bones the reproductive and survival life history characters recorded during their various life stages. She and her colleagues then compare their skeletal data with the detailed written behavioral life histories recorded by Jane Goodall and her Tanzanian staff.

There is an obvious connection between primate studies and human evolution, as Washburn believed, and tremendous interest in studying Gombe chimps and other primates was sparked in the 1960s by the world-renowned paleoanthropologist Louis Leakey

(d. 1972). As a conservationist, Leakey was concerned with documenting as much data as possible about the great apes before they would no longer exist. However, as a paleoanthropologist, he believed that the information learned from observing chimpanzees and gorillas could hold important clues to understanding our more ancient ancestors, in terms of social dynamics, types of environments encountered, and types of resources exploited.

Paleoanthropology concerns itself more with the fossil record of primates, and in particular, humans and their immediate ancestors—the Family Hominidae. Paleoanthropologists commonly use an interdisciplinary approach when conducting fieldwork to study chronology, habitats, and material culture. Within this team, the physical anthropologist is responsible for interpreting the fossilized bits of bone recovered from a site and reporting on its diagnostic features and importance framed within the body of knowledge culled by other team members, and then in light of the rest of the fossil record. To prepare, one must comparatively study the hard tissue anatomy (osteology and dentition) of a wide variety of extant and extinct primates and other mammals in order to make functional, morphological, and evolutionary inferences of ancestral human and nonhuman primate life histories.

Two successful examples of accomplished paleoanthropological teams at work in the field include the one led by Rutgers University professors Susan Cachel and Jack Harris, both of whom have been put in charge of continuing the heuristically important paleoanthropology research of the Lake Turkana, Kenya, Field School first started by Glynn Isaac and Richard Leakey in the late 1960s. Another group of well-known professors from the Institute of Human Origins (IHO) team, Donald Johanson and William Kimbel, have worked in the Afar region of Ethiopia for the past thirty years. Although Johanson is known worldwide for his key participation in the discovery of the fairly complete skeleton of *Australopithecus afarensis* named "Lucy," IHO's paleoanthropological research is responsible for the bulk of scientific discourse regarding hominid fossils recovered from sediments dated 3.5 to 2.0 million years ago in East Africa.

Studies of human variation, on the other hand, focus on the more recent chronological periods and primarily concern themselves with how and why humans differ biologically in today's world. Typically, this involves deciphering the immediate influence that culture elicits on human biological and mental development, or perhaps the extent to which culture acts as a buffer to natural selection among many modern human populations. Today these studies include human skeletal maturation and growth, population size and composition, epidemiology, and genetics. Extensions of human variability studies include forensic applications in legal cases when recovered osteological and dental remains are unquestionably human and the cause of death is unclear.

Physical anthropologist Harry Shapiro (d. 1990) was a true leader in the field with his work on the island survivors of the HMS *Bounty*, as well as documenting the effects of migration and the environment in modern human populations. A current leader of our field is Douglas Owsley, of the Smithsonian Institution, who is an expert in Native American studies and spends much of his time documenting the morphological variation in Amerindian skeletal remains. Owsley is also an expert in forensic anthropology and is commonly called upon by the FBI to help in difficult cases. The field of genetics has sparked a great amount of awareness among physical anthropologists interested in human variation. Researchers are turning to DNA studies to answer both micro- and macroevolutionary questions of who peopled the Americas and when they did. Although these studies are in their infancy, they are continuously fine-tuning their methods and show high promise for future research in physical anthropology.

—*Ken Mowbray*

See also: Great Apes; *Homo Sapiens;* Human Evolution; Primates

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Pioneer Species

See Succession and Successionlike Processes

Plankton

The term *plankton* is derived from the Greek word *planktos*, meaning wandering, and is used to describe any of a diverse array of prokaryotic (Bacteria and Archaea) and eukaryotic (Eukaryota) aquatic organisms that possess limited mobility and thus float, or passively drift, in the water column. Many taxa are holoplanktonic and spend their entire life cycle in the plankton, while others are meroplanktonic, spending only a portion of their life cycle in the plankton. Planktonic organisms are found in both marine and freshwater ecosystems. Marine ecosystems physically dominate the planet, inasmuch as oceans cover approximately 71 percent of the earth's surface. In comparison, freshwater ecosystems cover less than 1 percent of the surface of the earth but contain a larger proportion of life's diversity.

Plankton have traditionally been subdivided into two main groups—phytoplankton and zooplankton—based on their mode of nutrition. Phytoplankton manufacture their own food through photosynthesis (photoautotrophs) and are represented by a number of taxonomically diverse groups, such as cyanobacteria and other photosynthetic bacteria, and single-celled and multicellular photosynthetic eukaryotes. Phytoplankton are, therefore, limited to dwelling in the upper, sunlit waters of a body of water. These surface waters, known as the photic zone, constitute a layer of water that extends from the air-water interface to the depth at which 99 percent of all sunlight is absorbed. In the clear tropical waters of the world's oceans, the photic zone may extend as deep as 200 m, whereas in inland freshwater lakes, the maximum depth to which light can penetrate is around 100 m.

Zooplankton are heterotrophic organisms and thus must obtain their nutrition by feeding on other organisms or by maintaining intracellular symbiotic associations with unicellular photosynthetic organisms. A diversity of organisms are classified as zooplankton, including numerous single-celled eukaryotes (flagellated and nonflagellated), and metazoans. As collecting techniques have become more sophisticated throughout the years, it has been recognized that smaller-size organisms dominate plankton communities. Bacterioplankton include both heterotrophic and autotrophic bacteria; viroplankton include viruses that infect both prokaryotic organisms (bacteriophages) and eukaryotic organisms (viruses).

Although most plankton are less than 1 cm in size, plankton span a broad size range. The size classes used to describe plankton include: megaplankton (20–200 cm), mesoplankton (0.2 to 20 mm), microplankton (20–200 μm), nanoplankton (2–20 μm), picoplankton (0.2–2 μm), and femtoplankton (0.02–0.2 μm).

Biodiversity of the Plankton

A diverse array of organisms from numerous taxonomic groups have adapted to life in the plankton; however, autotrophic micro-organisms constitute the base of the food web in both marine and freshwater ecosystems. Thus, the greatest biodiversity of the plankton, known and unknown, is to be found in the microscopic forms.

Viruses

Viruses are noncellular genetic elements that are incapable of self-replication, and thus must infect and enlist the machinery of living cells in order to reproduce. Viruses encompass a variety of morphologies, but their basic structure is that of a nucleic acid (RNA or DNA) core packaged inside a protein coat or cell membranelike envelope. Aquatic viruses typically range in size from 20 to 200 nm and dominate the femtoplankton. Marine viruses are the most abundant life form in the ocean, occurring in densities as high as 100 billion per liter of seawater. Although marine viruses are known to infect a wide range of organisms, marine bacterioplankton and phytoplankton are the most common hosts of marine viruses. Viruses are generally host specific, and bacteriophages are believed to contribute to a significant percentage of bacterial mortality in the planktonic realm.

Bacteria

After viruses, bacteria are the next most abundant life form in the oceans today, occurring in densities of approximately 10 billion per liter of seawater in surface waters. The bacterioplankton includes diverse taxa such as cyanobacteria and prochlorophytes, proteobacteria, and other groups.

Cyanobacteria, formerly called blue-green algae, are oxygen-producing photosynthetic bacteria that possess either chlorophyll a and phycobiliproteins, or chlorophylls a and b, as their primary light-harvesting pigments. Cyanobacteria are widely distributed in both marine and freshwater ecosystems and dominate the picoplankton-size class in marine environments. Cyanobacteria include unicellular and multicellular forms, the degree of morphological complexity ranging from simple, coccoid, and rod-shaped forms to more complex, differentiated forms that possess specialized compartments, such as reproductive cells, heterocysts, and akinetes.

Marine cyanobacteria possessing phycobiliproteins include colonial, filamentous forms, such as *Trichodesmium*, and small coccoid forms, such as *Synechococcus* and *Synechocystis*. Freshwater cyanobacteria include such forms as the filamentous *Anabaena* and *Oscillatoria*, and the colony-forming *Microcystis*. *Microcystis* produces neurotoxins and hepatotoxins, and ingesting water contaminated by these toxins can cause mortality in vertebrates and gastrointestinal illness in humans.

There are a few derived cyanobacterial groups that possess chlorophyll b, but lack phycobiliproteins. These taxa were initially called prochlorophytes, reflecting previous speculations that they might be living representatives of the ancestral group that gave rise to the chloroplasts of chlorophyte algae and green plants. More recently, prochlorophytes have been shown not to be a distinct group, but to have independently arisen from different cyanobacterial lineages. These groups include marine taxa such as the coccoid *Prochlorococcus* and *Prochloron*, and freshwater forms such as the filamentous *Prochlorothrix*.

A diversity of heterotrophic bacteria of variable morphologies is found in the plankton of marine and freshwater ecosystems. Alpha-proteobacteria occur in both marine and freshwaters and include rods, vibrios, and filaments of various sizes. Beta-proteobacteria are dominant in freshwaters but rare in marine waters, and they are represented by straight to curved rods (1.5 μm long by 1 μm wide). Other proteobacteria are also present in lower abundances in both marine and freshwaters. The *Cytophaga-Flavobacterium* group is composed mostly of filaments 20 to 300 μm long; it is the dominant group in marine waters, although members of this group also occur in freshwaters. *Planctomycetales* are large cocci, more than 1 μm in diameter, that are found in both marine and freshwaters, often associated with macroaggregates.

Most of the earliest microfossils preserved in the fossil record are cyanobacterial, and most of them are represented by benthic mat-forming and stromatolite-building taxa. A few potential fossil planktonic forms are known; for example, *Oscilltoriopsis obtusa* is a 2-billion-year-old fossil from the Duck Creek Formation of Australia that morphologically resembles modern filamentous species of *Oscillatoria*.

Archaea (or Archaebacteria)

Archaea is another group of single-celled prokaryotes, many of which occur in harsh or extreme environments. Recent studies have shown that archaeans, while never dominant, are cosmopolitan members of the plankton in both marine and freshwater ecosystems.

Protoctista

Protoctista is a paraphyletic grouping of lower eukaryotes that includes all eukaryotes except metazoans and green plants. Protoctistans are predominantly single-celled forms, although several groups have developed colonial and multicellular morphologies. Protoctistans may be either photosynthetic, or heterotrophic and nonphotosynthetic.

Algae is the term traditionally used to describe the polyphyletic array of photosynthetic single-celled and multicellular eukaryotes, excluding land plants. Different algal groups utilize different combinations of pigments for photosynthesis, their chloroplasts having been derived from at least three independent endosymbiotic events with photosynthetic bacteria or from secondary endosymbioses with other chloroplast-containing eukaryotes.

Nonphotosynthetic protoctistans are represented by a polyphyletic array of predominantly single-celled eukaryotes. Formerly called protozoans, reflecting earlier ideas of their close evolutionary ties to animals or metazoans, the nonphotosynthetic groups encompass a diversity of unrelated forms with flagellated and amoeboid morphologies

Foraminiferans. Foraminiferans are a protoctistan group that appears to have diverged early in the history of eukaryotes. Distinctive characteristics of foraminiferans include the possession of anastomosing pseudopodia (reticulopodia) and an extracellular test, or shell, that may be organic in composition, composed of agglutinated material, or of biomineralized calcite, aragonite, or silica. Although most foraminiferans live in benthic marine habitats, a few lineages have diversified into the plankton. Meroplanktonic forms include *Tretomphalus* and other closely related benthic taxa. Members of this group live attached to sea grasses and marine macroalgae during most of their life cycle. Just prior to reproduction, gametogenic individuals develop an enlarged, spherical gas-filled chamber, detach from their phytal substrate, and ascend into the plankton, where they release flagellated gametes into the surface waters.

Holoplanktonic foraminiferal species are widely distributed in the open ocean from subpolar to tropical regions. Spinose species are found living in warm, subtropical to tropical waters, where they dwell in surface waters of the photic zone. Most spinose planktonic species are hosts to intracellular photosynthetic eukaryotic symbionts, such as dinoflagellates, chlorophyceans, and haptophytes. Although the photosynthetic products of the endosymbionts provide the host cells with a source of endogenous nutrition, spinose species (such as *Hastigerina pelagica* and *Orbulina universa*) are known to feed on a wide range of prey items, including copepods, crab zoea, and fish larvae. Nonspinose species, such as *Globorotalia truncatulinoides*, are generally herbivorous, feeding on diatoms and nonphotosynthetic flagellated eukaryotes. Many nonspinose species live in the photic zone as juveniles but descend into deeper waters as adults. Other nonspinose taxa, such as *Globorotalia* species, spend their entire life cycle at depth.

Although living planktonic foraminiferans are relatively sparsely distributed in the plankton, occurring in densities of from 1 to 10 per cubic meter, their empty shells form significant deposits in oceanic sediments, and also did so in the past. The earliest fossil planktonic foraminiferans are found in Middle Jurassic sedimentary rocks of Europe. Fossil planktonic foraminiferans appear to have undergone three episodes of evolutionary diversification in the past—during the mid-Cretaceous, the Paleocene to Middle Eocene, and the Early Miocene. Recent reconstructions of the evolutionary relationships of planktonic foraminiferans based on DNA sequence data indicate that modern planktonic foraminiferans are derived from at least two different benthic groups.

Euglenids. Euglenids are a group of primitive, single-celled eukaryotes that are most closely related to the parasitic trypanosomes. Euglenids possess a pellicle composed of helically arranged, interlocking proteinaceous strips. Primitive euglenids are nonphotosynthetic and phagotrophic. Most derived euglenids are photosynthetic, possessing chlorophylls a and b as their primary photosynthetic pigments, and beta carotene and other carotenoid derivatives as accessory pigments. The flagella of euglenids are typically covered with a single row of fine hairs. A pigmented eyespot located at the base of one flagellum is believed to function as a light-sensing organ.

Euglenids live primarily in shallow, freshwater habitats with high nutrient concentrations and, thus, are considered to be environmental indicators of eutrophication and pollution.

Radiolarians and acantharians. Radiolarians and acantharians are nonphotosynthetic, single-celled eukaryotes that possess axopodia (pseudopodia underlain by an axial bundle of cross-linked microtubules). Both groups are wholly marine, dwelling exclusively in the waters of the open ocean, but like planktonic foraminiferans, radiolarians and acantharians are found in relatively low densities, from 1 to 10 per cubic meter of seawater. Radiolarians and acantharians have traditionally been classified together in the same group, but recent studies based on DNA sequence data indicate that these groups may have separate and distinct evolutionary histories.

Radiolarians possess a perforate organic wall, or capsule, that surrounds the cell body, and intricate siliceous skeletons. The cytoplasm of radiolarians is highly compartmentalized and organized into specialized zones with specific functions. Radiolarian species with nonspherical, bilaterally symmetrical skeletons feed primarily on bacterioplankton, while species with small spherical skeletons feed predominantly on photosynthetic bacteria and eukaryotes. The large, gelatinous colonial species are omnivorous generalists, feeding on heterotrophic flagellates, photosynthetic eukaryotes, bacteria, and cyanobacteria. Several radiolarian taxa host dinoflagellate and prasinophycean endosymbionts that live in the cytoplasmic zone exterior to the capsule. The fossil record of radiolarians extends from the Recent all the way back to Cambrian times.

Acantharians possess a microfibrillar, meshlike capsule and a skeleton composed of strontium sulfate spicules. Most acantharians dwell primarily in the photic zone, as they possess photosymbiotic haptophytes. The fossil record of acantharians is much younger than that of radiolarians, the earliest fossil acantharians being Eocene in age.

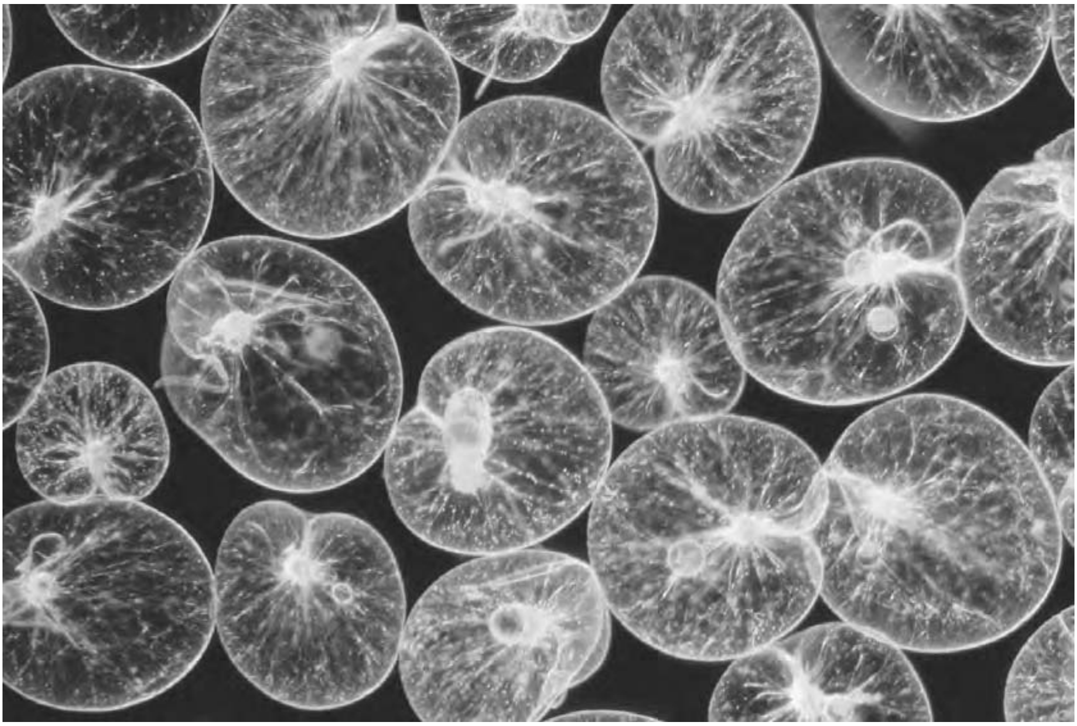
Heliozoans. Heliozoans are nonphotosynthetic, single-celled eukaryotes that possess axopodia, an organic wall, and siliceous or organic surface scales or spines. Heliozoans are primarily a freshwater planktonic group, but a few species, such as *Heterophrys marina,* are found living in marine waters.

Like foraminiferans, radiolarians, and acantharians, heliozoans use their web of radiating pseudopods to capture prey items from the water column. Studies have shown that heliozoans are ecologically important components of plankton communities in freshwater lakes; many species feed on photosynthetic and heterotrophic nanoplankton. Several species, such as *Heterophrys myriopoda,* are hosts to photosynthetic endosymbionts.

Alveolates. Alveolates are another morphologically diverse group of heterotrophic and photosynthetic protoctistans. Dinoflagellates, ciliates, and apicomplexans together make up the alveolate clade. Members of these three groups possess either cilia or flagella and a distinctive alveolar membrane system, which consists of flattened membrane-bound sacs located below the outer cell membrane.

Dinoflagellates are an important component of marine ecosystems. Nearly all dinoflagellates are planktonic marine forms, with only a few taxa found in freshwater ecosystems. Dinoflagellates possess a distinctive pattern of spiral movement, being propelled by two flagella—one longitudinal flagellum that extends in a direction opposite to movement, and a transverse flagellum that encircles the cell, lying in a girdlelike depression. Dinoflagellates also possess a theca, or test, made up of rigid cellulose plates. As a group, dinoflagellates include both photosynthetic and heterotrophic forms; approximately half of all free-living species lack chloroplasts and are heterotrophic. Photosynthetic dinoflagellates are yellowish-brown in color and possess chlorophylls a and c as their primary photosynthetic pigments, and beta and gamma carotenes, xanthins, and a unique carotenoid called peridinin, as accessory pigments. Heterotrophic dinoflagellates feed on a wide range of prey items, including bacterioplankton, photosynthetic and nonphotosynthetic single-celled eukaryotes, and metazoans such as copepods. Some dinoflagellate groups enter into endosymbiotic associations with other marine organisms, including planktonic cnidarians, foraminiferans, and radiolarians. Many dinoflagellates, such as *Noctiluca,* are bioluminescent and light up the waves in the ocean at night.

Several dinoflagellate groups produce toxins that can impact both human health and that of marine organisms. The dinoflagellate



Swarm of Noctiluca *plankton at sea surface in summer. Many dinoflagellates, such as* Noctiluca, *are bioluminescent and light up the ocean waves at night. (Frank Lane Picture Agency/Corbis)*

Pfiesteria is believed to have caused the massive fish kills that occurred in 1997 in numerous tributaries of coastal North Carolina. Planktonic dinoflagellates are responsible for "harmful algal blooms" (HAB), such as "red tides." Life-threatening paralytic shellfish poisoning may result from human consumption of filter-feeding marine mollusks and crustaceans that have been feeding on these dinoflagellates. Other dinoflagellates are responsible for neurotoxic shellfish poisoning and ciguatera fish poisoning.

Many species of dinoflagellates undergo an encystment stage during their life cycle, producing resistant cysts that are preserved in the fossil record. The earliest dinoflagellate cyst is the Silurian *Arpylorus*. No record of dinoflagellate cysts is found again until the Late Triassic.

Ciliates are another alveolate group that is widely distributed in the plankton of marine and freshwaters. Ciliates possess cilia, a special class of flagella, arranged in rows over the surface of the cell body. The cilia are anchored inside the cell via the infraciliature, a network of three types of fibers. In some ciliate groups, cilia cover the entire cell surface, while in other taxa the body ciliature is reduced or present only during certain stages of the life cycle. Some ciliates feed by phagocytosis, while others utilize a specialized oral apparatus called the cytostome. Most ciliates are omnivorous and feed on a diversity of bacterioplankton, nanoplankton, and microplankton. Several planktonic oligotrich ciliates enter into facultative symbioses, by sequestering and retaining functioning chloroplasts in their cytoplasm. This behavior has been observed in both marine and freshwater oligotrichs. Blooms of the red-pigmented, chloroplast-sequestering marine holotrich *Mesodinium rubrum* are responsible for nontoxic red tides that may, nevertheless, negatively affect marine habitats through oxygen depletion of the overlying waters.

Tintinnids are a specialized group of spirotrich ciliates that are an important component of the marine plankton. The cell body of tintinnids is enclosed in a cup-shaped organic test, or lorica, that may be covered with agglutinated particles such as sand grains, diatoms, or coccolith plates. Tintinnids feed on other small plankton, such as diatoms, dinoflagellates, coccolithophores, silicoflagellates, bacteria, radiolarians, and other ciliates. As a group, tintinnids are the most diverse in warm subtropical to tropical waters, but they occur in relatively low abundances. They have the lowest diversity but the highest abundances in colder water; for example, tintinnids are second only to diatoms in abundance in the Antarctic plankton. The fossil record of ciliates is almost exclusively that of tintinnids, which are first found in Ordovician rocks.

Haptophytes. Haptophytes, also known as prymnesiophytes, are a group of photosynthetic eukaryotes that possess two smooth flagella, a unique organelle called a haptoneme, and a body covered by organic or calcareous scales. Haptophytes possess chlorophylls a and c as their primary photosynthetic pigments. Haptophytes are a predominantly marine group, and they constitute a significant component of the plankton in today's oceans. Coccolithophorids, a haptophyte group bearing calcite scales (coccoliths), have an extensive fossil record extending back to the Late Triassic.

Stramenopiles. Stramenopiles are a morphologically diverse group of photosynthetic and heterotrophic protoctistans. Members of this group possess two flagella at some stage in their life cycle; one flagellum is smooth and the other is covered with tripartite hairs. Photosynthetic stramenopiles possess both chlorophylls a and c. Some of the photosynthetic stramenopile groups that are found living in the plankton include: diatoms (marine and freshwater), xanthophytes (freshwater), chrysophytes (marine and freshwater), silicoflagellates (marine), synurophytes, eustimatophytes, raphidophytes, and phaeophytes (marine macroalgae).

Diatoms are a diverse group of stramenopiles with numerous living and fossil species. Diatoms possess an elaborate frustule, or shell, composed of opaline silica. Most planktonic species are centric forms that form radially symmetrical frustules. Living diatoms are yellowish-brown in color and possess, in addition to chlorophylls a and c, accessory photosynthetic pigments such as beta carotene and xanthophylls. Diatoms are most common in waters with high nutrients. Some diatoms synthesize a neurotoxin identified as domoic acid that can accumulate in shellfish without any adverse affects, but that may be life-threatening to humans (causing amnesic shellfish poisoning) and to other vertebrates.

The earliest fossil marine diatoms are Early Jurassic in age; the earliest fossil freshwater diatoms are Paleocene in age. Fossil accumulations of diatom frustules are called diatomites or diatomaceous earth, and may be quite extensive in thickness. A well-known outcropping of a marine diatomite is the Middle Miocene Monterey Formation in California, which is mined commercially.

Chlorophytes. Chlorophytes, or green algae, are closely related to land plants and include prasinophyceans, chlorophyceans, and trebouxiophyceans. Chlorophytes include both single-celled and colonial multicellular forms that are characterized by the possession of at least two flagella of equal length. Chlorophytes possess chlorophylls a and b as their primary photosynthetic pigments, and carotenoid derivatives as accessory pigments. Chlorophyceans are a major component of the plankton in freshwater ecosystems, reaching high abundances in nutrient-rich waters.

Prasinophyceans are predominantly marine photosynthetic eukaryotes that may be either biflagellated or quadriflagellated. Their cell bodies and flagella are typically covered in distinctive scales. As mentioned above, prasinophyceans are found as endosymbionts in a few radiolarian taxa. Some prasinophyceans produce a highly resistant, sporopollenin-containing nonmotile stage called a phycoma. Prasinophycean phycomata are found in rocks as early as the Proterozoic, extending all the way up to the Recent.

Metazoan Zooplankton

Numerous metazoan, or animal, groups live in the plankton during some part of their life cycle. Many metazoan zooplankton feed or graze on phytoplankton, and their life cycles and population densities are synchronized with, or tied to, the availability of food. A large number of marine organisms have planktonic larvae that feed in the plankton before undergoing metamorphosis and settling out in a suitable habitat. Examples of organisms that produce meroplanktonic larvae include: corals, mollusks, gastropods, crustaceans, sea urchins, sea stars, annelids, and fish.

Holoplanktonic metazoan taxa found in marine waters include: snails (pteropods and heteropods), cnidarians (corals and jellyfish), ctenophores (comb jellies), crustaceans (copepods, ostracods, amphipods, and krill), and salps. Copepods are the most abundant and diverse group of metazoan zooplankton, dominating oceanic and coastal waters. Krill are shrimplike crustaceans that are abundant in regions of high productivity. In the Antarctic, krill are the primary food of baleen whales. The gelatinous zooplankton are made up of a polyphyletic array of metazoans that includes scyphozoans (true jellyfish), ctenophores (comb jellies), salps, and larvaceans. Other metazoan groups with holoplanktonic members include chaetognaths (arrow worms), pteropods (snails), and polychaete worms.

The holoplanktonic metazoan taxa that are important in freshwater ecosystems are rotifers and cladoceran and copepod crustaceans. Rotifers are small (100 to 250 μm) metazoans with a distinctive rotating mode of locomotion. They often account for more than 50 percent of the zooplankton in freshwater ecosystems, occurring in densities as high as 20,000 individuals per liter of seawater. Cladocerans, also known as "water fleas," are small, transparent crustaceans, and are often the most abundant metazoans in the zooplankton. Both calanoid and cyclopoid crustaceans are also ubiquitous components of the zooplankton in freshwater systems. Freshwater jellyfish (limnomedusae) are also found in various lakes in different localities all over the world.

Introduction of Invasive Species by Ballast Waters

An emergent problem of global concern that directly threatens the biodiversity of indigenous planktonic species in both marine and freshwater ecosystems is the introduction of invasive species and disease-causing agents via the ballast water of transoceanic ships.

In the Great Lakes region, two invasive cladoceran species have recently been discovered. *Cercopagis pengoi*, a predatory cladoceran native to the Caspian, Azov, and Aral seas, has been introduced into Lake Ontario. And *Bythotrephes cederstroemi*, the "spiny water flea," is another cladoceran species that appears to have been transported in ballast waters to

Lake Erie from the Port of St. Petersburg in Russia. The former species actively preys on smaller zooplankton and is expected to harm populations of the native cladoceran species. The latter species, *B. cederstroemi,* is planktivorous and is directly competing with the native species of *Daphnia* for food and resources. Both invasive species are expected to alter the size and composition of the indigenous plankton community.

In the marine realm, the Atlantic comb jelly (*Mnemopsis leidyi*), a species native to the western Atlantic, was accidentally introduced into the Black Sea in the late 1980s from the ballast water of a grain ship. This ctenophore both fed on meroplanktonic fish larvae and outcompeted the local fish populations for zooplankton, ultimately resulting in the crash of commercial fisheries in the Black Sea.

Of graver concern is the introduction of disease-causing agents, such as invasive species of phytoplankton that cause harmful algal blooms, into uncontaminated regions. Recently, high concentrations of pathogenic strains of *Vibrio cholera,* the causative agent of cholera, were detected in all samples of ballast waters collected from ships in the Chesapeake Bay that had arrived from foreign ports. Cholera is an acute diarrhoeal disease, epidemics of which can result in the deaths of thousands of people. The bacterium *Vibrio cholera* is an inhabitant of brackish and estuarine waters, and preferentially attaches to chitinous zooplankton, such as copepods. Plankton blooms triggered by climatic events, such as El Niño, have been suggested as the underlying cause behind some recent outbreaks of cholera.

—*Susan L. Richardson*

See also: Arthropods, Marine; Bacteria; Cnidarians; Lakes; Mollusca; Oceans; Protoctists

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Plate Tectonics

Plate tectonics is the theory that proposes that the earth's outer layer, the lithosphere, is divided into a dozen large, thick slabs, called plates, that are moving and changing in size; the interactions of these plates produce the major features on the earth's surface.

Traditionally the earth has been divided into three zones: the outer crust, the mantle, and the core at the center. Geologists now know that the earth's internal structure is somewhat more complicated than that simple three-part division indicates.. The crust and the upper part of the mantle are rigid, forming the lithosphere, the outer, brittle layer. Oceanic crust, basaltic in composition, is about 7 km thick, while continental crust can be 30 to 50 km thick and is composed for the most part of granitic rocks. The lithosphere is between 70 and 125 km thick. Below the lithosphere and extending downward to about 200 km below the surface is the asthenopshere, a hot, semimolten layer that moves, driven by heat. Hot material moves toward the surface, cools, and drops downward forming a circulation pattern called a convection current. Thus the interior of the earth is a heat machine driving all of the internal movements.

The entire mantle is 2,900 km thick, and the earth has a radius of 6,370 km. Intense geologic activity takes place at the boundaries of the plates. Plate tectonics is the unifying theory that relates many geological features that appear to be independent of one another. The theory is as important to geology as the theory of relativity is to physics, the atomic theory is to chemistry, and the theory of evolution is to biology.

Although the theory of plate tectonics had a number of forerunners, the modern concept was proposed in the early 1960s; within ten years it had been accepted by most geologists.

According to the theory, the plates move on the underlying semisoft asthenosphere, driven by convection currents generated by the heat from within the earth. The plates are pulled away from each other, slide past each other, or move toward each other. Where the plates are pulled away from each other, at a "spreading boundary," submarine mountain ranges, called midoceanic ridges, are created. They result from the upflow of hot mantle material (magma), which pushes the lithosphere upward. More or less simultaneously, as the plates pull away, tension cracks develop along the ridge crest, into which magma squeezes, sometimes solidifying there or erupting out on the seafloor forming lava flows and volcanoes. As the plates move away from the ridge they cool, shrink, and sink, causing the ocean floor to deepen away from the ridge. Plates may be entirely oceanic (basaltic), partly oceanic and continental (granitic), or entirely continental in composition.

The boundary, where two plates slide past each other, is called a transform boundary. The San Andreas fault in California is an example of this type. Numerous earthquakes occurring along its boundary are a result of plate motion.

The third type of boundary is a convergent boundary, where plates move toward each other. Where one plate has a continent on it and the other ocean crust, the plate with the continents, which is less dense, will ride over the denser oceanic plate. Here convection currents and gravity aid in pulling the plate downward in a process known as subduction. As the oceanic plate descends into the hot mantle, the downward-arched crust forms an ocean trench, while the deeper parts of the plate heat up even more because of friction. As the plate moves deeper toward the asthenosphere, melting takes place and magma is created. Magma, less dense that the overlying rocks, works its way upward, sometimes cooling below the surface but also erupting onto it forming volcanoes and lava flows.

When these rocks are exposed to the atmosphere on the surface, the earth's external heat engine, driven by solar power, comes into play. The hydrological cycle, circulation of the oceans, the various types of erosion, and the weathering of rocks, all dependent directly or indirectly on the external heat engine, work to wear down the landforms created by the earth's internal movements.

—Sidney Horenstein

See also: Geological Time Scale; Geology, Geomorphology, and Geography; Mountains; Oceans; Volcanoes

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Pleistocene Epoch

The Pleistocene Epoch ranges from 1,800,000 to 10,000 years ago and is the oldest division in the Quaternary Period. The boundary between the Pleistocene and the Holocene is defined loosely and is based on the start of the warm interval. The boundary is delineated by the melting of the continental ice sheets and the simultaneous rise of sea level and is placed closest to the midpoint in sea-level rise and ocean warming. The Pleistocene was first described by Charles Lyell in 1839 from strata in southern Italy previously lumped into the Pliocene. His basis for separating the two epochs was his recognition, in 1833, of the occurrence of modern North Sea mollusk species in the Mediterranean in the higher beds. The Pleistocene was described as a glacial epoch by Edward Forbes in 1846 without realizing that glaciation began at different latitudes at different times.

During the Pleistocene, glaciers advanced and retreated many times in the Northern Hemisphere, sea level rose and fell through a vertical range of 100 m, weathering rates and soil-forming (pedogenic) processes varied with temperature and precipitation changes, and habitats contracted and expanded, forcing species to migrate and adapt to environmental changes. It was during this time period that our own species evolved and rose to dominance. Today, we recognize that the advance and retreat of glaciers was complex and occurred as many as eighteen times, as recorded by glacial moraines, lake-bottom varve deposits, glacial ice sheets on continents, and oxygen isotope ratios in carbonates preserved in deep-water sediments.

Age of Glaciation

During the Pleistocene more than one-third of the world's land surface was covered by snow and ice. Northern Hemisphere glaciation actually began in the Pliocene and expanded in the Pleistocene. The glacial maxima and minima caused Northern Hemisphere climatic zones to shift southward by around 20 degrees latitude in North America and Europe; Asia was mostly free of ice, but it became a cold desert. Also as a result, tropical zones shrank and rain forests in Africa were fragmented into islands of forests amid savannas, and the Sahara Desert greatly expanded its boundaries.

The Pleistocene expansions of continental ice sheets in North America, Greenland, and Scandinavia caused the lowering of sea level by more than 100 m (roughly 330 ft). Vast quantities of water remained as ice and snow that was added to the glaciers. At this time, the continental shelves were exposed above sea level. Marine sediments were now exposed to weathering, erosion, and pedogenic processes. Rivers flowed across the shelves, cut downward, and produced large valleys, while soils formed between valley systems. Sediments that passed through these rivers were eventually deposited in the deep sea. The remnants of these systems today exist as submarine canyons.

Glacial Chronology

North American glacial and interglacial stages of the Pleistocene are as follows: Pre-Nebraskan, Nebraskan glacial (began 1,800,000 years ago), Aftonian interglacial (began 500,000 years ago), Kansan glacial (began 435,000 years ago), Yarmouth interglacial (began 300,000 years ago), Illinoian glacial (began 265,000 years ago), Sangamon interglacial (began 125,000 years ago), and Wisconsinian glacial (began 75,000 years ago). These stages correspond to the European stages of the Pre-Günz, Günz, Günz-Mindel, Mindel, Mindel-Riss, Riss, Riss-Würm, and Würm (Table 1). The Holocene (10,000 years ago to present) represents the postglacial age, from which we are likely to slip back into another glacial stage.

Detailed information on the chronology of the Pleistocene glaciation comes from oxygen isotope ratios in foraminifera skeletons preserved in deep-sea sediments. A fairly good record of oxygen isotope ratios for the last 160,000 years comes from glacial ice samples cored from the Greenland and Antarctic ice sheets since 1966.

Causes of Glaciation

Climate change and the cause of glaciation over at least the last 2 million years has followed a distinctive pattern termed the Astronomical Theory, developed by James Croll in 1875 and elaborated on by Milutin Milankovitch in 1924. The Milankovitch Theory states that there is a regularity and frequency of climatic fluctuations based on the: (1) eccentricity of the earth's orbit (change from circular to elliptical orbit around the sun), (2) obliquity of the ecliptic (the angle of tilt of the plane of the elliptic path), and (3) the precession of the earth's axis on which it rotates (ranging from 0 to 23.5 degrees). Together, these act as the primary driving mechanisms, also known as orbital forcing, of global climate change; in the Pleistocene and Holocene, they produced long-term periods of cooling and short, rapid periods of warming at cycles of 100,000, 43,000, 24,000, and 19,000 years. Evidence of astronomical variables and, hence, the cycles of climatic fluctuation, have been collected from coral reefs, pollen records, deep-sea cores, loess sequences, ice cores, and tropical lake records.

The cause of the onset of North Hemisphere glaciation is likely to have been related to the connection of North America to South America by Panama and the rise of the Isthmus of Panama in the latest Pliocene. The so-called oceanic conveyor belt in the North Atlantic Ocean was created by the restriction of ocean water flow into the Pacific from the Atlantic and caused the cooling and sinking of those warm surface waters, which deprived the Arctic Ocean of heat. The waters of the Atlantic are slightly more saline than the Pacific Ocean, because of the evaporative effects of the hot, dry trade winds from the Sahara Desert in Africa. Prior to the closing of the Isthmus of Panama, the Atlantic Ocean water mixed with that of the Pacific Ocean. After the closing, the slightly denser, more saline warm-water ocean currents of the Atlantic were diverted along the western mar-

Table 1

Glacial and Interglacial Stages of the Pleistocene Epoch for North America and the Alpine Region of Europe

North America	*Alpine Region*	*Years before Present*
Wisconsinian	Würm	75,000
Sangamon	Riss-Würm	125,000
Illinoian	Riss	265,000
Yarmouth	Mindel-Riss	300,000
Kansan	Mindel	435,000
Aftonian	Günz-Mindel	500,000
Nebraskan	Günz	1,800,000
Pre-Nebraskan	Pre-Günz	

Source: Levin, Harold L. 1999. *The Earth through Time*, 6th ed. Fort Worth: Saunders College Publications. (This material is used by permission of John Wiley and Sons.)

gin of the Atlantic Ocean northward toward the Arctic, where they cooled and sank before reaching the Arctic Ocean. The Arctic Ocean was effectively isolated from warm water inputs from the Atlantic Ocean currents, eventually cooling the whole Arctic region. The Northern Hemisphere was plunged into the "Ice Age" without the mediating effects of the warm water currents that originated from the equatorial region.

Extinction and Habitat Tracking during the Pleistocene

The expansion and contraction of the major ice sheets and mountain glaciers reflected the glacial (cold) and interglacial (warm) episodes that also caused habitats to contract and expand. These cooling and warming episodes forced species to migrate and adapt in response to environmental changes. For example, tropical fauna such as lions and elephants inhabited Trafalgar Square in central London; these organisms are now confined to tropical Africa.

The Pleistocene extinctions affected many large (greater than 40 kg) mammals in North America (73 percent: 33/45 genera lost); South America (80 percent: 46/58 genera lost); and Australia (94 percent: 15/16 genera lost). Europe and southern Africa suffered the fewest extinctions (5 percent: 2/44 genera lost). Two main hypotheses explain the pattern of extinction for the end-Pleistocene. The prehistoric kill hypothesis suggests that large mammals became extinct because of overhunting by humans. This is based on the coincidence of human arrivals with mass extinctions in North and South America and Australia, as well as a number of kill sites where human artifacts are associated with large mammal remains. Rapid climate changes near the end of Northern Hemisphere glaciation are also suggested as a mechanism for extinction, because of the rapid shifts from colder climate, open-grassland tundra to warmer, wetter-climate conifer-broadleaf forests during the latest Pleistocene.

Human Diaspora and Extinction

Between 300,000 and 200,000 years ago, *Homo sapiens* evolved from *H. erectus* in Africa. This is the species to which modern humans belong. *H. sapiens*, whose fossils and artifacts are found in Europe and Asia, exhibit rounder and higher-profile skulls with a more delicately structured and flattened face, a distinctive chin, and smaller teeth and jaw. Currently, two distinct species (based on DNA and nuclear gene-mapping) of *H. sapiens* are known to overlap in time and space in the late Pleistocene: Neanderthals (*H. neanderthalensis*) and Cro-Magnon (*H. sapiens*). Neanderthals lived from about 150,000 to 30,000 years ago and were stocky and slightly shorter than modern humans, with relatively large cranial capacity (1350 cubic centimeters), prominent brow ridges, projecting mouth, and receding chin. They developed the Mousterian stone culture, which is characterized by more sophisticated knives and scrapers than those of earlier stone cultures. Trace fossil evidence (for example, artifacts, injuries to the bone, and positioning of the bodies) also suggests that Neanderthals cared for injured and sick members of their group and performed burial rituals. Cro-Magnons, resembling modern Europeans with a flattened brow and projecting chin, occurred from about 34,000 to 10,000 years ago. They moved into regions inhabited by the Neanderthals and, within a short span of time, the Cro-Magnon replaced them either through competition for resources (for example, food, shelter, territory) or by tribal warfare. The Cro-Magnon culture developed into the Late Neolithic culture with specialized tools, cave artwork, decorative bone carvings, clay figurines, and jewelry.

By the end of the Pleistocene, from about

30,000 to 15,000 years ago, small groups of humans began to cross into North America via the Bering Straits land bridge between what is today Russia and Alaska (Boyd and Silk, 2000). By about 12,000 years ago, when the continental glaciers were melting rapidly, many groups of humans migrated to the south via an ice-free corridor from Alaska through the northern (Canadian) Rocky Mountains into the western United States. There is evidence in the form of jaw bones, teeth, and sculpted wood and bone, that humans made their way as far south as South America, to Peru and Chile, by 12,600 years ago. The Clovis people, named for their archaeological sites near Clovis, New Mexico, thrived from 13,000 to 11,000 years ago and produced distinctive projectile points that are often found embedded in or associated with animal remains. From 11,000 (end Pleistocene) to 9,000 (beginning Holocene) years ago, the Folsom people fashioned finely flaked and fluted, short points that were attached to shafts. These artifacts have been found at kill sites of extinct bison. By about 10,000 years ago, humans began to raise domesticated animals and turned to agriculture as climates warmed at the end of the Pleistocene.

Two important lessons about global climate change and biodiversity can be learned from geologic, paleontologic, and geochemical evidence in the Pleistocene record. First, sudden changes in climate over very short time periods, such as a warming event of several degrees centigrade in ten years, can occur without being influenced by human activities that include deforestation and the burning of fossil fuels. Second, there is evidence of a pattern of animal extinction based on human activities—mainly overhunting and, most recently, deforestation via the expansion of agriculture.

—Stephen T. Hasiotis

See also: Geology, Geomorphology, and Geography; Glaciation; Global Climate Change; Habitat Tracking; Human Evolution; Hydrological Cycle

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Pollination

Pollination involves the transfer of the male gametophyte in seed plants, or pollen, to the receptive surface of the female organs, the stigma, for fertilization of the ovule. Although many plants are capable of self-fertilization, only some weedy and ephemeral plants routinely do so. Some seed plants disperse pollen by wind, such as many conifers; the grasses, sedges, and rushes (Poaceae, Cyperaceae, and Juncaceae); and temperate species of oaks and beeches (Fagaceae), elms (Ulmaceae), birches (Betulaceae), and some willows (Salicaceae). The unparalleled success of the angiosperms, however, at least partly results from a symbiotic relationship with pollinating insects that began approximately 140 million years ago and that evolved to include some birds and bats 100 million years later.

Pollination of flowers by animals has many advantages. It allows less pollen to be wasted, and (probably most important) it allows reproduction of plants distant from each other. Growing distant from other individuals of the species, as many trees do in tropical forests, allows more efficient exploitation of resources; it avoids intraspecific competition, and helps prevent serious outbreaks of plant-feeding insects that specialize on that species. Because reproduction in most of the 220,000 species of angiosperms is entirely dependent on certain kinds of animals, gene flow is controlled by the foraging behavior of the pollinator. The diversity of this group has been attributed to sexual isolation among populations caused by pollinators, leading to the rapid formation of many species.

The main pollinating groups are certain birds, bats, and many groups of insects. Among each group there has evolved particular kinds that are highly specialized for feeding exclusively on the nectar and sometimes the pollen of flowers. These obligate pollinators almost always can hover in flight, and they have a long, extensible tongue for probing the recesses of flowers. Conversely, flowers have pollination "syndromes," or suites of features that adapt them for pollination by particular animals (Table 1). In the Western Hemisphere the main bird pollinators are the hummingbirds (Family Trochilidae) and honeycreepers (some Thraupidae). Sunbirds (Nectarinidae) are the main pollinators of Africa and Asia; honeyeaters (Meliphagidae) in Australia; and honeycreepers (Drepanidinae) in Hawaii. Bird flowers tend to be large, vivid red, with deep corollas. Among bats the main pollinators are some Pteropinae (fruit bats) of Africa and southeast Asia, though the Macroglossinae (nectar-feeding bats) are more specialized pollinators in southeast Asia and Australia. In the

Table 1
Specialized Pollinators and Characteristics of the Flowers They Visit

Pollinating Group	*Region*	*Flower Characteristics*						
		Anthesis	**Color**	**Size**	**Form**	**Scent**	**Nectar**	**Plant Growth**
Birds	Mostly tropical	Day	Vivid red	Medium to large	Tubular, zygomorphic	Minimal	Copious	Trees, vines
Bats	Tropical	Night	Subtle, pale	Large	Radial, open, brushy	Musty, fruity	Very abundant	Trees, cacti
Long-tongued flies	Tropical to xeric	Day	Blue, violet	Small	Deep tubular, radial	Minimal	Abundant	Herbs
Saprophagous flies	Tropical to temperate	Day and night	Green, light yellow	Large	Tubular vessels	Musky, putrid	None	Vines, herbs
Syrphid flies	Tropical to temperate	Day	White, yellow	Small to medium	Exposed, radial	Minimal	Moderate	Herbs
Butterflies	Tropical to temperate	Day	Blue, violet	Medium	Exposed/ tubular	Mildly sweet	Abundant	Trees, vines, herbs
Moths	Tropical to temperate	Night	White	Medium to large	Bell, to deep tubular	Fragrant	Copious	Vines, herbs
Bees	Tropical to xeric	Day	Various	Various	Various	Fragrant	None to abundant	Herbs to trees

Western Hemisphere, the Subfamily Glossophaginae in the family of leaf-nosed bats (Phyllostomidae) has specialized pollinators. Bat flowers tend to be large and fleshy, with numerous exposed, "brushy" stamens. Pollinating bats occur largely in the tropics and deserts, such as those that pollinate the large flowers of cacti. Some small monkeys and arboreal species of rats and opossums pollinate a few species of tropical trees. The proportion of angiosperms pollinated by vertebrates probably amounts to less than 1 percent of all species.

Insects, in contrast, pollinate perhaps 90 percent of all angiosperms. Flower visitors have been found in most orders, and, indeed, most species of insects have no particular adaptations for pollinating, even though they may be significant pollinators, particularly in the Coleoptera, nematocerous Diptera, and symphytan and lower apocritan Hymenoptera. For example, important generalized pollinators include some thrips (Thysanoptera) on large Asian dipterocarp trees; ceratopogonid midges on the chocolate tree, *Theobromia cacao;* as well as muscids and other kinds of calyptrate flies on umbellifers in northern latitudes. Various tiny Diptera become temporarily trapped within vessels of Dutchman's pipe vine (*Aristolochia*), *Ceropegia* milkweeds (Asclepiadaceae), and aroids (Araceae). The flowers of these plants occur deep in the vessels. Particular species of flies are lured to the vessels by musky or putrid odors and cannot escape because of slippery surfaces and false windows. When they are released by changes in the shape of the vessel, generally a day later, they are dusted with pollen. The most effective and pervasive pollinators, though, are the long-tongued flies (Bombyliidae, Acroceridae, Apioceridae, and Nemestrinidae), the flower flies (Syrphidae), Lepidoptera, the pollen or hover wasps (Vespidae: Masarinae), and, by far the most important, the bees (Apoidea). These groups alone comprise approximately 150,000 species.

There are about 20,000 species of bees, essentially all of which provision their nests with larval food made of nectar and pollen. Many forage on a particular family or even genus of plants (oligolectic), though the highly social honeybees (bumblebees, stingless bees, and especially *Apis*) visit diverse flowers (polylectic). Bees are intelligent insects, and individuals quickly learn which flowers are most rewarding, or how to force themselves into a flower, or even to steal nectar by chewing a hole in the bottom of the corolla from the outside. Although many zygomorphic flowers are pollinated only by bees, bees visit a wide range of flower types, so there is no typical "bee flower" syndrome.

Orchids (Family Orchidaceae) have the most impressive array of specialized adaptations for pollination. They are also among the most diverse families of plants (with approximately 25,000 species), and they evolved probably only within the past 40 million years. Such rapid diversification may be related to the exotic modes of reproduction. The flowers of some species mimic the shape of female wasps; males transfer pollen when they attempt to mate with the dummies. Other, South and Central American orchids secrete scents specific to one of nearly 200 species of orchid bees (Euglossinae). Male bees don't feed from the flowers, but collect scents that they use for displaying to females. Some orchids mimic the appearance and odor of mushrooms, and are pollinated by flies that normally congregate on mushrooms.

In the mid-Cretaceous, approximately 100 million years ago, angiosperms radiated explosively. There are only two fossil records from the Cretaceous of insects specialized for visiting flowers. One is a nemestrinid fly approximately 120 to 130 million years old, the other a bee, *Cretotrigona prisca*, perhaps 65 to 70 million years old. The fly fossil possesses a long proboscis and wing venation typical of a hovering fly, and it may have been the earliest specialized pollinator. *Cretotrigona* is a member of the recently evolved group of stingless bees, found throughout the world's tropics. Bees evolved from generalized sphecid wasps somewhere in the mid-Cretaceous. The fossil record otherwise indicates that pollinators of Cretaceous flowering plants were small, unspecialized flies, wasps, moths, and beetles. Insects were on the scene when angiosperms first appeared in the Cretaceous, and both quickly adapted to specialized pollination.

—*David Grimaldi*

See also: Angiosperms; Arthropods, Terrestrial

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Pollution

Pollution is the release or discharge of a substance, chemical, or heat energy into the natural environment, including the air, water, or soil, as a result of human activities. Pollution can be poisonous to living organisms and can modify and degrade habitats. It affects every ecosystem on earth and, therefore, changes the way in which the environment can provide living organisms with the habitat and conditions they need to survive. In this way, pollution threatens biodiversity.

Toxification and chemical contamination from industrial, agricultural, and residential sources can poison an ecosystem and render it unfit for life. Common chemicals, such as pesticides and herbicides, can persist in the environment and affect every level of the food web, including nontarget organisms. In particular, persistent organic pollutants (POPs), a group of chemicals including pesticides, dioxins, furans, and polychlorinated biphenols (PCBs), do not break down once they are released into the environment, instead bioaccumulating in the tissues of animals. Bioaccumulation is the process by which these fat-soluble chemicals build up in the fatty tissues of animals after they ingest them by consuming contaminated food or water. The chemicals are passed up the food chain, and the level of contamination is magnified higher up the food chain in a process called biomagnification. For example, a polar bear that eats a seal that ate contaminated fish will ingest the chemicals that accumulated in the tissues of both the seal and the fish, and it will further concentrate the chemicals in its own tissues. These chemicals can cause cancer, and, if they are ingested at high enough doses, they can kill an organism. Continual exposure at lower doses can, over time, cause the chemicals to reach lethal levels.

Chemical contamination, particularly by POPs and other organochlorine compounds, can also disrupt the endocrine system by mimicking estrogen and other hormones in the body. Moreover, they can lead to reproductive failure or dysfunction, developmental problems, decreased sperm counts, compromised immune systems, and birth defects and deformities. Some organochlorines can even cause genetic mutations. The presence of organochlorine chemicals in the food web has caused

Congested traffic in Cairo, Egypt. Emissions of nitrogen oxides and sulfur oxides from automobiles contribute to smog, which causes repiratory problems for humans and declines in plant populations. (UN photo)

population declines by altering or hindering the physiological processes involved in reproduction, development, and immune response. For example, in the 1950s and 1960s, the populations of brown pelicans, ospreys, cormorants, bald eagles, and other raptors declined in the United States as a result of DDT contamination. This pesticide was passed up the food chain and accumulated in the tissues of the birds. One of the breakdown products of DDT is DDE, which reduced the calcium content of their eggshells, decreasing their reproductive success rate and leading to a decline in populations (Miller, 1994).

Global climate change and stratospheric ozone depletion also affect biodiversity and can lead to its loss. Anthropogenic emissions of greenhouse gases such as carbon dioxide and methane, from factories, power plants, deforestation, and automobiles, increase the earth's average temperature on a global scale in a process called global warming. As the troposphere warms, climates, including temperature and precipitation patterns, will be altered and may no longer be suitable for the plants and animals inhabiting them. This loss of habitat will cause populations to decline unless organisms are able to migrate to suitable new habitats. The release of ozone-depleting substances such as chlorofluorocarbons (CFCs) contributes to the depletion of the stratospheric ozone layer, as well as to global warming. As stratospheric ozone levels decline, more ultraviolet (UV) radiation can reach the earth's surface. The increased UV radiation is harmful to plants and animals, and it has been linked to a decrease in phytoplankton populations, which form the base of marine food webs. It has also been linked to an increased incidence of cataracts and skin cancer in humans and wildlife. Some plants, such as loblolly pine, are sensitive to UV radiation; a drop of approximately 1 percent in the total yield for some food crops, including corn, rice, wheat, and soybeans, has been associated with each 3 percent drop in stratospheric ozone (ibid.).

The emission of nitrogen oxides (NO_X) and sulfur oxides (SO_X) also threatens biodiversity. NO_X emissions, primarily from automobiles, factories, and power plants, contribute to smog formation, which can cause respiratory and other health problems in humans and declines in plant populations near pollution sources. NO_X and SO_X emissions, primarily sulfur dioxide from industrial sources, combine with water vapor in the atmosphere to cause acid precipitation. Acid precipitation, including acid rain, acidifies soils and surface water (decreasing its pH). Acid rain can lower the pH of lakes and streams, making them unsuitable for aquatic species. Furthermore, acid rain has been shown to impair the growth of some vegetation.

Thermal pollution is caused by the discharge of cooling water from industrial sources and power plants into bodies of water. The cooling water absorbs heat generated during industrial processes, making the cooling water effluent warmer than the surface water that receives it. Thermal pollution raises the water temperature, thereby lowering the dissolved oxygen level in the water and reducing the amount of oxygen available for aquatic organisms. At the same time, higher water temperatures can increase the biological oxygen demand (BOD) of the aquatic ecosystem. BOD refers to the amount of oxygen required by the organisms living in the ecosystem. As water temperature increases, the bacterial metabolic rate can also increase, raising the BOD of the ecosystem. If the thermal pollution is great enough, the decreased dissolved oxygen content and the increased BOD may be sufficient to create a dead zone, a region in which no aquatic organisms can survive.

The release of effluent rich in organic wastes and nutrients can also raise the BOD, through a process caused eutrophication. The discharge from sewage treatment plants (a point source), and agricultural runoff (a nonpoint source) containing fertilizers and animal wastes, are common human sources of nutrients that can alter aquatic ecosystems. The organic wastes in the effluent provide a food source for aerobic bacteria, which demand more oxygen as they digest the organic matter. Nutrients, including phosphates (compounds containing phosphorus) and nitrates (compounds containing nitrogen), that are released by the sewage treatment plant, in the runoff, or by bacterial decomposition make possible the rapid growth of algae, phytoplankton, and aquatic plants. These algal blooms on the surface of bodies of water can prevent sunlight from reaching the plants growing below them. Because other organisms depend on those submerged plants for food, the food chain can be upset and the lake or stream can be rendered unsuitable habitat. Algal blooms can also reduce the dissolved oxygen content of water below the surface.

Waste disposal also alters and degrades the environment and impacts biodiversity. Hazardous waste, radioactive or nuclear waste, municipal and industrial solid waste, mine tailings, and household garbage all require land for disposal. Wastes disposed of in landfills produce leachate that can contaminate soils, groundwater, and surface water. Leachate forms as rainfall percolates through a landfill and leaches out toxic compounds and heavy metals from the waste. Landfills also contribute to air pollution by releasing hydrogen sulfide gas, methane, and volatile organic compounds produced by anaerobic decomposition of organic wastes. As a result, waste disposal can cause the loss of biodiversity by taking land and polluting air, water, and soils. For example, many landfills in the United States were created by filling in wetlands, displacing plant and animal life. Waste incinerators also pollute the environment by producing toxic ash and by emitting dioxins, toxins, and volatile organic compounds into the air.

Improper disposal of waste, such as littering and dumping in lakes, rivers, or the ocean also harms biodiversity. For instance, plastic six-pack rings and fishing nets in the ocean can choke or strangle marine mammals and other wildlife. In addition to solid waste disposal, marine pollution includes spills and discharges of chemicals, oil, and oily wastes. These pollutants poison aquatic life and sea birds and degrade aquatic habitats, coastal habitats, and wetlands. Moreover, many of these chemicals persist in the environment and can bioaccumulate in wildlife.

Pollution is often an unintentional by-product of beneficial industrial processes and sometimes involves substances that are not harmful in other contexts. Pollution impacts and threatens biodiversity because it can poison plants and animals, interfere with physiological processes, degrade habitats, and even alter animal behavior. Noise and light pollution do not usually harm wildlife directly, but they can cause animals to alter their ranges or to change their behavior. For example, lights can disrupt the nesting behavior of sea turtles (Meffe and Carroll, 1997). The effects of pollution are long lasting and may change in unknown ways over time. As a result, pollution will continue to affect biodiversity in known and unforeseen ways. In particular, the combination and accumulation of chemicals in the environment will continue to threaten biodiversity by contaminating environments and by inhibiting the basic physiological processes—especially reproductive success—that make all life possible.

Advances in technology have decreased pollution, but much remains to be done. In some cases pollution can be prevented by installing control technology and altering industrial processes. In other cases, switching to cleaner alternatives can eliminate the toxic by-products of industrial processes. Laws and regulations, new technology, new components, and economic incentives can increase efforts to control pollution.

Toxification and chemical contamination can be prevented by modifications to machinery and industrial equipment and processes. For example, closed-circuit manufacturing systems can limit the discharge of chlorine and other chemicals used to bleach paper. Unbleached and oxygen-bleached paper are alternatives to chlorine bleached paper that create less pollution. Alternative farming practices, such as integrated pest management, utilize natural methods instead of chemical pesticides to control insects and other pests. By using nontoxic alternatives to poisonous household chemicals, such as some cleaning products, and by decreasing the amount of chemicals and harmful products we use, we can reduce the amount of chemicals released into the environment. The Stockholm Convention on Persistent Organic Pollutants (POPs) is an international agreement that aims to prevent the use, production, and trade of POPs.

Global climate change can be mitigated by increasing energy efficiency and by controlling carbon emissions. By consuming less electricity and fossil fuel we can decrease carbon emissions. Renewable energy sources, such as solar, wind, and geothermal energy, produce electricity without the carbon emissions created by burning fossil fuels such as oil, gas, and coal. Hybrid automobiles use alternative fuel sources, such as hydrogen fuel cells, to power automobiles, along with varying amounts of gasoline or electricity. These automobiles emit less carbon dioxide than traditional automobiles. The UN Framework Convention on Climate Change and the Kyoto Protocol are international agreements that aim to reduce greenhouse gas emissions globally.

Stratospheric ozone depletion can be mitigated by controlling emissions of CFCs and other ozone-depleting substances (ODS). Alternatives to CFCs and other ODS have been developed, and using such alternatives can minimize the loss of stratospheric ozone caused by anthropogenic sources. For example, in the United States, CFCs are no longer used in spray cans. The Montreal Protocol on Ozone Depleting Substances is an international agreement to phase out ODS globally.

The emission of nitrogen oxides (NO_X) and sulfur oxides (SO_X) is controlled by installing control technology, such as scrubbers in smokestacks, that removes such pollutants from the discharge. Changing fuel sources—from those with high sulfur or nitrogen content, such as low-grade coal, to those with lower sulfur or nitrogen content, such as higher-grade coal or natural gas—also reduces NO_X and SO_X emissions. Increasing energy efficiency, using less electricity, and driving automobiles less also reduce the amount of NO_X and SO_X emissions.

Thermal pollution can be reduced by decreasing the amount of heated water discharged from power plants and other industrial sources. This decrease can be achieved by lowering the amount of electricity used, decreasing the amount of water used for cooling, and increasing energy efficiency. Allowing the heated water to cool in cooling ponds before reusing it or discharging it can also decrease thermal pollution. Heat from the cooling water can be transferred to the atmosphere by using wet or dry cooling towers (Miller, 1994).

Eutrophication can be controlled by using compost and other natural forms of fertilizer instead of artificial fertilizers. Runoff can be reduced by soil conservation and erosion control. Moreover, preserving wetlands and coastal areas can mitigate eutrophication, because they filter out and retain nutrients. Tertiary treatment at sewage treatment plants and industrial facilities is a process that removes nutrients, including phosphates, before effluent is discharged. Limiting the use of phosphates in household chemicals, such as laundry detergents, can also reduce the amount of nutrients discharged in sewage treatment plant effluent (ibid.).

Waste disposal and its effects on biodiversity can be reduced by composting, reusing and recycling products and wastes, and altering industrial processes so that they use fewer toxics and produce less waste. To minimize the amount of garbage we produce, we can purchase products with less packaging or with recyclable packaging. We can also buy products that last longer and repair broken items, instead of throwing them away and buying new ones. By decreasing the use of nuclear power, we decrease the creation of nuclear waste. Proper waste management, including the prevention of littering, ocean dumping, and other forms of improper waste disposal, is also important to minimize the pollution and other harmful effects of waste disposal. (ibid.)

To protect biodiversity, our goals should be to prevent pollution and reduce waste before it is created, rather than to clean up pollution and manage wastes after they are a problem. Once they are produced, pollution and wastes do not break down quickly; they have lasting effects on the health of the environment, wildlife, vegetation, and humans. Increasing energy efficiency, reducing consumption of harmful chemicals, reducing the quantity of garbage and other wastes, switching to nontoxic alternatives, and adopting environmentally sustainable manufacturing processes offer the greatest benefit for biodiversity and the environment.

—*Susan Park*

See also: Agriculture and Biodiversity Loss: Genetic Engineering and the Second Agricultural Revolution; Food Webs and Food Pyramids; Global Climate Change; Hole in Ozone Layer; Nitrogen Cycle; Protoctists

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Population Growth, Human

The date that the first "human" set foot on earth is more speculation than fact, but it is virtually certain that population growth throughout humankind's early history was painfully slow. Modern humans may have emerged more than 130,000 years ago in the form of *Homo sapiens sapiens*.

Life for early *Homo sapiens* was, of course, extraordinarily harsh, with humans wholly dependent on a hunter-gatherer form of existence for the large proportion of history. During much of that early period, it is doubtful that human numbers amounted to more than a few hundred thousand, given the constraints of the available food supply. Indeed, it may be considered a remarkable achievement that the human race survived at all. Our ancestors did find ways to survive, however, with the discovery of fire making possible a more varied diet and the eventual development of metals. Life was not completely migratory, and it likely featured at least temporary settlements near streams and natural shelter. But in the period from 10,000 to 8,000 B.C.E., the practice of sedentary agriculture is believed to have contributed to what might be termed the first population "explosion." Historical demographers generally place the world's population by the time of the birth of Christ at about 250 million—although it should be pointed out that there is wide variation in such estimates.

The first 1,000 years of the Common Era appear to have been a particularly difficult period for human survival, as numerous famines came and went throughout Asia and Europe. By the year 1000, the global population may have been virtually the same as it had been 1,000 years before. Even after that period, famines, plagues, mortality associated with the rise and fall of dynasties in China, and warfare continued to keep the population growth rate very low—in fact, nearly imperceptible. The Black Death in the fourteenth century may have reduced Europe's population by more than 25 percent and halved that of England. In Latin America, the arrival of Europeans is believed to have almost completely wiped out the indigenous population, from about 40 million in 1500 to less than 10 million a century later.

Most estimates suggest, however, that by about 1600 the decline in world population may have come to an end. But that is not to say that an explosion of population was imminent. In 1600 the global total may have been about 575 million;150 years later, it had grown to about 770 million, an annual rate of but 0.3 percent. Most of that growth was accounted for by Asia, whose 500 million people made up two-thirds of the world's total, almost the same as today.

The modern period (after 1500) saw modest growth in nearly all regions, with Africa and Latin America as two exceptions. The introduction of previously unknown diseases by European conquerors nearly wiped out much of the indigenous population of the Americas. From a peak of about 42 million in 1500, the population is thought to have dropped to as low as 12 million two centuries later. Although Africa did not experience such devastating losses, population growth was extraordinarily slow after 1600, much of that the result not only of the large numbers of Africans rounded up for the slave trade but also the social disruption that trade caused. Population growth in Africa did not resume until the mid–nineteenth century.

By 1800 the sum total of modern humans was approaching the 1 billion mark for the first time. For the human race's long battle simply to survive, victory was nearly in sight. Various watershed events—such as the development of sewer systems that greatly improved health in cities, the invention of washable cotton clothing, which might have reduced transmission of disease, and growing efficiency in the storage and distribution of food all made significant contributions. Later in the same century, the work of Louis Pasteur advanced the science of medicine in a few short decades—medicine's largest leap forward ever. As a result, the realization that "germs," such as bacilli and viruses, cause disease led to wholesale changes in hospital practices and to the use of immunization against such killers as anthrax, smallpox, and rabies. The importance of such discoveries cannot be overemphasized, since the unprecedented expansion of population numbers that was to come in the next century was a result of the "mortality revolution," not a rise in the birth rate.

As can be seen in the Table 1, the twentieth century was truly the "century of population growth," although growth had begun to accelerate in the nineteenth. It should also be remembered that, as the population grew, the absolute numbers of the population additions were necessarily larger. The century opened with 1.6 billion people on earth and closed with 6.1 billion.

Table 1
Number of Years to Add Each Billion to the World Population

World Population	Year	Years to Add 1 Billion
1 Billion	ca. 1800	All of previous human history
2 Billion	1930	130 years
3 Billion	1960	30 years
4 Billion	1974	14 years
5 Billion	1987	13 years
6 Billion	1999	12 years

Source: United Nations Population Division; Population Reference Bureau

The rapid increase in population growth was caused by the gradual increase in life expectancy that forever changed the span of human life, our expectations, and even economies. Consider mortality in the not-so-distant past: Abraham Lincoln's mother died when she was thirty-five and he was nine. Prior to her death, she had three children: Abraham's brother died in infancy, and his sister in her early twenties. His first love, Anne Rutledge, died at the age of nineteen. Of the four sons born to Abraham and Mary Todd Lincoln, only one survived to maturity.

This is a level of mortality that is unrecognizable today. As the twentieth century progressed, the elimination of many diseases and very sharp reductions in infant mortality changed prospects for the human lifespan to levels that would have been almost incomprehensible in 1890. In the United States, infant mortality in 1915 was such that one in ten infants died within a year of birth, and an approximately equal proportion did not survive to age five. Today, 993 out of 1,000 newborns survive to their first birthday.

As the twentieth century opened, the transformation of a world in which all population growth would shift to the developing countries of Africa, Asia, and Latin America had already begun. It would end with that transformation complete (see Table 2). Today, nearly every developed country is in population decline or on the verge of it (The United Nations definition of more and less developed countries is used here. The UN classifies the countries of Africa, Asia, Latin America, and Oceania as less developed. All other regions are more developed. Exceptions are made for Australia, Japan, and New Zealand, which are classified as more developed despite being in less developed regions.). Only the United States retains a prospect for continued robust population growth, with two-thirds of its growth attributed to fertility and one-third to immigration. But fertility decline was well underway in 1900 throughout Europe and North America. Widespread birth rate decline took place in the developed countries during the Great Depression years of the 1930s and two world wars, along with war mortality itself further reducing the pace of population growth during the century. In the 1980s what may be described as a total collapse in fertility took place in Western Europe, a collapse that quickly spread to the East because of the economic disruptions that followed the breakup of the Soviet Union and its satellites. Fertility is now so low that women in many European countries, at the birth rates of recent years, will average only about 1.1 to 1.3 children during their lifetime—unprecedentedly low levels that were not foreseen.

Throughout the twentieth century, the developed countries continued the process that became known as the demographic transition. This general pattern of demographic change theorizes that, as countries develop and become more urban, the high birth and death rates that characterized the preindustrial period will both begin a gradual decline. Fertility will fall as populations shift to towns and cities, where children become less of an economic asset. Rudimentary forms of family

Table 2
World Population, 1900, 1950, and 2000, and Projections for 2050

	1900	*1950*	*2000*	*2050 Estimate*	*% of Total World Growth 1900–1950*	*% of Total World Growth 1950–2000*	*% of Total World Growth 2000–2050*
World	1,650*	2,519	6,057	9,322	100	100	100
Developed Countries	543	814	1,191	1,181	31	11	0
Developing Countires	1,107	1,706	4,865	8,141	69	89	100

*All populations given in millions.

Sources: 1900, author's estimates. 1950, 2000, and 2050 United Nations Population Division. *2000 World Population Prospects, The 2000 Revision*. New York: United Nations.

planning, such as abstinence and withdrawal, become more widely practiced, and reduced family size follows. In many developed countries, this process was well underway in the nineteenth century. At the same time, advances in medicine and public health began to lengthen lives. The end of the demographic transition features low birth and death rates, and, if the average number of children declines to about two, population growth will eventually cease.

It is often pointed out that the demographic transition actually occurred at different times and in different ways from country to country, but the overall pattern has proven reasonably valid. That process is, of course, essentially complete in the developed countries, and, in fact, the transition had the surprise ending of extremely low fertility in much of the developed world; decline seems now to be the end of the story.

The major turning point in modern world population history came at about the middle of the twentieth century, when the mortality revolution spread to the developing countries. At that time, demographic rates in most developing countries still had the earmarks of the preindustrial condition. The level of infant mortality meant that 20 percent of newborns died in the first year of life, and a roughly equal proportion died before their fifth birthday. But medical advances that had taken centuries to emerge in the developed countries and were themselves still somewhat new spread rapidly throughout the world. The outcome was a level of mortality that dropped with unheard of speed throughout the developing world. At the time it could not be known, but the developing countries had begun their own demographic transition—but in a rather different way.

The decline in mortality from disease was so swift that fertility largely remained where it was, typically an average of six or seven children per woman. Developing country societies were still primarily agricultural, and the preference or perceived need for a large family remained. The result was a population growth rate that rose to a level that had never before been seen. The population growth rate rose to 2.5 percent per year, a rate that would double a population's size in less than thirty years.

The new population "explosion" gave rise to renewed fears of Malthusian principles. In his 1798 treatise, *An Essay on the Principle of Population*, the British clergyman and economist Robert Thomas Malthus had argued that, while population grew geometrically (that is, doubling in size during a fixed time period and increasing by twice as much in the next time period), the food supply grew by a fixed amount. The specter of starvation in the developing countries seemed quite real and, for a time, quite possibly was. Early population projections were quite pessimistic.

Several factors intervened to forestall a complete Malthusian calamity. For one, the Green Revolution greatly increased food production in many countries. But the second factor was just as important: in the 1970s, a growing number of developing countries determined that rapid population growth simply could not be sustained indefinitely if they were to make significant progress in raising overall health and living conditions. Population policies to slow population growth and provide family planning services spread rather quickly (India was the first country to adopt a population policy in 1952).

By 2000, an extraordinarily rapid fertility transition was underway in the developing world—although not in all countries. Fertility declined from about six children per woman in 1950 to slightly less than three. This is the second part of the developing countries' demographic transition. It differs, however, from that of the developed countries by its speed.

Much of the decline in both fertility and mortality has taken place in countries that remain largely agricultural and with relatively low levels of education. And it has done so in a matter of decades, not centuries.

The dramatic decline in developing country birth rates has been hailed by some observers as the end of Malthusian concern, but demographic arithmetic contradicts that point of view. The process of demographic transition is only partially complete. Given the still young age structure of developing countries, tremendous potential population growth remains. Fertility decline has barely begun in Africa and other countries, particularly in the Middle East, and it has stalled in others. Progress toward the two-child family remains very much in doubt. The projected population for 2050 given in the table above assumes that fertility decline will, in fact, be smoothly uninterrupted and be largely complete in many countries well before 2050. If that is not the case, future population may be very much larger than shown.

It is certainly true that demographic history has not been without it surprises, such as the postwar "baby boom" in the United States and the unexpected appearance of HIV/AIDS. But we can, at this stage, make at least one prediction for the population history of this new century. It will see a continued expansion of population in developing countries that may well be larger than that of the last. Whatever the outcome, we can be certain that future generations will look back on these as the "population centuries."

—*Carl Haub*

See also: Agriculture and Biodiversity Loss: Genetic Engineering and the Second Agricultural Revolution; Agriculture, Origin of; *Homo Sapiens;* Human Evolution; Population, Human, Curbs to Growth; Urbanization

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Population, Human, Curbs to Growth

As quickly as the population "explosion" of the post–World War II era became a cause celebre, developing countries began to consider ways to slow growth. It became apparent that population growth rates reached in the 1960s would cause their populations to double every twenty-five years, a situation that was without precedent in history.

The rapid increase in population growth in developing countries, as has been well documented, resulted directly from the swift spread of modern methods of public health and sanitation, preventive medicine, and health care. These methods had taken centuries to evolve in developed countries but could be exported quickly elsewhere. Death rates throughout Africa, Asia, and Latin America, particularly in the latter two regions, fell rapidly in the second half of the past century. The intentions, were, of course, good—but such efforts had an unexpected result. Declining mortality rates, particularly infant and child mortality, raised population growth rates to heights never anticipated. In fact, a major concern in the 1950s had been that repeats of past famines and epi-

A billboard in the city of Chengdu extols the one-child policy of the Chinese government, 1994 (Bohemian Nomad Picturemakers/Corbis)

demics might lead to rising death rates in developing countries.

One by one, developing countries realized that the pace of population growth had quickened remarkably. India, which had a population of about 350 million at independence in 1948, could easily have reached 1.5 billion by 2000 with its slowly rising life expectancy, had its fertility level of about six children per woman remained unchanged. Many countries came to the conclusion that something had to be done.

The most obvious direct tool to slow growth was family planning. The vast majority of couples in developing countries lived in rural areas where large numbers of children were seen not only as an economic asset but also as an emotional comfort and, often, a matter of pride. The reasons varied from region to region. In some areas, strong son preference might exert some upward pressure on family size, as couples sought at least one or two surviving sons for their support in old age. High infant and child mortality had long motivated a relatively large number of births. A woman's role in life, to bear children and tend house, made larger families attractive. Perhaps simply the lack of prospects for economic advancement under many colonial governments kept family size high.

Although there certainly were women in virtually every society who would have wanted to control their fertility, the notion of family limitation was relatively novel. Traditional practices—such as rhythm, withdrawal, abstinence, and a prolonged period of infertility resulting from breastfeeding—whether used intentionally or not, did keep the number of children a woman might bear below a possible maximum. But the use of modern methods of contraception, such as sterilization or the condom, were largely unknown.

Perhaps one of the great surprises of the twentieth century was that the use of family planning spread as widely as it did (see Table 1). It is surprising in the sense that the idea of family limitation was introduced in societies that had changed little in themselves. This is particularly true of modern methods of contraception, such as the pill, sterilization, and injection. The contraceptive pill and injection are often looked upon with suspicion and fear of side effects, while there can be considerable reluctance to seek a permanent method such as sterilization, particularly on the part of husbands.

Table 1

Percentage of Married Women Using Family Planning

	1960–1965	*1980–1981*	*Late 1990s*
Developing Countries	9	38	60
Africa	5	11	26
East Asia	13	69	82
South Asia	7	24	49
Latin America	14	43	67

Sources: Data for 1960–1965 and 1980–1981: United Nations Population Division. 1988. *Levels and Trends of Contraceptive Use as Assessed in 1988*. New York: United Nations; Data for Late 1990s: Population Reference Bureau 2002. *2002 World Population Data Sheet, Family Planning*. Washington, DC: Population Reference Bureau.

Yet contraception did catch on in a large number of countries, often for very different reasons. In some countries, such as Indonesia and Thailand, the use of family planning was popularized in a variety of innovative ways, such as meetings at which villagers discussed the health and economic value of family planning and announced publicly the method they were using. The inclusion of men in such meetings was particularly effective. Such activities were often accompanied by mass media campaigns such as the use of billboards and radio and TV messages that described the health benefits to both mother and child of a smaller family. Even popular soap operas incorporated such ideas or were specifically produced to dramatize the idea that large families result in poverty and reduced opportunities for all concerned.

In other cases, programs were less than voluntary or were outright coercive. The latter, to the extent that they truly were coercive, are contrary to the UN's principle that family planning should only provide couples the ability to decide their number of children—and the timing of those births—themselves. Some programs, such as China's, provide for penalties for violating the national policy of having one child and seeking permission for a second. Although excessively coercive measures are not part of the national family planning policies, such violations do occur. In South Asia, notably India and Nepal, sterilization "camps" that brought the procedure to the village level proved quite unpopular, particularly where pressure might have been used. Such campaigns initiated by Sanjay Gandhi in the late 1970s gave India's program a bad name, from which it has only recently recovered. Today, in Vietnam, the government policy of two children per couple, advertised widely on signs and billboards from large cities to highways to country lanes has received what truly seems to be a good reception from the people, without the use of any Draconian measures, other than some peer pressure.

Family planning's role as a limiting factor to population growth is often viewed in the light of "replacement level" fertility, which corresponds to an average family size of about two children per woman. That particular number of children is often specified, or implied, in national population policies because, at that pace of childbearing, population growth ultimately comes to an end and the total population size stabilizes. With replacement fertility, each couple simply replaces themselves, not increasing or decreasing the size of future generations. It is unlikely that a family size of fewer than two children would be a societal or government goal, since that would lead to long-term population decline. That is the very situation in which all of Europe, in fact every industrialized country except the United States, finds itself. This limit to growth, below replacement fertility, is a phenomenon that was truly unexpected.

It has long been the practice when making projections of global population size to incorporate what we might call an "end of growth" scenario as the medium projection, the one most often quoted by users. The custom has been to make the general assumption that fertility in a country will fall to the two-child family average at some point in the future and then remain at that level. The second half of that assumption has largely been for statistical convenience, in that the two-child family will result in stabilized, unchanging total population size, a population that neither grows nor declines. For nearly every industrialized country, however, that outlook has changed rather drastically.

Throughout Europe, the so-called end of growth scenario has become a discussion of how to end population *decrease*—or at least dampen its intensity. In many populous European countries, the rate of childbearing, both in formal and informal unions, is such that women would average only about 1.1 to 1.5 children each if birth rates do not rise, and they give little sign of it. Here the curbs to population growth that have emerged are sluggish economies or economies in actual recession, unemployment and lack of confidence in the economic future, longer periods of education in preparation for occupations that have become more technical, and, finally, changing "tastes," the desire to live well, travel, and have more time for oneself, rather than raise as many as two children. Here, we have something of a paradox, in that highly educated societies seem to move away from earlier, traditional family formation, and more frequently face the question not *when* to form families, but *if*. In the developing countries, higher levels of education are thought to result in smaller family size, but the notion of population decline is hardly a national goal.

Fertility reduction as a limiting factor on growth is a common element of most national policies, but it rarely occurs in a vacuum. Policies today call for a full menu of programs, both from educating larger proportions of women and keeping them in school longer, incorporating a full range of reproductive health services with family planning programs, improving child health, and involving men. This is certainly an ambitious series of tasks, but it is one that has been discussed extensively for many years, particularly since the landmark UN International Conference on Population and Development (ICPD) in 1994.

At a previous UN population conference in 1974, limiting factors to population growth were discussed under the general theme of the oft-quoted "development is the best contraceptive." This line of argument held that forcing family planning on the population would be counterproductive; it would be economic development that would motivate people themselves to seek such services. Ten years later, at the next UN population conference in Mexico City, recently available survey data showed clearly that family planning programs did find a ready clientele in developing countries and that lower birth rates were a result.

Now, more emphasis would be placed on increasing contraceptive supply and information on family planning.

At the 1994 ICPD, another shift in direction seemed to occur, when the argument was advanced that family planning was not simply a tool by which demographic targets might be achieved with women's rights taking a back seat. Although it can be argued that most programs already incorporated many aspects of what was now hailed as "reproductive health," family planning programs since 1994 have emphasized needed enhancements to improve prenatal care, delivery and postdelivery care, information on family planning methods, the prevention of sexually transmitted diseases, and child nutrition and immunization.

The 1990 UN Summit on Children emphasized a series of goals for child and maternal health that could be taken as a form of "fewer, healthier babies," although it was not itself designed to slow population growth. Still, greater emphasis on child health reinforces in the parents' minds that child survival has seen significant improvements in their country, lessening the sense that large numbers of children are necessary to ensure the survival of a few.

The general assumption made in end of growth population projections that family size will eventually decline to two children is not an unreasonable one. (Whether fertility decline stops at two children or falls well below is a question for another day.) It follows the general plan of the demographic transition that took place in the industrialized countries. Their societies became almost fully urbanized, and large families lost their appeal. It is not illogical to believe that today's developing countries will follow much the same path and, indeed, many are.

Such an assumption often implies a large number of growth-limiting circumstances that work in concert to reduce fertility in developing countries. Factors such as universal secondary education, greatly increased life expectancy, low infant mortality, and the involvement of women in decisions from the domestic arena to national government imply a fundamental transformation in society that must not only be accomplished simultaneously, but in a very short period of time. Transformations of this type took centuries in industrialized countries, and assumptions made today about the future of developing countries implicitly assume that such changes can occur in mere decades.

What has happened thus far is that fertility decline has actually occurred where societal changes have been only gradual at best. In Bangladesh, national policies to lower the birth rate saw little effect until population growth itself became a limiting factor. Rural land could no longer be subdivided among offspring, so that income was sought by migrating to cities. Here, children may be more of an economic liability than an asset, and the Bangladesh birth rate began to fall.

Finally, a factor has reappeared that had almost vanished from consideration: the appearance of epidemic disease. HIV/AIDS has emerged as one of the most tragic and unanticipated curbs to population growth in modern history. Its impact in a number of countries of Africa is such that the population of those countries is actually expected to decline in the near future—that, in countries in which women recently averaged six and seven children during their lifetimes.

The earth has undergone cataclysmic demographic changes in its recent history, and both the twentieth and twenty-first centuries will likely be remembered as the "centuries of population." The twentieth century began with 1.6 billion people and ended with 6.1. The twenty-first century is the one in which we expect that population growth may end in the developing countries, as it has elsewhere. But how that happens will be a complex interplay of factors that will vary in different countries. Finally, a demographer might at this point emphasize some of the mathematical implications. The future timing of fertility decline—how quickly or how slowly it actually takes place—will have a very large impact on the ultimate number of the earth's residents. That number could range anywhere from 6 to 20 billion, a range that carries with it huge implications for earth's future.

—*Carl Haub*

See also: Agriculture, Origin of; Human Evolution; Population Growth, Human; Urbanization

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Porpoises

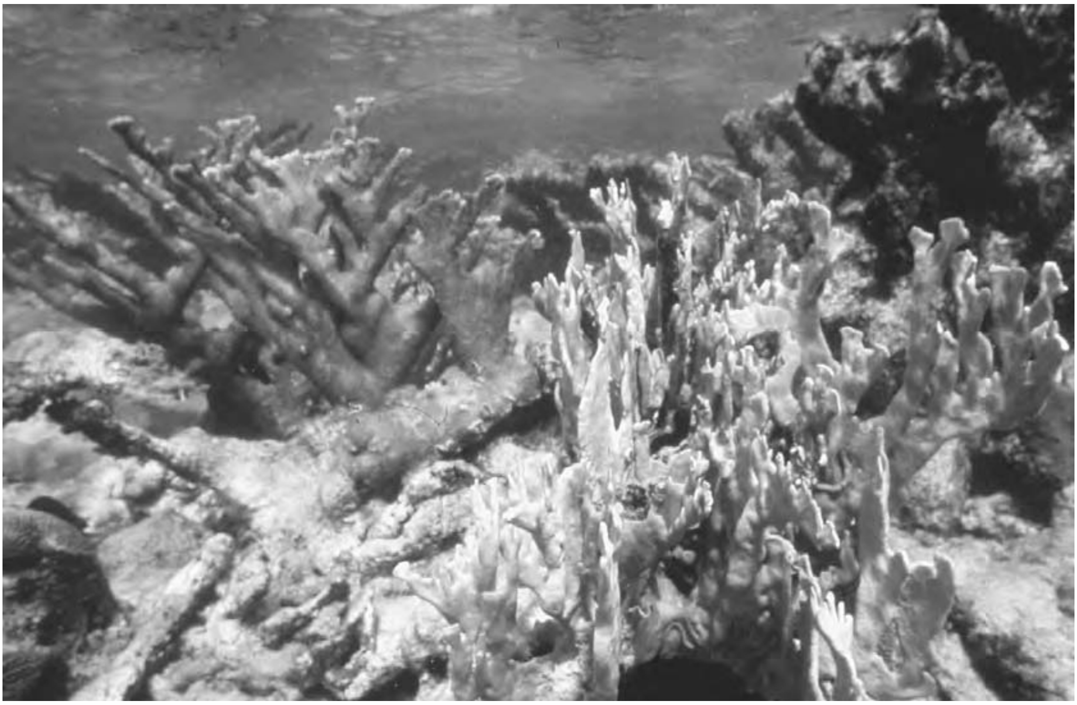
See Cetacea

Positive Interactions

Positive interactions are cooperative relationships between species that result in better growth, reproduction, and survival for at least one species involved in the interaction, without negatively affecting the other species (Morin, 1999; Stiling, 1999). Positive interactions influence biodiversity by creating alliances between species that allow them to coexist. The benefits of these associations are numerous. They include the provision of food, habitat, and more specialized services such as pollination, dispersal, predator defense, and reduction of physical stress.

There are two types of positive interactions, mutualisms and commensalisms (Morin, 1999; Stiling, 1999). Mutualisms occur when all species involved gain some benefit from the interaction. Well-known examples of mutualisms include the positive effects generated between fungi and algae that produce lichens found on rocks or trees, corals and microscopic algae that form the ocean's tropical reef systems, flowering plants and their insect pollinators, and fungi or bacteria and the roots of most plants on earth. Commensalisms occur when at least one species benefits from the interaction but the other species have a neutral response. Commensalisms include common and general relationships, such as trees providing living space or attachment sites for birds, bee hives, or orchids. In addition, animals including beavers, earthworms, and prairie dogs can physically modify or "engineer" habitats, creating more hospitable conditions or greater resources for other species.

Positive interactions vary in their strength and importance (Morin, 1999; Stiling, 1999). Some interactions are obligate mutualisms, in which species cannot survive without the assistance of their partners. These dependent situations often involve symbiosis, in which species live intimately associated with one another. Living close together facilitates energy transfer and protection. For example, microscopic animals and bacteria living in the guts of most vertebrates and termites are needed for



Coral reef in the Caribbean. Positive interactions between corals and their symbiotic algae are important for coral reef formation. (Sally Hacker)

the complete digestion of plants. Without these gut associates or symbionts, the majority of the energy and nutrients contained in plants would be inaccessible to the host species. In turn, the symbionts live in a world bathed with food and constant temperature. Corals and their single-celled algal inhabitants also provide similar benefits for one another. By harboring algae, corals garner a ready source of carbohydrates for growth. Algae receive nitrogenous wastes, an essential fertilizer needed for photosynthesis, and a protective internal environment within the host animal. Obligate positive interactions are not always symbiotic. A good example is the highly specific interaction between the figs and their fig wasp pollinators. There are more than 900 fig species on earth, each dependent on a particular fig wasp pollinator. These relationships have evolved by means of tightly coupled genetically determined traits that produce a high degree of specialization and dependence.

Many other positive interactions are facultative. They are beneficial to at least one participant, but not required for survival under all conditions (Morin, 1999; Stiling, 1999). Facultative interactions typically do not require close living arrangements, because of the lack of specificity in the relationship and the intermittent or minimal positive effects. These interactions are important under some situations—for example, when physical stress is high, resources are limiting, or during certain life stages. In this way, the interaction can be broken or resumed, depending on its usefulness. A good example is the relationship between the palo verde tree and saguaro cactus from the Sonoran Desert of North America. As seedlings, the saguaro cacti benefit from the physical and biological protection created by the palo verde tree. But over time, as the Saguaro grows and is less vulnerable to water stress and herbivory, the positive effects become neutral or negative, even though the two species live close together until they die. Another example is the seed dispersal services of fruit-eating birds, bats, and ants. Under some conditions, seed dispersal has advantages for plants, by providing new colonization sites or escape from predators. But if seeds are deposited in caves or other sites that are inhospitable, the interactions become negative.

Positive interactions can play a substantial role in promoting biodiversity by increasing species alliances and thus coexistence (Hacker and Gaines, 1997; Morin, 1999; Stiling, 1999). In the past, ecologists focused on the novelty and unique nature of positive interactions, but more recent theoretical and empirical research predicts that positive interactions are common and significant forces in nature. Their importance depends not only on their strength but also on the influence they have on other species in the community. Not all positive interactions are exclusive partnerships. Some positive interactions act in a general and flexible fashion that reaches many other, distantly interacting species. These indirect effects arise when a direct interaction is transmitted to a third species, providing food, habitat, or other services. In turn, the third species interacts with other members of the community that may receive some part of the benefit.

Saguaro cactus and palo verde tree from the Sonoran Desert. Saguaro cacti are positively influenced by palo verde trees as seedlings but not as adults. Note the growth of the palo verde tree around the saguaro cactus indicating a long association. (Sally Hacker)

A recent example from a coastal wetland community in Rhode Island illustrates how direct and indirect positive interactions can promote species diversity (Bertness, 1999; Hacker and Gaines, 1997). In this system, a number of plant species obtain membership in the community on account of the direct, positive effect of a plant species called black rush. The black rush has a turf growth form and creates a lawn that acts to decrease the harsh salt and oxygen conditions characteristic of the salt marsh. This simple service allows plants lacking similar ameliorating capabilities to flourish. The direct positive interaction has a multitude of indirect positive effects for insects that specialize on plants facilitated by the black rush. Experiments showed that without the direct and indirect effects of the black rush, a number of plant and insect species would become locally extinct, reducing species diversity by 60 percent. The black rush has a

Positive interaction between the black rush (background turflike plant) and the marsh elder (small shrub in foreground) from New England. Without the black rush, many plants and their insect predators could not survive, and species diversity would be lower. (Sally Hacker)

large effect on species diversity because of its strong but general multiple-species effect that creates a number of indirect opportunities for other species. Recognizing that complex interaction webs contain important direct and indirect positive associations allows an expanded view of the mechanisms controlling species diversity in a variety of natural systems worldwide.

—Sally Hacker

See also: Angiosperms; Annelida—The Segmented Worms; Arthropods, Terrestrial; Bacteria; Cnidarians; Coevolution; Communities; Coral Reefs; Food Webs and Food Pyramids; Fungi; Lichens; Nutrient/Energy Cycling; Pollination; Succession and Successionlike Processes

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Preservation of Habitats

The word *habitat*, in the sense of habitat preservation, often refers to two different but related concepts. Population ecologists define habitat as the places where individuals of a single population or species live. Community and ecosystem ecologists, however, extend the definition to the places where certain assemblages of species live. The latter definition is most commonly used by the public, but it is also what many scientists refer to when discussing habitat types or habitat maps.

Habitat types are frequently characterized by their primary structural features. In terrestrial areas, the dominant vegetation as well as other environmental features like elevation, rainfall, temperature, and soil type define the habitat. In freshwater and marine areas, benthic, or bottom, habitat types are defined features such as aquatic vegetation, corals, or sand flats in addition to other environmental variables such as water depth and wave exposure. Pelagic, or open water, habitats are more often defined exclusively by the physical and chemical properties of the water column.

Because of these overlapping meanings of habitat, habitat preservation may target areas needed by an individual species of concern, a particular vulnerable habitat type for a rare assemblage of species (such as undisturbed beach dunes), or some combination of habitat types to maintain the function of an ecosystem. Given the often limited funds available for habitat preservation, determining which habitats to preserve and at what scale is a complex task because there may be multiple priorities and objectives, some of which may conflict.

The efficient design of a habitat preservation plan consequently requires clear specification and prioritization of objectives as well as scientific evaluation of the different options for achieving the goals. In many cases, there are so many competing options for protecting different combinations of habitats that computer programs are required to compare the options and find the specific plan that is likely to be most effective at the lowest cost. The following sections focus on three general approaches for preserving habitats for species, communities, and ecosystems: identifying critical areas, considering the size of habitat areas, and using corridors to connect disjunct portions of habitat.

Identifying Critical Areas

In the past, national parks were often created in places like mountains and deserts with spectacular scenery and little apparent economic value. Other protected areas were designed to manage various game species rather than the habitats and ecosystem processes upon which these and other species ultimately depend. As a result, existing protected areas do not represent all habitats equally, and many habitat types have been nearly or completely lost to agricultural and urban uses. For example, in the United States, only 6 percent of land is protected, and most of these areas are found at higher elevations and on less productive soil (Scott et al. 2001). This trend is typical in many parts of the world, where the ecosystems most suitable for agriculture, such as dry tropical forests, prairies, and grasslands, are underrepresented in protected areas. According to a survey of protected habitats in tropical areas, where a total of 7.7 percent of the land was protected, lowland and montane moist and wet forests were overrepresented, and dry forests were underrepresented (Green et al. 1997). Freshwater habitats are also especially prone to destruction and degradation through channelization, damming, dredging, draining, and the introduction of invasive species. Preservation of marine systems has typically lagged behind efforts in terrestrial areas. Only a very small percentage (less than 1 percent) of marine habitats are protected.

Protected areas, generically defined by the World Conservation Union (IUCN) as “an area of land and/or sea especially dedicated to the protection and maintenance of biological diversity, and of natural and associated cultural resources, and managed through legal or other effective means,” (World Conservation Union, 1994) include a wide range of protection levels listed under many different names (such as national park, nature reserve, refuge, or sanctuary). To provide greater international consistency and comparability, IUCN created six broad categories to reflect the level of protection and management of protected areas: levels I–III provide strict protection (national parks, nature reserves, wildlife refuges); level IV involves active management to maintain a species; level V focuses on landscape or seascape conservation; and level VI focuses on sustainable use of natural resources (Green and Paine 1997).

Because existing protected areas fail to include many species, conservation efforts in the 1970s and 1980s focused heavily on greater habitat protection for threatened populations and species. These projects generally aimed to identify and protect the minimum suite of habitat areas that a population or species needed to avoid extinction, a goal shared by current Habitat Conservation Plans under the U.S. Endangered Species Act. Such conservation efforts have tended to focus on larger, more charismatic vertebrate species, such as spotted owls, gorillas, tigers, and giant pandas; many conservationists argue that by protecting the habitats of these so-called flagship or umbrella species, the habitats for many other species are protected as well. Since the 1990s, however, greater emphasis has been placed on the direct analysis and conservation of all biodiversity. These efforts have been conducted in a large number of ways, and there is no consensus on the best ways to identify and conserve biological diversity.

Several approaches to identifying critical areas for protection rely heavily on information about the distributions of relatively well-known taxonomic groups, such as flowering plants, butterflies, mammals, and birds (Olson and Dinerstein 1998; Myers et al. 2000). Hotspot analyses use computer algorithms to search for places, considered biodiversity hotspots, that contain the greatest number of species (species richness) across as many taxonomic groups as possible (Myers et al. 2000). For these studies, search algorithms can be configured in various ways, either counting total species richness, for example, or the richness of endemic species found only in limited areas.

Although such analyses have been conducted in terrestrial areas for many years, scientists recently conducted one of the first marine hot spot analyses, using centers of endemism for four groups of species (corals, snails, lobsters, and fishes) to select conservation priorities for coral reefs around the world (Roberts et al. 2002). Although supporters of hotspot approaches argue that these take maximal advantage of known biodiversity data to prioritize areas for conservation, critics frequently question whether the resulting priorities may be biased by differences in the availability and quality of data across groups. Hotspot analyses also seem to be inherently scale dependent. For example, different groups of organisms are likely to have overlapping patterns of hotspot diversity at some scales but not at other scales. Because comparable data across groups tend to be available only at relatively large scales, hotspot studies are generally constrained to much lower spatial resolutions than are useful for most conservation planning and management. As a result of this limitation, other approaches are necessary for identifying critical areas for species at smaller spatial scales. In addition, many conservationists believe that hotspot types of prioritization need to be tempered by triage considerations.

Rather than simply targeting the places with the highest levels of species richness, it may be more effective to preferentially target places: (1) with significant levels of biodiversity; (2) that are under increasing threat of losses; and (3) that possess reasonable opportunities and expectations for effective conservation. Although various hotspot, triage, and other approaches to prioritizing critical areas conceptually overlap and often complement each other to a large degree, divergent perspectives remain and seem to revolve around differences in the spatial and temporal scales of interest. Although some methods may be better suited for identifying longer-term (50-year) priorities on a continental scale, others are better suited for distinguishing options for effective local conservation (for example, small countries, states, and localities) over shorter time frames (3–20 years).

Another approach for integrating species distributions, known as Gap Analysis Program (or GAP), uses Geographical Information Systems (GIS), maps of protected areas, and computer algorithms to search for areas that contain species that are currently unprotected (Scott and Csuti 1997). Such analyses can be strictly limited to known occurrences of species, or it can be extended to expected species distributions through the use of additional data (such as land cover and climatic maps) and statistical models of species occurrences. Once the gaps in the protected status of species have been identified, additional computer algorithms can determine the most cost-effective combinations of sites that would need to be protected to adequately conserve these species. Various modifications are also possible, such as special weightings for the presence of endemic species. Because endemic species are unique to a region and may have special adaptations to their local environments, they are usually of special concern. Through weightings for endemicity, certain areas can be given special consideration for protection even if they are otherwise of low priority because of low species richness or because other resident species are already protected elsewhere.

Although GAP-type approaches were initially designed to maximize the protection of species, the basic protocol has also been directed to identify gaps in habitat protection. With the appropriate habitat maps or other data on habitat distributions, one can identify habitat types that are not adequately included within protected areas. Regardless of whether one is concerned with species or habitats, however, representation and redundancy are important criteria in the design of protected area systems. Representative systems contain either all species or all habitats in relative proportion to their abundance in nature. Redundant systems are ones in which all species are minimally represented by subpopulations in multiple areas, and all habitats are adequately replicated and dispersed, so that catastrophes are unlikely to cause complete losses of species or habitats. In practice, representation and redundancy need to be balanced so that all parts of biodiversity are present, but rare species and habitats are preferentially protected so that they are less easily lost via human accidents or natural disturbances. Although GAP-type and related reserve design approaches employ many simplifying assumptions that may not reflect the complexities of real environments, they provide systematic tools for identifying critical habitat areas for protection.

In addition to representation and redundancy, conservationists increasingly consider other landscape and ecosystem patterns and dynamics in selecting critical areas for habitat protection (Franklin 1993). Landscapes and seascapes, whether human-dominated or relatively natural, are made up of mosaics of habitat types, with populations in these environments frequently depending on some combination of these habitats in close proximity. For example, although seagrass meadows are frequently considered to be nurseries for many coral reef fishes and mangrove forests provide nurseries for invertebrates, all seagrass and mangrove areas are not of equal importance for any given species. Rather, those nursery habitats that are relatively healthy and close to other habitats used by that species are likely to be most critical for maintaining local populations. Many wetland species, such as turtles and amphibians, also require adjacent upland areas during various stages of their life cycles. Unfortunately, although much U.S. legislation regulates development of wetlands, no legislation adequately protects the adjacent upland habitats and these areas are frequently lost (Burke and Gibbons 1995). Spatial configurations of multiple habitats, in addition to full representation and redundancy, are important factors in the planning of reserve systems and other protective measures.

Most landscapes and seascapes are shaped by continual change brought about by periodic disturbance of various intensities (fires, landslides, storms, pollution, and outbreaks of disease or predators) and ecological succession. Disturbance and succession together regenerate the mix of habitat types upon which species and ecosystems depend. Given the dynamic nature of landscapes, it is often important to protect various areas not just for existing habitats, but also for the new habitats that will be created in these areas through ongoing ecological processes (Pickett et al., 1997). This is equally important for ephemeral, early successional communities, such as those that appear immediately after a fire, and climax communities that take a long time to develop. The long-term maintenance of biodiversity in protected areas is likely to depend on the ability to design systems that allow for (or mimic through active management) ecological dynamics that structure the diverse habitats in nature.

Finally, for many highly mobile species, the combination of existing and future protected areas will almost certainly not be large enough to sustain viable populations. Consequently, landscape- and seascape-level analyses need to extend beyond protected areas to identify ways in which surrounding habitats can be managed to maintain these mobile species. Such research includes reevaluation of how cities and suburbs can be planned in harmony with natural areas, how agricultural production can become more environmentally friendly and support greater biodiversity, how waterways can be better managed to sustain a broader range of aquatic habitats, and how destructive types and intensities of fishing can be reduced and ultimately eliminated. These environmental problems are socioeconomically and ecologically complex, but biodiversity conservation depends on finding ways that human activities can coexist with the mix of habitats upon which biodiversity depends.

Considering the Size of Habitat Areas

The issue of the size of protected areas is closely linked to concerns for identifying and protecting critical habitats. Not only do existing protected areas not represent the full range of habitats, but most protected areas are too small to sustain the biodiversity that they are intended to protect. According to the World Commission of Protected Areas, as of 2000, there were 30,000 protected areas in the world covering 13.25 million square kilometers, and 59 percent of these areas are smaller than 100 hectares. As a general rule, larger species, especially carnivores with high metabolic demands (for example, cougars, grizzly bears, and harpy eagles), require large areas to sustain the prey populations upon which they depend. Large areas also include and sustain greater diversity and redundancy of habitats, providing for a greater amount of biodiversity and the continuation of more natural ecosystem processes. Consequently, most conservationists conclude that large, contiguous areas of protected habitats are a critical tool for maintaining both species and ecosystem functions.

During the 1970s and 1980s, the debate over the ideal reserve size was largely based on species-area relationships and island biogeography theory. Species-area relationships are plots of the numbers of species found in discrete places (for example, islands of various sizes in an archipelago) against the estimated area of those places. Essentially, the larger the area sampled the more species will be found, although the relationship is not linear (hence species-area curves). As area increases, fewer and fewer species are added because the area gradually approaches saturation from the larger, regional pool of species. MacArthur and Wilson (1967) developed the theory of island biogeography around these and other empirical relationships. They argued that the number of species on an island represents a dynamic equilibrium between immigration and extinction of species. The rate at which species colonize an island is related to the island's distance from the nearest landmass; because the landmass serves as a source of species, the closer an island is to it, the higher the rate of immigration. Larger islands, however, support larger population sizes, and therefore have lower extinction rates. Consequently, for two islands the same distance from the nearest landmass, the larger one will have a greater number of species. Species-area relationships are important because they demonstrate that, all else being equal, any decrease in available habitat area results in a decrease in the number of species that can be supported by that area.

Based on the similarity between real islands and protected areas within human-dominated landscapes, island biogeography theory has been applied to protected areas in fragmented landscapes to estimate the number of species that protected areas or habitat patches can support. Although some researchers have also attempted to extrapolate predictions as to whether particular areas are adequate for preventing extinction of particular species or even ecosystems, the theory is based on general statistical patterns and assumes equilibrium conditions that may be ill-suited for most practical habitat management. For specific conservation applications, other theories that more directly address metapopulation, metacommunity, and landscape dynamics are likely to be more useful to decision makers.

Because funds for acquiring and managing protected areas are always limited, and many people were (and still remain) interested in devising general principles for the design of protected areas, a debate emerged in the 1980s about whether it was better to design systems made up of a few larger areas or systems of numerous smaller ones. This debate, labeled with the acronym SLOSS (Single Large Or Several Small), was derived in part from island biogeography theory but was more directly concerned with conservation issues. Researchers discussed, for example, whether for a given species, a single large population or multiple smaller populations might be more vulnerable to extinction from environmental catastrophes or disease. More recent thinking about reserves, however, de-emphasizes the pursuit of general, multipurpose designs. Rather, given all the site-specific variables and options about what to protect and what not to protect, the design of protected areas should be conducted around specific objectives. If a system is intended to protect a very rare species made up of three remaining populations, for example, a small reserve around each population may be better than a single, larger reserve around one population. If the goal is to provide the greatest possible protection to a relatively intact ecosystem, however, a single, large area may be more effective than other scenarios.

Larger habitat patches, or protected areas, tend to proportionally minimize the degradation of habitat that often occurs near their perimeters. Such edge effects, caused by dramatic changes in the ecological characteristics at certain edges (either habitat transition areas known as ecotones, or reserve boundaries), effectively decrease the size of core protected areas for sensitive species (Laurance and Bierregaard, 1997). Alteration of physical variables (for example, light levels, wind disturbance, and humidity in forests) or biological variables (such as the invasion of harmful, invasive species or predators, including human poachers) may contribute to negative impacts on populations near these edges. Because small and narrow areas have larger perimeters relative to their areas, protected areas or habitat patches with this shape will suffer disproportionately from edge effects compared to larger and rounder patches.

Another way to increase the effective size of protected areas is to create buffer zones that surround core areas and help minimize some of the human-caused edge effects. Within these buffer areas, relatively benign human activities are typically allowed, while more harmful activities are prohibited. Buffer areas are one way that management of protected and surrounding areas can be integrated to achieve larger landscape and ecosystem objectives that are not possible in the core protected areas themselves.

Using Corridors to Connect Disjunct Portions of Habitat

Habitat corridors offer another way for managing ecosystems beyond the immediate boundaries of core protected areas. In the past, most species lived in landscapes of well-connected habitats, but human activities increasingly fragment these habitats into smaller and smaller patches. The concept of wildlife corridors was developed to minimize the impact of fragmentation and enhance connectivity. Corridors are linear strips of land linking habitat patches. Ideally, they allow species to move among different areas for breeding, birthing, feeding, roosting, annual migrations, and dispersal of young animals away from their parents and to escape from predators or disturbance. Corridors may be a natural feature of a landscape, such as a riverbank, or they may be created intentionally to connect existing protected areas that are too small to sustain wide-ranging or area-sensitive species (such as cougars, grizzly bears, and tigers). Corridors can be many sizes, from a narrow hedgerow only a few meters long to wide swaths of habitat and protected areas, such as the Yellowstone to Yukon initiative, spanning 3,200 kilometers.

Simply selecting habitats that appear to be connected on a map does not ensure they are useful as corridors. Effective corridors need to consider what species will use them and what dispersal patterns those species follow. The habitat, width, length, and location, and the human activities in the area are important considerations in corridor design. Monitoring of corridors that pass under or over roadways in Banff National Park's Bow Valley has revealed that ungulates and carnivores prefer different corridor designs. Grizzly bears did not use corridors that were close to human settlements, preferring those near streams or drainage areas. Elk, in contrast, preferred corridors far from carnivores and with clear visibility and adapted quickly to the road bypasses. Corridors are also important for small and mobile species, like birds and insects. Studies of a threatened bird in the southeastern United States, the Bachman's sparrow, found that corridors allowed higher colonization rate of certain patches.

Understanding natal dispersal patterns can be helpful to corridor design. Mammals typically disperse less than the diameter of five home ranges. Based on this, Harrison (1992) suggested minimum corridor widths based on species' home range sizes, ranging from 22 km for wolves in Alaska to 0.6 km for deer in Minnesota. Seasonal migration patterns are also an important consideration in identifying corridors.

Given that there are limited funds for conservation, some have questioned the value of corridors relative to other options as a conservation strategy (Simberloff et al., 1992). One concern is that corridors may actually lead animals into unsuitable habitats or may facilitate the spread of invasive species into core habitat areas. Human activities (such as hunting, livestock, and grazing) or roads may also interfere with the effectiveness of corridors.

Unfortunately, the study of real wildlife corridors (versus model corridors) is relatively new, and the full utility of corridors remains unknown. The few studies that do exist, however, generally suggest that well-designed corridors can be effective conservation tools for some species in certain landscapes (Beier and Noss, 1998).

—Daniel Brumbaugh and Melina F. Laverty

See also: Benthos; Communities; Coral Reefs; Dams; Habitat Tracking; Nurseries; Preservation of Species

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Preservation of Species

The conservation of species involves the use of strategies and techniques that can be classified into three broad approaches: in the wild, in captivity, and in-vitro (germ cells). Knowledge of these approaches is essential to understanding how conservation management practices conserve biodiversity in real life applications.

In the wild, or in-situ, conservation is defined by the Convention for Biological Diversity (1992) as "the conservation of ecosystems and natural habitats and the maintenance and recovery of viable populations of species in their natural surroundings, and in the case of domesticated or cultivated species, in the surroundings where they have developed their distinctive properties." Essentially, this definition translates to conserving species in their natural environments so that they can exist naturally. The understanding of the biological, ecological, and social underpinnings of in-situ conservation is one of the active research areas of conservation biology.

For common or nonthreatened species, in-situ conservation management practices may require little active effort other than monitoring species' populations and maintaining them at viable levels in their natural habitats (self-sustaining populations). This adaptive style of conservation management involves managing populations with little interference unless a problem (threat) develops, or potentially can develop. Such management practices are typical of how state and federal natural resource agencies in the United States manage most game species, notably fish, birds, and mammals. For vulnerable, threatened, and endangered species, more active, interventionist, in-situ conservation strategies and techniques are required. For example, the black rhino (*Diceros bicornis*) is one of the most endangered species in the world, numbering fewer than 2,400 individuals in the wild. This rhino has declined precipitously on account of poaching for its horn for the traditional medicine market. Today, the remaining rhinos have been translocated to secure natural parks and private game reserves, where they are tracked and protected by armed wardens twenty-four hours a day.

The creation and management of multiple-use biological reserves, nature reserves, protected areas, and national parks are the cornerstone of in-situ conservation efforts. They address the loss and degradation of species' habitats. These areas are created to protect species and their habitats and, thereby, to hinder their extinction in the wild. Initially, the creation of such natural resource areas focused on protecting habitat for keystone species, such as caribou (*Rangifer tarandus*) in the Arctic tundra, or particularly charismatic vertebrate species such as elephants (*Loxodonta africana*), gorillas (*Gorilla gorilla*), and the large cats—and thereby, provide protection for the smaller, lesser-known plant and animal species coexisting in these habitats. Today, the creation of biological reserves increasingly focuses on management and protection of ecosystems and maintaining the ecological integrity of such systems. Landscape approaches are employed, and international intergovernmental cooperation is fostered to protect such reserves that cross country borders—for example, the management of the Serengeti Plains ecosystem involves national parks and reserves that are managed by Kenya and Tanzania.

Although such in-situ techniques have focused largely on terrestrial species and habitats, these concepts and methods are now being used to address the conservation of marine species and ecosystems. The Commonwealth of the Bahamas, in addition to its pioneering efforts in establishing land and sea national parks, recently initiated one of the world's first marine reserve networks. The Center of Biodiversity and Conservation at the American Museum of Natural History is supporting Bahamian marine conservation through two innovative research projects: a regional-scale initiative to study complex factors affecting marine reserve networks; and a local habitat-mapping project at Andros Island, site of the third largest barrier reef in the world. These in-situ conservation measures are attempting to understand the function of marine reserve networks through an interdisciplinary approach that involves physical, biological, and social scientists as well as representatives from the government of the Bahamas, local fishing communities, and conservation organizations.

Professional natural resource managers and conservationists recognized that in-situ conservation strategies need to involve local communities and to become more community-based. In-situ conservation practices routinely include outreach efforts to local com-

A biologist monitors eggs in a peregrine falcon's nest, Big Sur, California (Galen Rowell/Corbis)

munities to build a support base. One novel approach for heightening public awareness that is highly successful involves the designation of an endangered or endemic (native) species as a symbol of national pride. RARE Center for Tropical Conservation (based in Arlington, Virginia) pioneered this approach in its conservation efforts throughout the Caribbean region. The islands of St. Vincent, St. Lucia, and Dominica adopted national conservation strategies through the promotion of their endemic parrots as ambassadors for habitat protection and forestry reforms (Butler, 1992).

Local communities will increasingly play a vital role in conserving animal and plant species within their local environments. Because of biological, social, and financial constraints, species can not be protected only in reserves and park areas. Wildlife and plant species exist outside reserve boundaries, and these populations will need to be managed too or their genetic diversity will be lost. Many species are migratory and pass through habitats where they may come into conflict with man. Corridors and multiple-use areas are in-situ conservation methods employed to address such concerns. Where local communities at one time exploited species for hunting and harvesting, today they are involved in the management and protection of these same species. Locals are actively involved as park wardens, tourist guides, and resource biologists.

For example, the U.S.-AID funded "Campfire" (Communal Areas Management Programme for Indigenous Resources) program in Zimbabwe involves local, rural communities in the management of African big game species, such as leopard (*Panthera pardus*) and Cape Buffalo (*Syncerus caffer*), on their tribal lands. These rural communities directly profit from the hunting revenue generated, and such revenue provides support for schools and medical clinics. In return, it creates more habitat for the wildlife populations that coexist with human populations outside national park boundaries. In Argentina's grasslands, or "Chaco" region, local governments and communities are involved in an in-situ attempt to sustainably manage blue-fronted Amazon parrot (*Amazona aestiva*) and tortoise populations in their natural habitats. Under a strictly regulated harvesting program, local communities harvest a limited quota of parrots for international export as pet birds. The sales revenue from these parrots returns to the local community and funds a local, provincial university to biologically monitor this species. In addition, an incentive program exists to conserve the natural habitat for these species and to discourage the use of these natural areas for domestic species, such as cattle. Prior to the establishment of this model-harvesting program, Argentina exported more than 80,000 blue-fronted Amazons from 1985 to 1990 (CITES, 2002). This large-scale exploitation was unsustainable and threatened the species. Today, only 800 to 1,000 parrots are exported annually.

In captivity, or "ex-situ," conservation is defined by the Convention on Biological Diversity (1992) as "the conservation of biological diversity outside their natural habitats." Essentially, this definition translates to conserving species outside their natural environments, usually in zoos, aquaria, botanical gardens and arboreta, and in gene banks. Often these ex-situ conservation facilities exist outside the range countries for these species, in Europe and the United States. Already a number of animal species are extinct in the wild but survive in captivity, such as Pere David's deer (*Elaphurus davidianus*) and Przewalski's horse (*Equus caballus przewalski*).

Captive breeding or propagation plays a key role in these ex-situ conservation efforts. The purpose for this captive propagation is varied and includes scientific research, mostly for physiological, nutritional, and behavioral studies; production of individuals for in-situ reintroduction programs; maintenance of genetic diversity; and production of self-sustaining (self-maintaining) populations in captivity so that no individuals are taken from the wild. Captive animals and plants also educate the public about the need to conserve species in the wild. In many developed countries, such as the United States, large populations reside in urban areas and never see wildlife in their natural environments. Yet their awareness and appreciation of wildlife is essential to building a support (policy and financial) basis for in-situ conservation efforts and the alteration of environmentally destructive practices, such as pollution.

Ex-situ conservation programs for animals are limited by the number of species that they can address, the amount of space they have for specimens, their focus on vertebrate species, their genetic variability, and their ability to represent only a fraction of the genetic diversity found in the wild. Such programs are also limited by the ability of captive populations to undergo genetic adaptation to artificial conditions and to withstand the loss of their survival skills and knowledge of their natural environments. To achieve their long-term goals, ex-situ conservation efforts require continuity with a large, continuing investment of funds and a steady institutional support policy. Only a few private institutions and some government-managed facilities can afford to make such far-ranging commitments. The American Zoo and Aquarium Association, whose membership includes 185 accredited zoos and aquariums throughout North America, helps to ensure the survival of targeted wildlife species through its Special Survival Plan (SSP) program. They currently administer ninety SSPs covering 119 individual species. Studbooks are fundamental to the successful operation of SSPs, as each contains the vital records of a captive population of a species, including births, deaths, transfers, and lineage.

Opponents of ex-situ conservation efforts argue that such efforts are too costly, too risky, do not address the threats to the species in their natural environments, and maintain the species under artificial conditions. However, conservation biologists are recognizing that for some endangered species, ex-situ conservation can complement in-situ conservation efforts and become part of an integrated conservation strategy. If the remnant wild population is too small or inbred, or if all the remaining individuals in the wild are outside of protected areas, in-situ conservation efforts by themselves may not be enough to avoid extinction. If part of a holistic conservation approach, captive breeding and propagation can play a role in helping these species to survive, but they should not be viewed as an overall cure for the threats to biodiversity.

Examples can best help illustrate this point: The California condor (*Gymnogyps californianus*) was rescued from extinction by an intense captive breeding program by the San Diego Zoological Society and the Los Angeles Zoo (Synder and Snyder, 2000). However, this captive effort was integrated into the U.S. Fish and Wildlife Service's overall recovery plan for the species. Key recovery plan actions addressed: the purchase of critical habitat for the species, the Bitter Creek National Wildlife Refuge; the removal of lead shot in the condor's habitat and supplemental, "lead-free" carcass feeding; reintroduction of captive, bred condors into the wild, initiated with the release of the first generation of captive-raised condors; and establishment of a second population in the wild and outside of California to protect it against the occurrence of a natural disaster—a population has been established in the Grand Canyon National Park, a former natural habitat. In Puerto Rico, the highly endangered Puerto Rican parrot (*Amazona vittata*), of which fewer than one hundred specimens exist in the wild, survives in its rain forest habitat through intensive in-situ management efforts that include the fostering into active nests in the wild of parrot chicks produced ex-situ, thereby increasing natural reproduction.

Similar reintroduction programs exist for endangered mammals and reptiles—the red wolf (*Canis rufus*), the Arabian oryx (*Oryx leucoryx*), Przewalski's horse, the Cuban crocodile (*Crocodylus rhombifer*), the Jamaican inagua (*Cyclura colleli*), and the endemic plowshare tortoise (*Geochelone yniphora*) of Madagascar. In South Africa, captive-bred cheetahs (*Acinonyx jubatis*) are being released into natural populations to increase the genetic diversity of the wild populations. A key component to the success of the above ex-situ conservation efforts is that they have actively involved government natural resource agencies that are legally responsible for the conservation of these endangered species. It is far more difficult and complex to foster such efforts when all the remaining individuals held in captivity are in private collections. An example is the critically endangered Spix's macaw (*Cyanopsitta spixii*). Despite suitable habitat in the wild, this Brazilian endemic parrot is extinct in the wild; the only successful captive breeding has occurred outside of Brazil in private collections, thus hindering reintroduction efforts. The International Union for the Conservation of Nature's Captive Breeding Specialist Group provides expertise for assessing the contribution that ex-situ captive breeding programs can provide and their inclusion in conservation efforts for a species.

In-vitro conservation is a special case of ex-situ conservation and involves the use of a species' cells and tissues, along with biotechnological techniques in a laboratory environment, to assist species conservation. It can involve maintenance of germ (that is, eggs and sperm) and somatic (body) cells in a sterile, pathogen-free environment under artificial conditions. In-vitro techniques are most commonly used in the conservation of plants, and they are widely used for vegetatively propagated and recalcitrant-seeded species (species whose seeds can not be dried or frozen without lost of viability). This method provides an alternative to field gene banks and is a useful solution for recalcitrant, sterile, or clonally propagated plant species. The future for long-term in-vitro conservation efforts lies in the storage of frozen tissue cultures at very low temperatures—for example, in liquid nitrogen-cryopreservation.

With the cloning of domestic species, such as Dolly the sheep, the use of in-vitro conservation techniques for wildlife species has recently attracted much research. Borrowing techniques from human fertility clinics and livestock breeding, reproductive technologies are playing an increasingly greater role in species conservation. These techniques include: artificial insemination for species that are difficult to breed in captivity, such as giant pandas (*Ailuropoda melanoleuca*); interspecies embryo transfers, such as producing the endangered mountain bongo antelope (*Tragelaphus eurycerus*) from embryo transfers to the more common eland (*Taurotragus elands*); and test-tube fertilization.

One of the newest in-vitro techniques that has become available is interspecies (or "cross-species") nuclear transfer (Lanza et al., 2000). This cloning technique involves growing two kinds of cells in culture dishes: cells from the animal being cloned (somatic cells, such as skin tissue can be used) and recipient eggs from the species to which the surrogate mother belongs. Next, the nucleus of the egg is sucked out with a needle, and the whole cell from the future clone is injected into the enucleated (that is, emptied) egg. The egg is then given an electric shock to fuse the contents of the clone's cell with the cytoplasm of the egg. Through chemical stimulation, the fertilization event occurs and the egg divides to form new cells. This mass of cells is implanted in the uterus of the surrogate mother. In January 2001, a healthy baby gaur, Noah, was born to a cow named Bessie. Gaurs (*Bos gaurus*) are a threatened oxlike species that range from India to southeast Asia. The clone, Noah, was the first clone of a threatened species, and the first animal created from interspecies nuclear transfer. Frozen skin tissue from a deceased male gaur at the San Diego Zoo that had never reproduced in captivity, provided the cells for cloning.

Cloning faces the same opposing arguments that conventional ex-situ, captive breeding programs encounter: it is extremely expensive; it requires laborious efforts to produce a few successes; reintroduction with cloned animals will be no more successful than conventional ex-situ reintroduction programs; and it fails to address the conservation problems that endangered species face in the wild. Yet it does show the promise of increasing genetic diversity in captive populations, and if such efforts can be integrated with in-situ conservation efforts, they may help in the short term. They represent just another tool in the toolbox of conservation approaches. Cloning or the ability to resuscitate endangered populations from clones is not a justification for allowing further development or habitat loss. Ultimately, in-situ conservation efforts will always be more successful in the conservation and management of all species. However, ex-situ conservation approaches can provide some short-term relief for endangered species until in-situ conservation measures can be implemented and sustained. The recovery of the California condor attests to the success of such approaches.

—Rosemarie Gnam

See also: Conservation Biology; Endangered Species; Organizations in Biodiversity, The Role of; Preservation of Habitats; Sustainable Development; Systematics

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Primates

Primates are an order of mammals that includes humans, apes, monkeys, and prosimians (see Figure 1). Prosimians are sometimes referred to as lower primates, where the rest of the order is referred to as higher primates. In general, primates have a large range of variability in body size. The smallest primate is the pygmy mouse lemur from Madagascar. It is only 20 cm (8 in) from its nose to its tail and weighs only 30 gm (1 oz). This species is dwarfed by the largest primate—the lowland gorilla of Africa, which weighs in at about 180 kg (400 lb). The physical characteristics of primates reflect several evolutionary trends. Perhaps the most important of these is the adaptation of the hands and feet for grasping. The characteristics associated with this trend include highly mobile digits with opposable thumbs and flat fingernails instead of claws on the hands and feet. In addition, primates have very sensitive pads on the undersides of their fingers and toes that facilitate gripping.

Another important trend is the progressive increase in the relative and absolute size of the brain. The visual cortex and cerebral cortex have increased in size and complexity, while the olfactory centers of the brain have decreased in size. This is associated with increased dependence on sight and a decreased importance of smell. A trend toward a gradual foreshortening of the muzzle reflects the decline in the importance of smell and increased importance of vision. Forward projecting eyes provide primates with depth perception, so important to living and moving around in trees. Primates also have eye sockets encircled or enclosed in bone, to protect these very important organs. Finally, all primates show a tendency for erectness, or upright posture during feeding, locomotion, or rest. The more centrally placed foramen magnum in the base of the skull (where the spinal cord attaches to the head) reflects this tendency.

Most primates are omnivorous, with diets that include plants, insects, and occasionally small mammals. Most primates are diurnal

Figure 1

Primate Taxonomy

- Order Primates
  - Semiorder Euprimates
    - Suborder Strepsirhini
      - Infraorder Lemuriformes
        - Superfamily Lemuroidea
          - Family Lemuridae
            - Subfamily Lemurinae
            - Subfamily Hapalemurinae
        - Superfamily Indroidea
          - Family Indridae
          - Family Lepilemuridae
            - Subfamily Lepilemurinae
          - Family Daubentoniidae
        - Superfamily Lorisoidea
          - Family Lorisidae
          - Family Galagidae
          - Family Cheirogaleidae
          - Family Pseudopottidae
    - Suborder Haplorhini
      - Hyporder Tarsiiformes
        - Superfamily Tarsioidea
          - Family Tarsiidae
      - Hyporder Anthropoidea
        - Infraorder Platyrrhini
          - Superfamily Ateloidea
            - Family Atelidae
              - Subfamily Atelinae
                - Tribe Atelini
                - Tribe Alouattini
              - Subfamily Pitheciinae
                - Tribe Pitheciini
                - Tribe Homunculini
            - Family Cebidae
              - Subfamily Cebinae
              - Subfamily Callitrichinae
                - Tribe Callimiconini
                - Tribe Callitrichini
        - Infraorder Catarrhini
          - Parvorder Eucatarrhini
            - Superfamily Cercopithecoidea
              - Family Cercopithecidae
                - Subfamily Cercopithecinae
                  - Tribe Ceropithecini
                    - Subtribe Cercopithecinia
                    - Subtribe Allenopithecina
                  - Tribe Papionini
                    - Subtribe Papionina
                    - Subtribe Macacina
                - Subfamily Colobinae
                  - Subtribe Colobina
                  - Subtribe Presbytina
            - Superfamily Hominoidea
              - Family Hylobatidae
              - Family Hominidae
                - Subfamily Homininae
                  - Tribe Hominini
                  - Tribe Gorillini
                  - Tribe Panini

(active during the day), although many (especially the smaller species) are active during the night (nocturnal). Primates are typically sociable and often live in complex social groups. Exceptions include smaller primates, especially nocturnal ones, which tend to be solitary. Baboons live in the largest groups, sometimes consisting of more than one hundred members. Relative to other mammals, primates have a tendency for prolonged periods of infant dependency and a long period of socialization. This is related to their complex social behavior, which must be learned over the animal's lifetime.

Primate ancestors were tree dwellers, and, with the sole exception of humans, all primates spend some time in trees. Consequently, all primates retain characteristics that are adapted to tree living, even though some have since adapted to living primarily on the ground. Almost all primates are quadrupedal (that is, they walk on four legs) to some extent, but the different species exhibit a wide range of locomotion. Some are uniquely adapted to brachiating (swinging) under tree limbs (for example, gibbons), and others (for example, sifakas) have unique adaptations for clinging and leaping from tree trunk to tree trunk.

Female and baby orang-utan in Borneo (W. Perry Conway/Corbis)

Primates inhabit a wide range of habitats, from dry desert savannas to lush tropical forests. Geographically, primates are primarily restricted to tropical areas of the world, including Central and South America, Africa, India, and southeast Asia. Two exceptions are the Barbary macaque, which can be found in northern Africa and on the Rock of Gibraltar, and the Japanese macaque, which can be found on both of the main islands of Japan.

—Ken Mowbray and Shara Bailey

See also: Great Apes; *Homo Sapiens;* Human Evolution; Monkeys

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Protoctists

In the genetic-, evolutionary-, and morphology-based five-kingdoms-of-life taxonomy, protoctists are defined as nonbacterial organisms that are neither plant, animal, nor fungal; ranging from unicellular to colonial, and from microscopic to macroscopic, protoctists are in evolutionary history the first organisms with cells that have nuclei and chromosomes. To this group belong all the beings once called protozoans—a term that must be scrapped because, literally, it means "first animals" or "pre-animals." But the protoctists are as likely to be "pre-plants"—that is, to have photosynthetic inclusions in their cells yet not display the advanced tissue organization or development from an embryo characteristic of true plants. A typical example of a protoctist that illustrates the necessity of organizing this miscellany of eukaryotic organisms into their own kingdom—and the inadequacy of the obsolescent term *protozoa*—is the microbe *Euglena*. Like an amoeba or sperm cell, *Euglena* is capable of locomoting itself through the aqueous medium, and thus it has "animal-like" characteristics. Yet, like a plant or algal cell, *Euglena* has green plastid—chloroplasts—in its cell. Neither plant, animal, nor "pre-animal," it is a protist. The term *protoctist,* from Greek words meaning, roughly, "first established being," was coined by John Hogg in 1860.

Unicellular members of the protoctist kingdom are known as protists. Although the name is ungainly and obscure, protoctists are of fundamental importance to biology, ecology, medicine, and, perhaps most intriguingly, an evolutionary understanding of who we are. In terms of biodiversity, they include many important globally distributed groups, such as amoebae; green, red, and brown algae; ciliates; diatoms; dinomastigotes (more often, if less correctly, known as dinoflagellates); flagellates (which should more logically be called mastigotes); foraminifera; kelp; radiolaria; and slime molds. Evolutionarily, the protoctists were central players in two crucial transitions: the symbiotic genesis, some 2 billion years ago, of gene-trading bacteria into cells with nuclei; and the aggregation of these new cells with nuclei and chromosomes into the colonial ancestors to plants, animals, and fungi. (Although some still consider the green algae to be primitive plants, they are probably best considered protoctists, since they do not, like all other plants, develop from an embryo that itself comes from a fertilized egg.) Their study holds the keys not only to these major evolutionary transitions, but also to that major theme of our lives as individual animals—sex and reproduction. For it was in the protoctists, these free-living cells some of which look like bodiless eggs and sperm, that the origins of our kind of sex, meiotic sex, first evolved. Thus, although less important to medicine and genetic research than the bacteria, and less important to behavioral research and food production than animals, plants, and fungi, this previously overlooked and highly diverse kingdom is of great importance to understanding the evolution of eukaryotic cells, the origins of meiotic sex, present and past ecology, and the evolution from unicellular beings of multicellular plants, animals, and fungi.

History of Taxonomic Status of Protoctists

The term *protoctista,* coined by British biologist John Hogg in 1860, was used by him to refer to "organisms that are clearly neither animals nor plants." The great German champion of Charles Darwin's evolutionary ideas, Ernst Haeckel (1834–1914), had already proposed a new kingdom—Monera ("first beings")—to accommodate the taxonomically equivocate microbes whose existence, revealed by the microscope, had now, with the increasing acceptance of Darwin's theories after 1859, to be grappled with in evolutionary terms. If microbes were our ancestors, and those of plants and animals, they could no longer be considered a drawing room curiosity, or only as pathogens.

Thus in 1956 biologist H. F. Copeland of the Sacramento City College in California proposed a four-kingdom refinement of Haeckel's Monera, clearly distinguishing (as Haeckel had not) between the nonnucleated prokaryotes (bacteria), and cells with nuclei (eukaryotes). Little attention was paid to Copeland's system, and the entrenched two-kingdom, plant-animal system held on. But with advances in microscopy and molecular biology in the 1960s and 1970s, the plant-animal dichotomy became increasingly untenable. Cornell University biologist R. H. Whittaker, whose studies showed how distinct bacteria and fungi are from plants, proposed a five-kingdom system, using the term *protists*. Copeland had used *protoctists,* but only to refer to single-celled organisms (leading to continuing the confusion surrounding the term *protozoan*), and this term was resuscitated by biologists Lynn Margulis and Karlene Schwartz in their further refinement of Whittaker's system.

Diversity of Protoctists

Today an estimated 200,000 species of protoctists exist, grouped into from seventeen to forty-five phyla, depending on who is doing the classifying. They are still actively being discovered. The smaller members of the great group are the protists. Protoctists range in size from tiny micromonads and chlorella algae, cells about a micrometer in diameter, to giant brown kelps meters across, at the shores of the ocean; most, however, range from 5 to 100 μm in size. Some, such as the giant amoeba *Pelomyxa palustris,* which survives on reduced oxygen levels in muddy, freshwater ponds, have nuclei but no mitochondria in its cells: it thus is a potential "missing link" between early cells with nuclei and modern ones, almost all of which have mitochondria outside the nucleus involved in oxygen metabolism and energy acquisition in an oxidizing atmosphere. Despite the existence of *Pelomyxa* and other unusual protoctists, the metabolic diversity in this group is almost identical to that of plants, animals, and fungi—most protoctists are oxygen-breathing forms with mitochondria and, sometimes, plastids (called chloroplasts if green) in their cells. Their diversity thus tends to be morphological and behavioral, rather than biochemical or metabolic, as in the bacteria.

One area of diversity in this group that is of note is their genetic diversity. Unlike the plants and animals that arise from sexual merging of eggs and sperm, parts of protoctists can be grafted and then breed true. That is the case, for example, with protoctists with many waving appendages known as undulipodia (sometimes called, incorrectly, flagellates; the waving structures are fundamentally different from the flagella of bacteria). The protoctists known as ciliates have distinct patterns of cilia (undulipodia) which, if removed and replaced in a different location of the cell, will continue to be found at that place when the cell reproduces. Such genetics is the equivalent to a finger's being surgically grafted onto the leg of a man, whose children then appear with fingers on their legs. This genetic lability of ciliates was one of the first indications that protoctists have genetic apparatus outside the nucleus. That discovery in turn led to the finding that all protoctists, the smaller ones of which were the first protists (equivalent to the first eukaryotes), are multiple-genome beings. Protists began from merged genetic systems of from two to four or more types of bacteria. Exploration of the genetic, morphological, and behavioral diversity of protoctists continues to play an important role in investigations of the evolution of mitosis, meiotic sex, and the establishment of mitochondria.

Amoebae

We have already mentioned the giant amoeba. It looks like a wine flask and is the largest member of the Class Arcamoebae in Phylum Archaeprotist (which includes all primitive mitochondrialess protists). Other amoebae, members of the Phylum Rhizopoda, are food-engulfing protists with retractable "limbs" called pseudopods ("false feet") that extend in a wobbly mass as the cell changes shape. There are many species of amoebae; most have chromosomes and undergo mitosis. These protoctists, whose nuclei can be removed and replaced, are used in experimental studies of the relationship between cell nuclei and cytoplasm, the area around the cell. Some amoebae are enveloped in tiny calcified shells, called tests. Some tests are made from sand and the shells of other organisms, held together by organic glue. Amoebae not only display the basic cell type of animals but also contain proteins, such as actin (used in animals as muscle tissue), found in "higher" organisms. With fossils from a billion years ago, this multifarious group is also known to form resistant structures, called cysts, able to withstand drying, digestion by animals, and other environmental insults.

Golden, Green, Red, Yellow-Green, Brown, and Eyespot Algae

Some words that may seem taxonomic—for example, *plankton*—are in fact ecological words; *plankton* refers to free-floating microscopic organisms, usually algae, whose transport is subject to wave movements. Technically, algae are defined as photoautotrophic protoctists—protoctists that make their own food photosynthetically. They all produce oxygen from photosynthesis, but the appellation does not include plants, which form from embryos. Nor does the group contain oxygen-producing bacteria such as cyanobacteria and chloroxybacteria. These latter beings are, nonetheless, still often called algae (especially cyanobacteria, which have historically been called "blue green algae"), in a looser way designating oxygen-producing photosynthesizers. There are more than 300 species of golden algae, whose photosynthetic cell parts, or plastids, are golden yellow in color and called chrysoplasts. Some scavenge silicon from the water and use it to make elaborate skeletons. Green algae, put by Copeland in the plant kingdom, are really protoctists, photosynthetic cells with nuclei that are neither plants nor cyanobacteria.

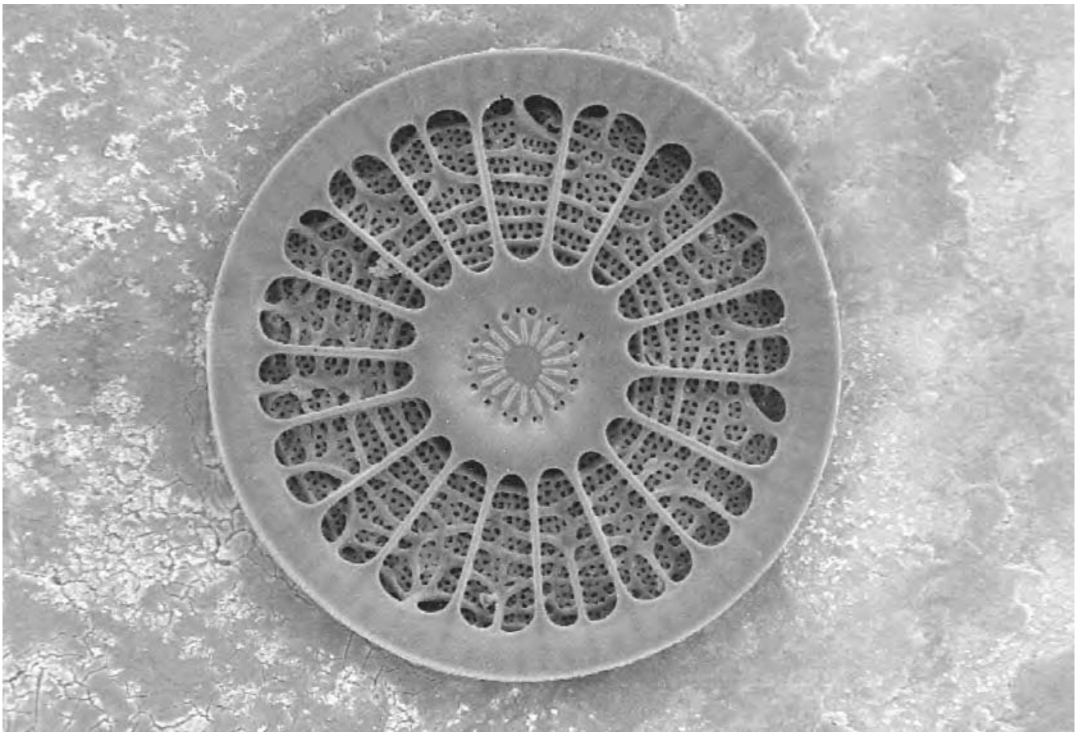
There are thousands of species of green algae. Like plants, they contain chlorophylls a and b. There are two major groups: the chlorophytes, which form (like some plants) swimming, spermlike cells with undulipodia tails, and the gamophytes, which lack undulipodia. Green seaweed is a kind of green algae, and some closely allied species, such as those of *Volvox* and its relatives, show many variations on multicellularity—giving us a window into how it may have evolved. Brown algae contain the brown pigment fucoxanthin as well as chlorophyll a. About 4,000 species of red algae or rhodophytes are known. They contain the red pigment phycoerythrin, which allows them to grow 180 meters beneath the ocean surface, where they capture longer wavelengths of the sun's radiation. They are used in the production of agar and some foods. The yellow-green algae have a characteristic plastid called a xanthoplast, which links them to the Eustigmatophyta, eyespot algae whose plastids appear to play a role in photolocation, "seeing."

Ciliates

Although not always visible on adult cells, ciliates are named for the hairlike undulipodia that protrude from their cells, called cilia, arranged into characteristic structures called kinetids. Most are unicellular, with complex cell structures, although some species, such as *Sorogena,* are multicellular and grow stalks that release "spores" that germinate into swimming cells. More than 8,000 species are known. The complex cell structure revealed by the electron microscope allows scientists to divide these organisms into three basic groups. The postciliodesmata have cell tail structures known as postciliary fibers. The rhapdophorans lack these fibers. The third group, the cyrtophorans, reconstruct the pattern of their ciliated cell surface prior to reproduction. Some ciliates "hunt" by extending cords with poisons at the end; the body part resembles a fishing line with lure, and it is even reeled in. Sex in ciliates, which do not require sex to reproduce, involves the making of a subsidiary nucleus and exchanging it with a neighboring cell. These activities evince the protoctistan penchant for variations on the theme of sex in nucleated cells that has become more or less fixed in sexually reproducing plant and animal lineages. In the relatively familiar organism *Paramecium,* a ciliate, the extra nucleus will fuse with itself in a process known as autogamy if no partner is available. Most ciliates are incapable of photosynthesis, although *Paramecium bursaria,* which contains within it the green alga (see above) *Chlorella,* thrives in sunlight. (If the *Paramecium bursaria* is restricted by darkness, however, it digests its inner gardens before it dies.)

Diatoms

Ubiquitous in the world's oceans, and traditionally classified as plants within the algal division Bacillariophyta, diatoms are better classified as photosynthetic protoctists. Single-celled or colonial, they are often of spectacular symmetry and beauty. Cell walls ("frustules" or "valves") are hardened by silica. Diatoms are important players in global ecology, and also were in the past; indeed, mineral beds up to 1,000 feet in depth, called diatomaceous earth, are composed of their fossil remains. Diatomaceous earth is used in paints, varnishes, and toothpastes, and as an insulator superior to asbestos. The varied exoskeletons of diatoms range in shape from flowerlike to crown-shaped. The centric ones, disk-shaped, look like flowers or pillboxes, whereas the pennate ones like *Navicula* resemble boats. Made from silica, which they take from solution in the water, diatoms are so good at constructing their miniature hard parts that they can grow even in water where human instruments fail to detect measurable amounts of silica. The frustules are composed of two valves. Pennate diatoms have a split, or raphe,



Microscopic view of a diatom (Jim Zuckerman/Corbis)

between their valves, along which they move. Diatom valves split after reproduction; each one goes to an offspring cell. In many, each offspring then grows a smaller valve to fit the original one. After shrinking a third in successive cell divisions, the diatoms then recapture their original size by flinging off their valves to nakedly conjugate in a mating act that reestablishes their larger size. Usually tan or brown, diatoms used to be classified with the golden algae.

Mastigotes (Flagellates)

The microbial world is still very new to science. In this world are no true plants or animals but only bacteria and thousands of species of protoctists still being classified and investigated. *Protoctists* is a new and relatively unusual word. But the older words are more reflective of familiarity than conciseness of meaning. Nowhere is this more true than in the eclectic group of organisms that are neither photosynthetic nor ciliates, but instead have undulipodia. Undulipodia are whiplike structures (cilia and human sperm tails are examples) composed on the inside of tiny tubes, called microtubules, in specific formations, usually nine pairs arranged in a circle and often surrounding a central pair. The mastigotes, often called flagellates, possess these undulipodia. Early scientists conflated them with the completely different tail-like structure of bacteria, flagella. The mastigotes are rapid swimmers, and they would be considered algae if they were photosynthetic. Instead, they are often called zooflagellates. But true flagella are rotating rods composed of flagellin proteins and found only in bacteria. The small undulipodiated swimming cells are not “zoo”—that is, not animals. In this group of mastigotes, then, can be found amoebomastigotes, diplomonads, retortomonads, kinetoplastids, bicoecids, opalinids, choanomastigotes, pyrsonymphids, and parabasalids. Fine examination with the electron microscope is necessary to distinguish among these groups. Choanomastigote (choanoflagellate) cells look like individual cells from a sponge, one of the simplest sorts of animal. Kinetoplastids, another sort of mastigote, are named for their kinetoplast, a special large mitochondrion. These beings have been well studied, because they are involved in frightening tropical diseases such as leishmaniasis, sleeping sickness, and Chagas’s disease. Other sorts of mastigotes are harbored within the complex microbial communities that break down wood into sugars and other food in the hindguts of wood-eating termites.

Dinomastigotes (Dinoflagellates)

Dinomastigotes have two cell tails, undulipodia: the first is inserted into a characteristic groove of their shell, which is made of cellulose (sometimes hardened with silica); the other circles the equator of the cell. Their name comes from their habit of slowly turning: *dino* means “whirl” in Greek. Fond of warm, marine waters, they provide food for whales and many other organisms. Some are bioluminescent, lighting up according to internal biological clocks, and also when disturbed. Some have evolved light-sensitive membranes, some even with miniature lenses that rove about the surface of the cell—tiny eyes.

Foraminifera

These giant marine unicells, familiarly called forams, may grow to several centimeters in diameter; they feed on algae and ciliates, even nematodes and the larvae of crustaceans. They are usually sand-dwelling, and many contain dinomastigotes, red algae, or other photosynthesizers, so that they behave as “marine plants,” which they definitely are not. Forams are a main part of the diet of many invertebrate animals. Their complex shells, building up on the ocean floor, are used to date other fossils and as markers for geologists searching for petroleum reserves. Regular fossil forms, 10 cm in width, show up as nummulites, or “coin stones,” in many places, including the limestones used to build the Egyptian pyramids.

Radiolaria

Their spiny silicate shells radiating like solid stars, radiolarians may possess up to several hundred spikes, technically known as axopods, shooting out from their bodies in all directions. The axopods, the identifying characteristic of this group, are used variously to row, to catch small protists, and to locomote like tumbleweeds. Axopods attached to prey are used like high-tech straws to suck the nutritional contents of trapped protists and even small animals into the cytoplasm. The axopod spines allow some radiolarian species to float on the ocean’s surface to look for food. They also increase the ability to accumulate nitrogen and phosphorus in the nutrient-poor open ocean, by increasing surface area. Radiolarian spines or spicules may be made from strontium sulfate or silica. Two main types of radiolarians exist, the polycystines and the phaeodarians. Polycystines have multiple sets of chromosomes; most plants and animals have two in their cells. Their skeletons are composed of hydrated amorphous silica, the substance of opal. The opaline skeletons begin as minute silica deposits linked with the internal cell membranes. Skeletons of phaeodarians, not directly evolutionarily related, are less well known but contain silica as well as other materials. Freshwater radiolaria are known as heliozoans and can be found stuck to rocks at the bottom of streams and ponds.

Slime Nets and Molds

Slime nets, usually marine microbes, move on a special net made from the secretion of their own slime, the so-called net plasmodium, which itself moves. Slime net microbes that grow to abundance on marine grasses, which support clam and oyster beds, can be associated with shellfish destruction. Cellular slime molds are interesting because they combine individual life with colonial, organismlike structures each generation. They never grow undulipodia. Amoebae break loose from a spore case suspended on a slender stalk. Although the amoebae look like neighboring amoebae, they will aggregate, under the influence of a small organic compound called cyclic AMP, when food is unavailable. The aggregating amoebae mount each other, forming a slug that continues to grow and may move in concert as a single being. Dictyostelids, for example, can be found moving across rotting logs or damp soils. The moldlike slime, which looks like tiny yellow or gray stalks, upon higher magnification is often a slime mold, not a fungus, despite its name. These protoctists consist of tightly aggregated amoebae cells behaving in social concert. The noncellular slime molds don't form slugs. They grow to be more extensive than the cellular slime molds, as they form slimy masses that move in which the cells lack their original structure and form a single entity—really a huge multinucleate cell called a plasmodium. If food is nearby, the cells lose their undulipodia and grow by nuclear division rather than whole cell division. The swimmers and amoebae can also engage in sex, but only with their own kind (swimmers or tail-less forms). The plasmodial mass can give rise to swimmers (mastigote stages) at any time. These organisms feed on bacteria and plant material from decaying logs. They possess a protein, myxomyosin, similar to the actinomyosin that contracts when we use our muscles. Still another group of slime molds are the parasitic slime molds, called plasmodiophorans or plasmodiophorids. These molds do not move but hide out inside plant tissue (they especially like members of the mustard family, such as cabbages and radishes). They feed by taking in plant juices in a growing plasmodial stage. Parts break off into individual cells to swim through the soil to find new plant victims.

Protoctist Diversity

Despite the abbreviated introductions to the above groups, which seem to us the most important, other protoctist groups, such as ellobiopsids, chytrids, and oomycotes, exist. Much of earth's limestone and chalk cliffs is calcium carbonate formed not by animals but by chalk-making protoctists (haptophytes and coccolithophorids). These ocean-going organisms are involved (before dying and being added to fossil mineral deposits) in global cycles of sulfur and carbon, and they may, through their production of gases, play a role in global weather and climate. Many other protoctists, not always recognized as such, do likewise. The suffix *phyte* means "plant," but haptophytes are not at all plants. So, too, *mycos* means "fungi," but many organisms previously classified with the fungi swim—and so belong better with the protoctists. For example, the oomycotes, or chytrids, are protoctists previously considered to be fungi; as we learn more, as instrumentation and microbiological techniques become more powerful, and more organisms are discovered, and as taxonomic categories become more reflective of evolutionary history, more microbes are sure to be added to this overlooked jungle of evolutionary and ecological diversity, the protoctists.

Some 213,000 species have been tallied, and every paleontologist agrees that the vast majority are extinct. Probably millions of species of these amazingly diverse beings, from which the original animals evolved, have come and gone.

—Dorion Sagan and Lynn Margulis

See also: Bacteria; Carbon Cycle; Classification, Biological; Climatology; Five Kingdoms of Nature; Fungi; Global Climate Change; Lakes; Microbiology; Mollusca; Paleontology; Soil

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Pteridophytes

Ferns and their allies belong to the Pteridophytes, a group of four phyla comprising nearly forty families that include some 9,000 to 12,000 species worldwide. Of these, 97 percent are true ferns, the Polypodiophyta (or Pterophyta, or Filicinophyta). They can vary in size from tree ferns with 12-foot leaves to mosquito ferns just 1/16 inch long. The other phyla are Psilophyta, made up of two genera in the whisk fern family (Psilotaceae); Lycopodiophyta, made up of the club moss or ground pine family (Lycopodiaceae), the spike moss family (Selaginellaceae), and the quillwort family (Isoëtaceae); and the Phylum Equisetophyta, containing only the single genus *Equisetum* in the horse tail or scouring rush family (Equisetaceae). Pteridophytes are the earliest plants to appear on land, approximately 400 million years ago, during the Devonian Era, before the rise of flower- and seed-bearing plants. Pteridophytes are second only to flowering plants in terms of their diversity among living land plants. The pteridophytes dominated the flora of the Carboniferous Era, and their fossil remains yield most of the world's coal and oil. The three types of pteridophytes other than true ferns are considered "living fossils," which have changed little since the Mesozoic. Today in North America north of Mexico, ninety-three species of pteridophytes are known, and of these twenty-six species are listed as endangered.

The K/T Boundary Fern Spike

Looking deep into the geological past, we find that the end of the Cretaceous Era and the start of the Tertiary Era is marked by the presence of a vast number of fern fossils and little other evidence of life. This phenomenon is known as the K/T boundary fern spike. At that time, the devastation caused by the impact of a meteor nearly 10 km in diameter in Yucatan, Mexico, wiped out most living species on earth. Scientists believe that some fern species survived the fires and dense cloud cover around the world because ferns are very tolerant of shade, and their underground rhizomes can survive fire, sending up new shoots that will grow in soil covered with ash. The death of most other plants and animals gave these ancient pteridophytes a competition-free environment in which they flourished briefly before a succession of new life appeared in the Tertiary.

Structure and Life Cycle of Ferns and Their Allies

Morphology. Most ferns have thin, wiry roots that are shallow and grow from the bottom and sides of the rootstock, called the stock, trunk, or rhizome. The roots hold the plant in place and absorb water and minerals. The rhizome may be short and thick, or more often longer, narrow, and growing horizontally at ground level, either partially or shallowly buried or above ground, but in all cases sprouting stems and leaves from the upper surface. The structure of rhizomes is comparable to that of the stem of a flowering plant. It contains the conducting tissues xylem and phloem, and the supporting tissues called sclerenchyma fibers. The rhizome is perennial and commonly covered with scales or hairs. A fern leaf is called a frond or blade and may be evergreen or annual, according to the species and ecological conditions. The stalk, also called the stipe, stem, or petiole, supports the leaf. The stalk is usually flat or concave in front and rounded in back and often covered with hairs or scales.

Immature fronds start life as tightly coiled shoots that look rather like the curled top of a violin; hence they are called fiddleheads. The way they uncoil as they grow is called circinate vernation. Fronds come in a great array of shapes and sizes, varying from a simple single leaf to extremely compound laciness. The divisions of a compound leaf are known as leaflets or pinnae, and the entire leaf is called once-cut or pinnate. The part of the stem that carries the leaflets is the axis or rachis. A frond is called twice-cut or bipinnate when the leaflets are decompound, or cut into subleaflets or pinnules. If the subleaflets have divisions too, they are named lobes or pinnulets, making the frond thrice-cut, lacy-cut, or tripinnate.

Reproduction. The reproductive structure of ferns and their allies consists of the sporangia, containing the dustlike spores that serve instead of seeds to generate a plant with male and female sex organs that in turn gives rise to the next generation of spore-bearing fern. Sporangia tend to be arranged in a group, called a sorus, of usually sixty-four or sometimes thirty-two or sixteen spores, depending on the species. Sori occur on the underside of fronds that grow after the first, purely vegetative, growth of the season. Young sporangia are pale and darken as the spores mature. In some genera, the entire sori may be protected by a membrane called an indusium, or by a cuplike structure, while in other ferns sori with no protection are called naked.

In most ferns, the sporangia are formed of stalked capsules only one cell thick. Some of the cells that grow in a row are thicker, making them function like a spring as the sporangium matures and dries out. Finally, increased tension bursts open the sporangium, at which spores may fall nearby or float on air or water to great distances. When conditions such as moisture, temperature, light, and soil composition are suitable, a spore will germinate into a tiny green, heart-shaped plant called the gametophyte or prothallus. Sex organs develop on the underside: the antheridia, which produces numerous sperms or antherozoids, and a number of archegonia, each containing a single female cell. Fern sperm require a damp environment, since they can reach archegonia only by swimming through free water to their destination. Hybridization, or the fertilization of one species of fern by a different one, is not uncommon, because antheridia form before archegonia mature, increasing the chance that a gametophyte may fertilize another one, rather than itself. Under ideal circumstances, the sporeling fern, which looks simpler in structure than its mature form, grows from the fertilized gametophyte to produce the sporophyte, or spore-bearing fern.

Reproduction of allied species. These more primitive relatives of ferns also reproduce through a separate gametophyte stage, but there are some differences. Club mosses and quillworts always have only one sporangium per leaf, located at the base. Although some club mosses have bisexual gametophytes like ferns, quillworts and other club mosses have two kinds of sporangia, a larger one that becomes a female gametophyte and a smaller one that develops into a male. Horsetails produce their sporangia on structures called sporangiophores, which are grouped into a cone-shaped point usually on top of the main shoot or on the end of branch shoots in some species. Each spore has four armlike elators that begin to flail in response to moisture in the air, helping to disperse the spores. Horsetails also reproduce vegetatively quite readily, since they grow in sections that, if broken, can grow roots and generate a full plant. Many true ferns also reproduce vegetatively by extending new rhizomes that sprout, and often a hillside or grove of ferns will prove to be a single genetic plant.

Human Uses of Ferns and Their Allies

Ferns have played a role in human economies since earliest times. Although the bracken can sometimes be mildly toxic, the young, still-curled frond tips called fiddleheads, or croziers, of brackens and other species are often eaten, either cooked or raw. The bracken fern root was once the food staple of the Maori people of New Zealand, and many people today consider fiddleheads a delicacy. Several species can also serve as teas that in some cultures are considered to have medicinal properties, as does the allied *Equisetum*. Before the invention of modern pesticides, dry bracken fronds were used as a mattress stuffing to repel insects such as bedbugs, and their antimold and insect-repellent properties made fresh brackens an effective packing material for the transport and preservation of fish, fruits, and vegetables. As early as 800 C.E. in Europe, ferns as well as fern ashes were used both as a dye and a fixative for dyes, giving a soft, earthy color as well as helping to preserve fabric.

Ferns such as *Lycopodium clavatum* produce huge amounts of tiny, powdery spores, which have been used like talcum powder for the skin as well as to coat condoms. "Lycopodium powder," as the spores were known, is also explosively inflammable and was once a popular feature of magic shows, theatricals, and firework displays. Dry fern fronds make excellent fuel and have even been used as money in barter. Early U.S. pioneers called the fern ally common horsetail (*Equisetum arvense)* the "scouring rush," because the high concentration of silica in its leaves gives it a scratchy texture that works like fine sandpaper or steel wool, suitable for polishing pewter or brass and scouring cookware. In the Middle Ages, horsetails were used to polish armor. At that time, people also thought that fern seeds could make you invisible by sympathetic magic. The logic was that only flowers produce seeds, and therefore fern flowers must be invisible. The myth said that these flowers bloomed on midsummer night, and whoever was touched by the seeds then would remain invisible until daybreak.

Ferns have been decorative items ever since the so-called Victorian fern craze, or pteridomania, that was made possible in the 1830s when the London resident Dr. Nathaniel Bagshaw Ward discovered that he could grow ferns, which often died in England's industrially polluted gardens, in an airtight glass box, or terrarium, he invented and marketed as the Wardian Case. By the mid-1800s ferns dominated Victorian society, both as design elements in everything from garden furniture to building decoration, and as houseplants that required little light in typically ill-lit rooms. The modern horticulture industry sells a great variety of ferns for use in floral arrangements, as houseplants, and as outdoor ornamentals. They are particularly useful as shade-loving perennials that flourish where many flowers cannot.

Environmental Aspects of Ferns

Because it's less expensive to collect than grow them, there has been a commercial demand for wild ferns since the Victorian era, which contributes to the present loss of fern species. Fern diversity has also suffered from environmental degradation and loss of habitat, such as clear-cutting forests; human-induced forest fires; replacing ecologically mixed environments with monocultures or human habitations; habitat invasion by alien species; land pollution through agriculture, industry, improper waste disposal, and inadvertent toxic spillage; and redirection, pollution, and siphoning off of waterways and their surrounding landscapes. On the plus side, horsetails have been used in gold prospecting, because of their great capacity to concentrate metals in their leaves, while recent studies indicate that bracken ferns have the potential to remove arsenic from polluted soil by drawing great quantities of it into their leaves.

As conservation agents, ferns play a role in a great variety of environments. In eastern North America the Christmas fern (*Polystichum acrostichoides*) helps to control erosion, because its fronds rise nearly vertically to pierce through the spring leaf litter on the forest floor, then gradually droop until frost lays them low, trapping the fall leaf accumulation. Species such as the rock-cap ferns (*Polypodium vulgare*, *P. virginianum*, and *P. appalachianum*), which grow on rock ledges, and those that grow on rocky slopes, such as the fragile fern (*Cystopteris protrusa*) and the maidenhair fern or the narrow glade fern (*Adiantum pedatum* and *Athyrium pycnocarpon*), also serve to hold organic matter that falls on the densely growing mat of fronds and roots and help convert rocky litter to soil. On sand banks and river edges, the ostrich fern (*Matteuccia struthiopteris*), which propagates vegetatively by sending out a network of underground roots to form colonies, stabilizes land against the current's pull, while the cinnamon fern (*Osmunda cinnamomea*), the royal fern (*Osmunda regalis*), and the chain fern (*Woodwardia virginica*), which grow in swampy areas, form little hummocks or islands that aid in making marshy land more solid.

—*Mick Wycoff*

See also: Botany; Bryophytes; Cretaceous-Tertiary Extinction; Draining of Wetlands; Ecosystems; Evolutionary Biodiversity; Interior Wetlands

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Punctuated Equilibria

Punctuated equilibria is a term coined in 1972 by paleontologists Niles Eldredge and Stephen Jay Gould for a mode of evolution they considered common—and not broadly understood or appreciated in the world of evolutionary biology up to the 1970s. They contrasted it with the notion of phyletic gradualism—that is, the supposition that evolution is largely a matter of the slow, steady ("gradual") transformation of entire species over time, under the general guidance of natural selection. Eldredge and Gould (1972) attributed phyletic gradualism to Darwin and claimed that it had been the general view in paleontology and evolutionary biology ever since 1859.

The core notion of punctuated equilibria is based on the empirical observation of stasis: contrary to Darwinian expectations, most species seen in the fossil record tend to remain very stable—recognizably the same, often for millions of years, from the moment of their first appearance to their very last. This great stability is the "equilibria" part of the term. The observation had been made by a number of paleontologists in Darwin's day, but it had largely been forgotten—most likely inasmuch as stasis was not what was expected to be observed in the new science of evolutionary biology of the late nineteenth century.

Eldredge and Gould claimed that stasis is nearly universal among all sexually reproducing species, especially those that have left a fossil record over the past 540 million years. Although once considered in itself a controversial claim, the reality, frequency of occurrence, and importance of stasis has since come to be acknowledged by the large majority of paleontologists and, increasingly, evolutionary biologists, such as experimental, population, and ecological geneticists.

Thus evolutionary change is concentrated in relatively rapid bursts, estimated to last only 5,000 to 50,000 years—rapid in geological terms, but not especially fast given what is known to be possible in terms of genetic change in modern populations of organisms. This, the "punctuated" part of the term, was considered especially controversial when it was introduced: the phenomenon was often confused with outmoded and discredited ideas of "saltationism," which postulated evolution by sudden jumps through macromutations or other such undocumented genetic processes. In contrast, however, the original term was always firmly associated with the notion of allopatric speciation (see Speciation), as developed especially by the geneticist Theodosius Dobzhansky and the avian systematist Ernst Mayr in New York in the late 1930s and early 1940s. True speciation—as opposed to the model of "phyletic gradualism"—had never been fully explored, let alone accepted, in paleontology.

Stasis recognizes the considerable geographic variation that is developed by many species: the term does not imply that there is no variation within a species. It simply means that the variation seen within a species at any one time is not likely to be transformed into substantial directional change over geological time. Stasis is thought to come about, not because organisms lack sufficient genetic variation to evolve, or because natural selection is weak, but rather because, as environments change, species tend to change their locations—occupying familiar habitat whenever they can get to it. Once there, species tend to remain unchanged, a phenomenon known as "habitat tracking."

The other, and perhaps most important, cause of stasis comes from the fact that most species are fairly widespread, and they are broken up into many localized populations that play roles in their local ecosystems. Circumstances of life are bound to be different in all of these different ecosystems, so that there would be no way for natural selection to change the phenotypic and genotypic properties of all the organisms within a single species in one direction for any great length of time (see Species for more discussion of the geographic structure of species populations).

There are a number of ideas closely associated with punctuated equilibria. One is the notion of "species selection," which grew out of the paradox that, if natural selection is not constantly changing the appearance of organisms within a species over geological time, how then to explain the many examples of long-term, apparently directional, evolutionary trends? For example, one would predict that the fossil record of human evolution would involve a progressive enlargement in the size of the hominid brain—based on the realization that chimpanzees have brain sizes in the range of 400 to 450 ml, while the average brain size of a modern human being is 1,350 ml. And, sure enough, that is what the fossil record shows: the earliest hominids (genus *Australopithecus*) had brains roughly in the chimpanzee range; earliest members of the genus *Homo* evolved from these ancestors about 2.5 million years ago and had larger brains, around 750 ml. Later, *Homo ergaster* and *Homo erectus* had still larger brains (approximately 1,000 ml).

These data were traditionally interpreted in straightforward phyletic gradualism fashion: gradual evolution over 4 million years took the brains from 450 ml to 1,350 ml, as natural selection would be expected to favor a gradual increase in brain size (hence in presumed intelligence) over time. In contrast, though, fossil species such as *Homo erectus* show great stability (that is, stasis) in brain size over time, and it is now accepted by the majority of paleoanthropologists that brain size increase in human evolution occurred in a stepwise fashion associated with true speciation. In other words, human evolution accords very well with the notion of punctuated equilibria.

How, then, to explain the increase in brain size? Eldredge and Gould (ibid.) suggested that such examples of directional evolutionary trends could be reconciled with punctuated equilibria simply by recognizing that closely related species in a lineage may well compete for space and resources; in the case of hominids, those with bigger brains might be expected to win out over their smaller-brained relatives, thus driving their ancestors to extinction in a form of "species selection." Indeed, it was Charles Darwin who originally thought that most extinction came about in precisely that way, with newly evolved, superior species actively driving their less endowed, earlier-evolved kin species to extinction simply by out-competing them. The modern view of extinction, however, holds that most extinction events occur through physical stress to ecosystems, rather than through competition between species within an ecosystem—the exception being the current wave of extinction engulfing the planet's species now, an event caused by the presence of ourselves, *Homo sapiens*.

Paleontologist Elisabeth S. Vrba, however, pointed out that true species selection should have reference to properties of entire species. Brain size, however, is a property of organisms, even though we can calculate an average brain size for entire species and see that the averages differ. She suggested instead that many evolutionary trends could arise simply because some lineages speciate (and thus evolve) and go extinct more quickly than others, and the reasons for this might have more to do with the biological properties of the component organisms themselves—a phenomenon she called the "effect hypothesis." In other words, it would be incorrect to consider the trend in brain size increase in human evolution "species selection," as the survival of the progressively bigger-brained species was due, not to selection of entire species, but simply to the competitive success of the individuals within the bigger-brained species.

—Niles Eldredge

See also: Evolution; Habitat Tracking; Human Evolution; Natural Selection; Paleontology; Speciation; Species

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Radiolaria

See Protoctists

Red Algae

See Protoctists

Replenishment of Genetic Stocks

See Agriculture, Benefits of Biodiversity to

Reptiles

"Reptiles" is a vernacular name that refers collectively to a hodge-podge of amniotes that are not birds or mammals: turtles, crocodiles, tuataras, lizards, snakes, and amphisbaenians. The antique scientific concept Reptilia promotes confusion and misunderstanding of evolutionary history and the diversity of amniote vertebrates. For much of the later nineteenth and most of the twentieth century, Reptilia was taken to mean a group composed of the ancestors of living reptiles, as well as the ancestors of all mammals and birds—but not including the living bird and mammal subsets. Because no scientifically or evolutionarily cogent generality can be made about this arbitrarily circumscribed grouping of taxa—either anatomically, physiologically, or ecologically—the term *reptile* is now a deeply entrenched popular rather than scientific term. A better classification is the following (with the "reptile" groups addressed herein in italics):

- Tetrapoda (terrestrial, four-legged vertebrate animals)
  - Lissamphibia ("living amphibians")
  - Amniota (those animals that have extraembryonic membranes associated with the developing embryo)
    - Theropsida (including the modern group Mammalia, not addressed here)
    - Sauropsida (including many fossil groups not addressed here)
      - "Anapsida" (including the *turtles*)
      - Diapsida
        - Archosauria
          - *Crocodilia*
          - Dinosauria (including the modern group Aves)
        - *Lepidosauria*
          - *Rhynchocephalia* (including the Tuatara)
          - *Squamata* (including lizards, snakes, and amphisbaenians)

The sauropsids ("reptile" ancestors and their descendants) and theropsids (mammal ancestors and descendants) appeared in the Upper Carboniferous (about 315 million years ago), so the ancestral amniotes must have appeared somewhat earlier. Early sauropsids were anapsid, meaning that they lacked temporal openings in the skull; from these early sauropsids we have two surviving groups, the turtles (Testudines, known from the Lower Triassic), and the Diapsida (those sauropsids that have ancestors with two temporal openings in the dermal bone part of the skull, including the lepidosaurs and the archosaurs [which includes birds], which are known from the Permian, 270 to 225 million years ago).

Turtles. The turtles (Testudines) are a small group of about 250 species that are known from the Lower Triassic (240 million years ago). The hallmark of the turtles is the shell, dorsally formed by expanded ribs and expanded and fused dermal bones found in the skin of their ancestors; and the plastron, formed apparently by expansion and fusion of dermal bones in the skin and ventral musculature of their ancestors. At present there are two major evolutionary groups of turtles. One group, the Cryptodira, retracts its neck into the shell by forming a vertical S-shape in the neck. This is the predominant group worldwide, and it includes all of the turtles familiar to those in the developed world (excluding Australia). A smaller group, the Pleurodira, retracts its head into the shell by forming a lateral S-shape in the neck. These turtles are found in South America, Africa, and Australia. Turtles are remarkable because, with exceptions, they are the only vertebrates that can be picked up with impunity by humans, are edible, and have therefore been severely reduced in numbers worldwide.

Pleurodira. The side-necked turtles contain 2 families (Chelidae and Pelomedusidae) of aquatic and semiaquatic turtles.

Chelidae. There are 11 genera and 46 species, of which 6 genera (27 species) are found in the Indo-Australian region, and 5 genera, 19 species in South America. Some of the strangest turtles are in this group, including the aquatic (and bizarre looking) *Chelus*, which feeds hydraulically on small fishes, and the Australian *Rheodytes*, which very actively pumps water in and out of its cloaca, which acts as a gill. The snake-necked turtles of Australia also have extraordinarily long necks, which gave them their common name.

Pelomedusidae. The pelomedusidae (5 genera, 25 species) are, on average, more normal looking turtles than the chelids, with representatives in South America and Madagascar.

Cryptodira. Cryptodira ("regular" turtles) contain several families, ranging from pelagic sea turtles to the terrestrial giant tortoises.

Carettochelyidae. The pignosed softshell (1 genus, 1 species) is a close relative of the Trionychidae and is found in the rivers of extreme northern Australia and southern New Guinea. The shell is covered with pitted soft skin and the feet are modified into flippers.

Trionychidae. The softshell turtles (22 species in 6 genera) are distributed from the eastern United States to north-central Mexico, although the bulk of the diversity is found in Africa across tropical Asia to New Guinea, northeastern China, and Japan. Although most of the species have shells of about 30 cm long, some of the Asiatic members become enormous, with shells well over a meter in length.

Dermatemydidae. Like the Carettochelyidae and Trionychidae, the Central American river turtle (1 genus, 1 species) has a shell covered with soft skin and attains a shell length of 65 cm. The single species has a distribution from Vera Cruz, Mexico, to the Caribbean side of Honduras.

Kinosternidae. The mud and musk turtles

(4 genera, 25 species) are ubiquitous omnivorous bottom-walkers within their range from southeastern Canada through most of the eastern United States to northwestern Mexico and south to Argentina. Most are quite small, but at least two of the species in Central America attain shell lengths to 38 cm. Some or most are capable of anaerobic respiration for considerable periods of time.

Dermochelyidae. The leatherback sea turtle (1 genus, 1 species) is a pelagic turtle with flippers that allow it to "fly" through the water. The adult shell is composed of bony platelets covered by oily skin. The leatherback attains an enormous size, with the dorsal shell to 1.9 m. Like the other sea turtles, it lays eggs in nests on beaches, but unlike other sea turtles, because of its well-developed countercurrent system it is able to maintain a relatively high core body temperature, which allows it to enter areas of cool and cold water.

Cheloniidae. The sea turtles (4 genera, 6 species) are widespread in all tropical and warm-temperate seas. All species are endangered to various degrees, generally because of human disturbance of their nesting beaches.

Cheydridae. The snapping turtles (3 genera, 3 species) are aquatic species found in eastern North America south to Pacific Ecuador, and also in southern China and Indochina. The aquatic alligator snapping turtle of the southern United States is one of the largest turtles in the world, weighing up to 91 kg and with a shell length of 66 cm. The common snapping turtle is another aquatic member of the family, found over the entire New World part of the family's distribution. The big-headed turtle of southern China and Indochina is deeply endangered through habitat loss and hunting pressures; it is found in high gradient streams, where it will climb out on branches overhanging the water to sun.

"Emydidae." The pond turtles (31 genera, 85 species) are found throughout temperate and tropical North America south to northern South America, with one species in southern South America; North Africa north of the Sahara and Europe to tropical Asia as far as the Philippines, southern Japan, and eastern China. Some of the pond turtles may be more closely related to the testudinids, so recognition of the group as an evolutionary unit is clearly provisional. Life histories of the emydids is quite variable, from completely terrestrial species (for example, *Terrapene* and *Pyxidea*) to semiaquatic (*Clemmys*) to large (shell lengths to 80 cm) aquatic river turtles of the Asian tropics (*Orlitia*).

Testudinidae. The tortoises (10 genera, 41 species) are all completely terrestrial species with predominantly herbivorous diets. Although a few species reach very large sizes (Galapagos tortoises, Aldabra tortoise, and the African spurred tortoise), most species attain a shell length of no more than 30 cm; some of the species in southern Africa (for example, *Homopus*) are truly tiny turtles, with shell lengths of about 10 cm. Tortoises are found disjunctly in the warmer parts of North America and in the tropics of southern Central America and South America; they are also widespread in the Mediterranean region south to South Africa and across tropical and temperate Eurasia to Borneo. At least one species (*Testudo horsefieldi*) is found in the cold-temperate areas of west central Asia, otherwise a habitat exclusive of testudinids.

Diapsida. The Archosaurs and Lepidosaurs are the two groups of diapsids that have persisted to the present, the earliest diapsids having appeared in the Upper Pennsylvanian (280 million years ago). Archosaurs include the dinosaurs (including their highly successful subgroup, the birds) and crocodilians, and the Lepidosaurs include the Rhynchocephalians

An eastern collared lizard (Daniel A. Northcott/Corbis)

and Squamates. The only archosaurs addressed here are the crocodilians.

Crocodilians. The Crocodilia are an old group of archosaurs, appearing in the Middle Triassic (230 million years ago). They are the closest living relatives of avian dinosaurs (that is, birds). Although fossil members of the Crocodilia were terrestrial and in some cases cursorial, all living members of the group are semiaquatic carnivores that have taken on many specialized characteristics. Nevertheless, the crocodiles share many characteristics with birds, such as pneumatic bones, vocalization between mother and young, nest building and extended care of young, uncinate processes on the ribs, and details of the circulatory system. Most of the diversity of the Crocodilia is extinct, but three semiaquatic groups persist: the alligators and caimans; the crocodiles; and the gharial.

Alligators and caimans (Alligatoridae) are evolutionarily quite close to each other. Two alligators persist, in the southeastern United States, and the other in the lower reaches of the Yangtze River in eastern China, at least the Chinese alligator being quite threatened in the wild. The tropical caimans (3 genera, 5 species) are found from southern Mexico to Argentina. The American alligator is the largest, up to 5.5 m; the other caimans and Chinese alligator generally get no larger than about 2 to 3 m in length.

The crocodiles (Crocodylidae) are a very closely related group of 14 species in 3 genera. The dwarf crocodile (1 genus, 1 species; to about 1.5 m) is found in West Africa, and the false gharial (1 genus, 1 species) is found in peninsular Thailand to the Great Sunda Islands of Indonesia. There are 12 species in the genus *Crocodylus*, all very closely related and distributed in aquatic habitats in Africa, India, and southern China south and east to northern Australia and Melanesia, as well as two species in Antilles and southern Mexico to northern South America. The crocodiles vary considerably in the width of the snout, from broad to very narrow. Crocodiles get quite large, with the salt-water Crocodile (*C. porosus*) reaching 7.5 m in length.

The gharial (Gavialidae) is a relict of a once-abundant group of fish-eating crocodilians noted particularly for its very narrow snout. The gharial attains lengths of up to 6.6 m and lives in the drainages of the Brahmaputra (Bhutan and India), Indus (Pakistan), the Ganges (India and Nepal), and the Mahanadi (India), with small populations in the Kaladan and the Irrawaddy.

Lepidosauria. The lepidosaurs are an ancient group (found from the Upper Permian, 240 million years ago) and form the sister taxon of the archosaurs (which includes birds and crocodilians). Lepidosauria includes two groups of which one, the Rhynchocephalia, contains only two relict species, and the other, the Squamata, includes all lizards, snakes, and amphisbaenians.

Rhychocephalia. This group, widespread in the Mesozoic, is now reduced to two very closely related species, the tuataras (*Sphenodon punctatus* and *S. guntheri*), found solely on offshore islands near New Zealand. The Tuataras are lizardlike in general appearance, to about 60 cm in total length, but the details of their anatomy are quite unlike those of lizards. The Tuataras were widespread on New Zealand until the colonization of the island by humans, whereupon their commensal rats and pigs rendered tuataras extinct on the mainland.

Squamata. The Squamata contain the lizards, snakes, and amphisbaenians (some 7,994 species) and is where most “reptile” species diversity resides. Squamates are united by their possession of paired penes, as well as their ability to shed their entire epidermis in a single piece at regular intervals. Although the evolutionary history of squamates is reputed to be well known, with the skeleton of an evolutionary tree more or less universally accepted since the early1920s, the addition of molecular data suggests that what we think we know (and what is presented below) about squamate phylogeny may be very seriously incorrect. What is clear is that the snakes and amphisbaenians are imbedded within the lizards, so the traditional classification regarding these three entities as coordinate suborders within the Squamata is clearly mistaken. For purposes of this discussion, the following classification is adopted:

- Squamata
  - Iguania—iguanian lizards
    - Acrodonta—chisel-toothed lizards
      - “Agamidae”—chisel-toothed lizards, excluding chameleons
      - Chamaeleonidae—chameleons
    - Pleurodonta—iguanas and allies
      - Corytophanidae—casque-headed lizards
      - Crotaphytidae—collared lizards
      - Iguanidae—iguanas
      - Hoplocercidae—tropical tree lizards and allies
      - Leiosauridae—South American ground lizards
      - Liolaemidae—South American swifts and rock lizards
      - Opluridae—Madagascan swifts
      - Phrynosomatidae—North American swifts, sand lizards, and horned lizards

- Polychrotidae—anoles and allies
- Tropiduridae—South American fence and tree lizards
- Scleroglossa
  - Gekkota—geckos and allies
    - Eublepharidae—lidded geckos
    - Gekkonidae—geckos
    - Pygopodidae (including the diplodactyline geckos)—pygopods and Australian geckos
  - Scincomorpha—skinks and allies
    - Xantusiidae—night lizards
    - Lacertidae—rock lizards and allies
    - Gerrhosauridae—plated lizards
    - Cordylidae—sungazers
    - Teiidae—whiptails and allies
  - Anguimorpha
    - Anguidae—alligator lizards
    - Xenosauridae—xenosaurs
    - Helodermatidae—Gila monsters and beaded lizards
    - Varanidae—monitor lizards
  - Dibamia
    - Dibamidae—dibamids
  - Amphisbaenia—worm lizards
    - Bipedidae—ajolotes
    - Blanidae—European worm lizards
    - “Amphisbaenidae”—worm lizards
    - Trogonophiidae—chisel-toothed worm lizards
    - Rhineuridae—spade-snouted worm lizards
  - Serpentes
    - Scolecophidia—blindsnakes
      - Leptotyphlopidae—threadsnakes
      - Typhlopidae—blindsnakes
      - Anomalepididae—early blindsnakes
    - Alethinophidia
      - “transitional alethinophidians”
        - Anomochilidae
        - Uropeltidae—shieldtailed snakes
        - Cylindrophiidae—pipe snakes
        - Aniliidae—false coral snakes
      - Macrostomata
        - Xenopeltidae—sunbeam snakes
        - Loxocemidae—Mesoamerican python
        - Boidae—boas
        - Pythonidae—pythons
        - Bolyeriidae—Mascarene boas
        - Tropidophiidae—dwarf boas
        - Caenophidia (advanced snakes)
          - Acrochordidae—wart snakes
          - Viperidae—vipers
          - “Colubridae”—colubrids
          - Atractaspididae—mole vipers
          - Elapidae—cobras, kraits, coral snakes, and sea snakes

Iguania. The Iguania are a group (approximately 100 genera, approximately 1,000 species) of predominantly scansorial diurnal lizards that use their tongues as the primary prey-prehension organ. The group is divided into two quite different assemblages, the Acrodonta, or chisel-toothed lizards, in which the lateral teeth are fused to the jaw in adults. This group includes the bizarre chameleons (Chamaeleonidae) and the residue assemblage from which they are derived (the “Agamidae”). The “agamids” are widespread in the tropics of Asia and Africa as well as Australia. An evolutionary subset of this group, the chameleons, are found in extreme southern Europe, throughout Africa and Madagascar, and in southern India. Acrodont diversity ranges from big herbivores (*Uromastyx*) to small ant-specialists (*Moloch*) to the chameleons, which can project their tongues to more than a body length to capture prey. The Pleuronta are composed of the iguanians that lack the morphological derived dental characteristics of the acrodonts and so far are supported as a natural group only by molecular evidence. This group is composed of ten groups of uncertain relationship to each other. The pleurodonts have somewhat greater morphological diversity than the acrodonts, ranging from the marine and terrestrial iguanas of the Galapagos, to tiny twig anoles in the Antilles, to horned lizards, and a broad array of small scansorial insectivores. Collectively, the pleurodonts range from southern Canada to near the tip of Tierra del Fuego in South America, Madagascar, the Galapagos, and Fiji and Tonga in the Pacific. The far outliers on Fiji and Tonga are clearly part of the iguana group.

Scleroglossa. The scleroglossan squamates are all of the snakes, amphisbaenians, and noniguanian lizards. The obvious characteristic of this group is that the tongue is not the primary prey prehension organ, and in most groups is primarily part of the sensory apparatus. The scleroglossans fall into several major subgroups: gekkotans, dibamians, scincomorphs, anguimorphs, snakes, and amphisbaenians, all of which are known from the later Mesozoic. The enormous majority of the species diversity of squamates is in this group, which ranges concomitantly from sand-swimming snakes to delicate geckos and hard-scaled skinks. Within the Scleroglossa are major groups:

Gekkota. The Gekkota (geckos and their allies) are a large group (100 genera, approximately 1,000 species) found worldwide in all warm-temperate and tropical areas. Almost all geckos are nocturnal, with loud voices, transparent scales covering the eyes, velvety skin, and broad toe-pads that allow them to scurry across vertical surfaces. Nevertheless, the morphological diversity is large, extending from tiny leaf-litter lizards in the American tropics to giant geckos up to nearly 70 cm in New Caledonia, as well as a snakelike group (the pygopods) of Australia that are diurnal, with large scales and adapted to eating large prey. The group is cast into several distinctive families, the Gekkonidae, Eublepharidae, and Pygopodidae.

Scincomorpha. The scincomorphs form an amorphous group of lizards of dubious monophyly that range from large diurnal active foragers to aquatic snail eaters to small fossorial and leaf-litter lizards. Within the scincomorphs are a number of families of poorly understood relationships.

The Teiidae (40 genera, 245 species) are found in temperate and tropical America and includes large (to more than a meter) and moderate-size species that are fast, active foragers, as well as semiaquatic swimmers, and common sharp-nosed whiptail lizards to very small skinklike leaf-litter species. A considerable number of species of teiids have been found to be unisexual.

The Lacertidae (29 genera, 215 species) are a group of Eurasian and African lizards that are similar to teiids in having large plates on the heads, being diurnal active insectivores, and having small scales on the body. Most are terrestrial or rock-living, but a few live on sand dunes.

The Xantusiidae (3 genera, 19 species) are an enigmatic group of lizards superficially similar in some ways to geckos, such as in having a transparent brille covering the eye, but otherwise they are typically scincomorph. They live in cloud forests to deserts in the western United States south to Panama and in Cuba. Some species are unisexual.

Skinks, Scincidae (100 genera, 1,090 species) are an enormous taxon found worldwide in temperate and tropical climes. The typical skink is a medium-size lizard with shiny cycloid scales each supported by osteoderms that make their scaly covering almost impervious to insect bites. However, the morphological diversity is huge, from many lines of legless lizards (and those with reduced limbs) to long-legged arboreal skinks in the islands of the South Pacific. Some lines have replaced their eyelids with transparent brilles; some have "windows" in the lower eyelid that allow them to see with their eyes closed, and many have developed direct internal development of the young.

The sungazers, Cordylidae (2 genera, 42 species), are a taxon found solely in southern and eastern Africa. One of the genera (*Platysaurus*) lays eggs and is strikingly flat, living in rock crevices. The other genus (*Cordylus*) has live young, but show great morphological diversity, from relatively smooth crevice dwellers, to snakelike species with strongly reduced limbs. Some species have such heavy osteoderms in their spiny skin that they are armored.

The nearest relatives of the cordylids are the Gerrhosauridae (6 genera, 30 species) of Madagascar and sub-Saharan Africa. The gerrhosaurids lay eggs, and are otherwise more skinklike than are the cordylids.

Anguimorpha. The anguimorphs are superficially similar to the scincomorphs in primitively having osteoderms in the skin, tails that break off, and in general having a skinklike body form. Some evolutionary biologists think that the snakes are members of this group, although the evidence is confusing.

Anguidae are the best-known family (13 genera, approximately 105 species) in the group with species ranging from the highly arboreal *Abronia* of Central America to the serpentiform *Ophisaurus* of North America and Eurasia; other groups of anguids occur throughout Central and South America, as well as the Antilles.

Xenosauridae (2 genera, 5 species) are a small group of anguimorphs that are semiaquatic or, when terrestrial, found in wet microhabitats. One genus is found in eastern China and the other is found in Mexico and Nuclear Central America.

Varanidae (2 genera, 50 species), the monitor lizards, are considered by some to be the closest relatives of snakes. They range in size from about 25 cm to about 3 m (the Komodo Dragon). Most of the living species diversity is in Australia, but the range of the group includes sub-Saharan Africa as well as tropical Asia and Indonesia.

The Gila monster and beaded lizard (Family Helodermatidae, 1 genus, 2 species) are distinctive species found from the southwestern United States south to Guatemala along the Pacific slope and are the only venomous lizards. The venom is secreted by nonmuscularized glands derived from salivary glands, which drain passively into the mouth, where deeply grooved teeth conduct these fluids into the tissue of prey. Human deaths have been documented by these species, which are highly dangerous, even though their disposition is generally phlegmatic. The two species range from strictly terrestrial (Gila monster) to arboreal (at least some populations of beaded lizards).

Amphisbaenia. The amphisbaenians are clearly scleroglossans, but beyond that the evidence is confusing. The group first is evident in the Cretaceous and is composed of about 150 species, cast into about five families, although that is in a state of flux. The size range is 10 to 70 cm. They range throughout the tropics of the New and Old Worlds, excluding Australia, and including the extreme southern parts of Europe and Florida. Skulls of amphisbaenians are very heavily constructed, and most species are heavily built legless burrowers, some of which will, from under the surface of the soil, attack mice and other vertebrates that are above them. Distinctive features of the amphisbaenians are a median tooth on the upper jaw and the scales of the body being arranged in distinctive rings. The Bipedidae (1 genus, 3 species) are restricted to Mexico, live in permanent burrow systems, and retain a well-developed pectoral girdle and forelegs and feet, with which they burrow. The Blanidae (1 genus, 2 species) are the most primitive group of legless amphisbaenians, being found in southern Europe and Turkey. Other than those taxa, the bulk of amphisbaenians are cast into three families, the Trogonophiidae of East Africa and Arabia, which have their teeth fused to the underlying bone and are the only live-bearing group; the Rhineuridae, a group with spade-shaped heads, and the rest, being cast into the obviously unnatural residue of species called "Amphisbaenidae."

Dibamia. Similar to the Amphisbaenia in terms of enigmatic placement evolutionarily is the Dibamia, a group coextensive with the Dibamidae (2 genera, 10 species). The dibamids are small, limbless, attenuated burrowing lizards found in eastern Mexico and in southeastern Asia and the Philippines through Indonesia to western New Guinea (a distribution that implies a very old history). The vestigial eyes are covered by a scale, and they lack ear openings. Males have flaplike hind limbs, presumably used in copulation. It has been suggested that they are related to anguids, skinks, geckos, amphisbaenians, and snakes.

Serpentes. The snakes, like the Amphisbaenia, are sometimes treated as a coordinate taxon with the lizards. That is clearly an error, as the snakes are imbedded within the lizards and should be considered just another, albeit very large (2,920 species) and diverse, group of legless lizards. The snakes appeared in the fossil record in the Cretaceous. Interestingly enough, one species in the highly derived macrostomatan group retains (or regained) legs, implying that legs were lost either many times within the snake lineage or have been regained at least once. Evidence suggests that snakes evolved from burrowing, possibly nearly blind ancestors. Living snakes fall into three major "flavors": those that are nearly blind and burrowing, those that are more derived but are not highly adapted for eating very large prey, and those that have highly kinetic skulls that allow them to eat very large prey, in some cases items many times larger in diameter than their skulls.

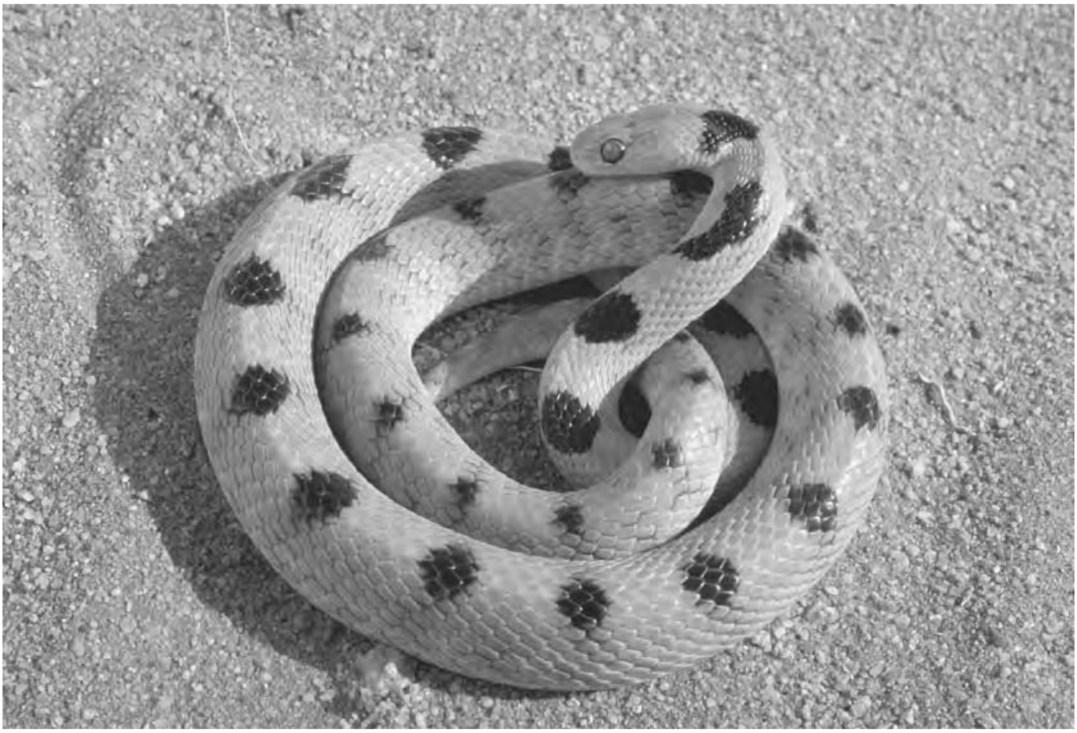
Scolecophidia. The scolecophidians are three groups of primitive snakes that are superficially similar looking in the way their eyes are reduced essentially to retinas underneath the scales of the head. In the Typhlopidae (225 species, worldwide tropics) and Anomalepididae (New World tropics, 16 species), the maxillae are rotated to form paddles that pump ants or termites down the throat of the snake. The thread snakes (Leptotyphlopidae—worldwide tropics and subtropics, 91 species), on the other hand, have more normal maxillae and, presumably, use their jaws in a more normal fashion.

Alethinophidia. The "advanced" snakes, with exceptions, have eyes that focus, and that is where most of the species and morphological diversity in snakes lies. It is composed of two groups, the Anilioidea and the Macrostomata, which differ most saliently in the level of skull kinesis. The Anilioidea have strongly built skulls reminiscent of varanoid lizards, while the Macrostomata have more delicately built skulls that exhibit a rather incredible degree of kinesis, allowing them to engulf very large prey items.

"Transitional groups." This transitional collection of primitive alethinophidians is not monophyletic; it is composed of several families that have a spotty distribution around the globe: Anomochilidae (1 species in Sulawesi), Aniliidae (South American tropics, 1 species), Cylindrophiidae (southeastern Asia, 2 species), and Uropeltidae (the pipe snakes of tropical India and Sri Lanka, 8 genera, 44 species). All are leaf-litter burrowers and eat arthropods and small vertebrates.

Macrostomata. Within the Macrostomata are several very small relatively primitive relict lineages: Xenopeltidae (sunbeam snakes, Southeast Asia, 2 species); Loxocemidae (1 genus, 1 species, western Mexico and Central America); Erycidae (the sand boas, 2 genera, 7 species, western North America, Africa, Arabia, and central and southwestern Asia); Bolyeridae (2 genera, 2 Recent species, of which one has become extinct in historical times, Round Island in the Indian Ocean); and Tropidophiidae (4 genera, 16 species, Central America, northern South America, and the Antilles). In addition, there are two groups of these transitional macrostomatans that are very well known to the public; these are the boas and pythons. The boas (Boidae: 4 genera, 22 species) are found in the tropics and subtropics of North and South America as well as Madagascar. The boas all bear living young, and although most species do not get larger than about 2 m, at least the semiaquatic anaconda of South America is the largest (although not the longest) snake, in some cases weighing 500 kg. Unlike other snakes, male boas retain "spurs," which are vestigial hind legs. A smaller relict group, the sand boas are found in western North America and West Africa (3 genera, 14 species). The pythons (Pythonidae: 9 genera, 33 species) are similar to the boas but lay eggs and are found entirely in the tropics of the Old World, including Australia. One of these, the reticulated python of southeast Asia, has been documented to grow to 11 m and has successfully eaten people.

Caenophidia. Within the Macrostomata is a group of highly derived snakes, referred to as the Caenophidia. They do not appear in the fossil record until the Oligocene-Miocene boundary, so either their enormous diversification has taken place relatively rapidly, or the fossil record is illusory. Within this group, the elephant-trunk snakes (2 genera, 5 species) are the most ancient family. This group of snakes are completely aquatic and live in southeastern Asia from the Philippines to northern Australia. The Viperidae (vipers: 17 genera, 241 species, worldwide tropics and temperate regions excluding Australia), Atractaspididae (mole vipers: 10 genera, 65 species, Africa and southwestern Asia), and Elapidae (cobras, coral snakes, and sea snakes: 61 genera, 236 species; worldwide tropics and Indo-Pacific Ocean) have extraordinarily well-developed venom delivery systems. This has been accomplished by shortening the maxilla, which allows the enlarged posterior teeth (a hallmark of the Caenophidia) to be brought anteriorly. The shortening of the maxilla has also allowed it to become increasingly movable, to the degree that the Atractaspididae and Viperidae have fangs that are so large that if they were not rotated backward they would be too large to keep in the mouth. This latter group includes the well-known rattlesnakes and huge bushmaster (which gets to at least 3 m). The Elapidae include the New World coral snakes, and the Old World radiations of cobras, taipans, tiger snakes, and relatives. The largest single radiation of elapid snakes is in Australia, in which better than 80 percent of the snake fauna are in this venomous group. Included within the Elapidae are the sea snakes, a group of obligate aquatic snakes,



Tiger snake, South Africa (Gallo Images/Corbis)

most of which are live-bearing. At least one of these, the black-and-yellow seasnake, is pelagic and has a range that extends from East Africa through the Indian and Pacific oceans to the Pacific coast of tropical America. The elapids are among the most venomous snakes on the planet, although they tend to be somewhat less aggressive than pit vipers.

The Colubridae are by far the largest snake family (295 genera, 1,600 species), as well as the most poorly understood, found worldwide in temperate and tropical areas (although with only a very few and marginal representatives in Australia). They show enormous diversity, from specialized burrowers and sand-swimmers, to constrictors, aquatic fish-eaters, arboreal vine snakes, and even arboreal gliders. Although most colubrids are not dangerous to humans, it appears that primitively most groups of colubrids were rear-fanged and mildly venomous, and many species are quite dangerous to humans, particularly in southeastern Asia and sub-Saharan Africa. For most of the period of snake systematics, the Colubridae have been considered an unnatural group, possibly ancestral to the other caenophidians; especially implicated are the Elapidae and Atractaspididae. In recent years, considerable work has been done on relationships within this difficult taxon, and major groups are becoming elucidated. The colubrids are composed of several groups. The "Colubrinae" is a group of about 100 genera found worldwide in temperate and tropical regions (except for most of Australia), mostly composed of nonvenomous (or mildly venomous) generalized snakes such as racers and rat snakes; considerable variation is present, however, from small sand-swimming taxa (for example, *Chilomeniscus*) to arboreal, dangerously venomous species (such as *Thelotornis*).

The Homalopsinae are a small (11 genera) peculiar group of southeast Asian to Indo-Australian species that are extremely aquatic and characterized by having ribs that closely approximate ventrally. The "Lamprophiinae" are a group of 44 genera found in sub-Saharan Africa and Madagascar that are mainly terrestrial to fossorial, although a few are arboreal. The "Natricinae" include the typical harmless water snakes of North America and Europe, but their range also extends through Eurasia to the East Indies and includes many burrowing taxa and even some rear-fanged species (for example, *Rhabdophis tigrinus* of southeastern Asia), which are dangerously venomous. The Pareatinae represent a small (3 genera) group of southeast Asia that are specialized on eating snails and slugs. The Xenodermatinae (6 genera) are found from Borneo to Assam, India, Japan, and southern China and are composed of small, forest leaf litter–inhabiting snakes. A large group, the Xenodontinae (with more than 90 genera, found throughout the Americas) are highly diverse in body morphology, ecology, and behavior, with the bulk of the evidence of their evolutionary propinquity coming from molecular studies. The typical xenodontine is a small, nondangerous rear-fanged crepuscular snake, although aquatic, diurnal racer, burrowing, and racer subgroups are known. At least some (for example, *Philodryas*) can be painfully venomous.

—Darrel Frost

See also: Adaptive Radiation; Classification, Biological; Evolution; Evolutionary Biodiversity; Geological Time Scale; Linnaean Hierarchy; Phylogeny; Species; Systematics; Zoology

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Rivers and Streams

Water flowing down a slope under the influence of gravity and confined to a channel is a river or stream. Geologists use the term *stream* to indicate any size channel, but in some places rivers are large, streams smaller, and brooks and rills even smaller. Streams receive their water from precipitation, melting snow, and groundwater that seeps into the channel from below the surface. They lose water by evaporation, sinking into the ground, and by discharge at their terminus or mouth. The size of a stream at any given place is dependent on the drainage area above that point. The discharge is the amount of water flowing past the point for a specific amount of time and is indicated as cubic meters per second. For large streams the amount of water can be measured in millions of cubic meters per second.

Rivers and streams are powerful transporting agents as they roll and push material on their bed down the channel. This is described as the bed load, but rivers and streams can also carry large amounts of suspended matter, usually fine grained, giving the river a muddy look. In addition, rocks can skip along the riverbed in short hops, a process called saltation. Rocks that sit motionless on a streambed are too heavy for the stream to move under the existing conditions. Rivers also carry dissolved materials derived from the weathering of rocks. All of this material—bed load, suspended and dissolved materials—is simply known as the load; the total amount a stream can carry is termed its capacity. The largest-diameter particle a stream can carry is defined as its competence, which is determined by velocity and is dependent on the discharge and steepness of the stream channel or gradient. Higher gradients cause rivers and streams to flow faster.

Rivers carve the valleys they are in, and, except for glacially carved valleys, the tributaries meet the main stream at the same elevation. Many streams encounter resistant layers of rock that form ledges in the channel, causing the water to drop precipitously downward over rapids and if high enough over waterfalls.

From the air or a map, it is clear that stream networks have a drainage pattern of connecting tributaries, a pattern that reflects the underlying geology. Dendritic patterns are treelike and are developed on homogenous layers of rock that are horizontal, while parallel drainage develops on homogenous rocks with a steep slope. A trellis pattern develops on inclined layers, and radial drainage on circular mountains with a central peak such as a volcano. So-called deranged drainage is located on a recently glaciated surface; it has many lakes, and the streams have not had time to develop a clear pattern. Over time rivers evolve and cycle through stages that generally begin with down-cutting as the primary erosional direction, eventually becoming lateral as erosion reduces the landscape's relief.

A profile along the length of a stream will usually be steeper at its headwaters and gentler downstream, forming a concave curve. The velocity of a stream may not decrease downstream, even though the gradient is less steep, because it is offset by other factors such as increased volume of water and changes in channel width and depth. For example, if the channel width decreases, and all other factors remain the same, a given volume of water will flow faster through a narrow channel than one that is wider.

As a stream flows toward its mouth, more and more tributaries join it, increasing the amount of water flowing in the river, increasing the discharge, and increasing the width of the channel. The doubling of the velocity increases the amount of sediment that a stream can carry by a factor of twenty, while also increasing the particle size.

The drainage basin contains all the streams that contribute to the main river and is separated from the adjacent basin by a drainage divide. It can be imagined as shaped like a large spoon, steep on the sides and nearly flat in the middle.

The lowest elevation of a stream is its base level, at its mouth, where it terminates in a body of water or in an interior basin, thus making base level the lowest elevation to which a stream can erode. As a stream slows down, it drops its sediments, larger particles first, until its velocity is zero, when all the sediments eventually settle out. As a stream flows down its channel, the sediment load

A mountain stream in the American West (USGS/Capps, S.R.)

becomes progressively well sorted by size, density, and composition as the particles are weathered and eroded during transportation. Thus the sediments, for the most part, are of the same size and composition.

When a river enters a body of water, a large fan-shaped pile of sediments is deposited, forming a delta. Here the river breaks up into a number of branches called distributaries. During flooding, one distributary is usually preferred over the others, bringing sediments to that section of the delta. Over time all the distributaries will be flooded, enlarging the delta in all its sections.

On desert floors, where the stream terminates, the fan-shaped deposit is called an alluvial fan. Often rivers that flow into desert areas dry up for a period of time, because the water evaporates, sinks into the ground, or there is just not enough water to supply them. When this happens they are called intermittent streams; sometimes streams flowing through a desert, such as the Nile River in Egypt, have water flowing all year round, because the constant supply from its headwaters is greater than the loss in the desert. These types of streams are described as *perennial*.

As a stream begins it journey, minor irregularities in the channel, due perhaps to different materials, cause the velocity of the stream to fluctuate, resulting in more erosion where it is faster and deposition where it is slower. Curves, or "meanders," begin to form and enlarge. Not only do they get wider but they also shift downstream, eroding as they do a flat, broad plain covered with sediment. This plain, the flood plain, is covered with water when a stream overflows its bank, when discharge exceeds the capacity of the channel. Often the river will deposit its coarsest (and heaviest) sediment where it overflows the banks, to create a low, ridgelike deposit, the levee. An individual meander does not last forever; during flood stage streams may cut a channel across the meander. The abandoned loop becomes an oxbow lake, separated from and independent of the river.

Flooding occurs when input from tributaries exceeds the capacity of the streams to hold the water. Rainfall frequency, permeability and porosity of the subsurface (which determines the infiltration rate), saturation level, and slope steepness are some of the factors that affect runoff rate. The greater the runoff, the greater the amount of water entering the stream. Vegetation can reduce flooding by being a physical barrier, thus slowing down the flow; it also holds together the soil and at the same time increases its permeability.

During a flood the water level rises; its elevation is called a stage; when the water overflows its banks, that is flood stage, the maximum discharge. It is at maximum discharge that a river crests and moves downstream until it returns to normal flow.

It is surprising that people choose to live on flood plains, but sometimes they are unaware of the hazard: they take a chance, it is scenic, a flood may occur only rarely, and flood control structures make people feel safe. Farmers appreciate the flood because the fine sediments deposited on the flood plain fertilize the soil. Cities are built adjacent to rivers, using them for transportation. There are many factors that create flooding in urban environments: asphalt and concrete reduce infiltration; buildings occupy space, raising the flood stage; storm sewers discharge water into streams; and vegetation is removed.

Silting may also increase the potential for flooding, by reducing the capacity of channels. A number of engineering solutions have been adopted to reduce flooding: retention ponds, storage of flood waters in quarries, flood control dams, dredging of silt from stream channels to widen or deepen the riverbed, and raising levees. However, the process of channelization may cause flooding downstream, or severe flooding may result when an unexpectedly high flood flows or breaches the levee. Once the flood occurs, the levees make it difficult for the flood waters to return to the channel.

Flood control dams have adverse effects, hindering navigation and the movements of organisms; they also destroy habitats, and the resulting reservoir creates a new base level into which sediments are deposited, reducing their effectiveness and eventually making them useless. The loading of the earth's crust with water and sediment has in some places pushed it down, resulting in earthquakes at a number of dam sites.

The amount of water flowing in a stream channel can be quite variable throughout the year. In some places along the channel it flows fast, and at others, where it flows over a flat surface, the water may move quite slowly. Organisms living in the water and adjacent to it on the riverbanks must be adapted to changing water conditions. When the river is flowing swiftly, not only does the turbulence add plentiful oxygen to the water; in addition, the animals must be able to attach themselves to a surface or dig themselves into if they are not to be washed away. As the water approaches the mouth of the stream, it can slow down and may contain suspended sediment, reducing the amount of oxygen and limiting photosynthesis in bottom-dwelling plants. In general, however, slower-moving water supports a greater diversity of plants and animals than more swiftly flowing water.

—Sidney Horenstein

See also: Freshwater; Hydrologic Cycle; Lakes

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Rodents

Rodents are small to medium-size mammals (5 grams to 65 kilograms), with one pair of ever-growing, rootless upper and lower incisors. Most are herbivorous, though some are partly or exclusively insectivorous, or partly carnivorous. There are more than 2,100 living species (sorted into more than 460 genera in 27 families) in the Order Rodentia, and they constitute nearly half of the approximately 5,000 species of living mammals. Rodents are indigenous to every land area except Antarctica, New Zealand, and a few Arctic and oceanic islands, and some species have been introduced even into those places through their association with humans. Rodents are also the only terrestrial placental mammals occurring naturally in Australia and New Guinea.

Significant interactions occur between humans and species of rodents. Humans utilize rodents as a source of food through hunting and husbandry, for coats derived from their fur, as subjects used in biomedical and genetic research, and for pleasure in the form of household pets and zoo exhibits. Because living rodents form such a large group of species, and occur in so many kinds of habitats (from desert to tundra, from subterranean burrows to forest canopies) over so much of the planet's surface, study of their species-diversity, biology, geographic distributions, and evolutionary history are pragmatically and intellectually satisfying to researchers in a wide range of disciplines.

At some point in their evolutionary history, humans experienced a transition in resource use from nomadic hunting and gathering to sedentary agricultural practices. Through this transition humans inadvertently became, and remain, a reliable source of shelter and food for some rodents, primarily those species with the innate genetic and behavioral adaptive abilities to exploit resources available in anthropogenic habitats. The impact of these commensal species upon human populations is usually not benign. Some crops are damaged before harvest; stored grains are eaten by rodents, and what is not consumed is contaminated by their excrement. Water-impounding earthen dikes and dams leak and may even fail because of burrowing by some species, and objects (from water pipes to electrical wiring) are damaged by their gnawing. Certain species are natural reservoirs for disease, and these may be, or have been, transmitted to humans by arthropods, resulting in sickness or death.

As documented by fossils, the evolutionary history of rodents extends back 56 million years (to the Late Paleocene) in North America and Asia, and the actual origin of the group is probably even older. Approximately 26 extinct families have been described, containing more than 220 genera. The closest living relatives of rodents may be the lagomorphs (rabbits, hares, and pikas), and both groups may have evolved from a common ancestor. Some of the earliest lagomorphs represented by fossils are difficult to distinguish from primitive rodents.

Throughout their evolutionary history, rodents have been successful and significant members of terrestrial faunas. They are diverse in number of species and morphologies that represent different evolutionary lines of descent, and they provide stunning examples of parallel evolution (similar structures evolving in different evolutionary groups). Because of this history, the classification of rodents is a challenge to zoologists. Rodent specialists agree with definitions of most families but disagree about the grouping of families into suborders. Past classifications have either omitted suborders altogether and arranged the families into superfamilies, or into from two to sixteen suborders.

The most recent classification, and the one followed here, arranges families into five suborders. It is loosely based upon a combination of the classical arrangements of the jaw and associated musculature (protrogomorphous, sciuromorphous, hystricomorphous, or myomorphous), histologic structure of incisor enamel layers, comparative anatomy of the head and postcranial skeletons and different organ systems, embryonic development of extra embryonic fetal membranes, and analyses of mitochondrial and nuclear DNA sequences. These five suborders represent a hypothesis of relationships among rodent families, and this classification may be modified by the discovery of new fossils, reanalyses of published data, and new analyses of data from new sources, most probably derived from rodent genomes. The five suborders, their contained families, and general native distributions are outlined below.

Suborder Sciuromorpha: Aplodontidae (mountain beaver; western North America), Sciuridae (tree squirrels, ground squirrels, flying squirrels, marmots, chipmunks, and prairie dogs; worldwide), Gliridae (dormice; Eurasia and Africa), and Castoridae (beavers; North America and Europe). **Suborder Myomorpha:** Dipodidae (birch mice, jumping mice, and jerboas; Eurasia, North Africa, and North America), Muridae (rats, mice, hamsters, voles, lemmings, muskrats, gerbils, zokors, blind mole rats, bamboo rats, and African mole rats; worldwide), Geomyidae (pocket gophers; North and Central America, northern South America), and Heteromyidae (forest spiny mice, pocket mice, kangaroo rats and mice; North and Central America, northern South America). **Suborder Anomaluromorpha:** Pedetidae (spring hare; sub-Saharan Africa) and Anomaluridae (anomalures; sub-Saharan Africa). **Suborder Sciuravida:** Ctenodactylidae (gundis; North Africa). **Suborder Hystricognatha:** Hystricidae (African and Asian porcupines), Erethizontidae (North American, prehensile-tailed, stump-tailed, hairy dwarf, and thin-spined porcupines; North, Central, and South America), Petromuridae (dassie rat; southern Africa), Thryonomyidae (cane rats; sub-Saharan Africa), Bathyergidae (blesmols; sub-Saharan Africa), Dasyproctidae (agoutis and acouchys; Central and South America), Agoutidae (pacas; Central and South America), Dinomyidae (pacarana; South America), Caviidae (guinea pigs, cavies, and maras; South America), Hydrochoeridae (capybara; South America), Octodontidae (rock rats, degus, viscacha rat, plains viscacha rat, coruro, and tuco-tucos; South America), Echimyidae (American spiny rats; South America), Myocastoridae (nutria; South America), Capromyidae (hutias; West Indies), Chinchillidae (plains viscacha and chinchillas; South America), and Abrocomidae (chinchilla rats; South America).

All rodents have an upper and a lower pair of persistently growing, rootless incisors, with hard enamel layers on the front surfaces of each tooth and softer dentine behind. The differential wear from gnawing creates perpetually sharp, beveled, and chisel-like edges. Between incisors and cheek teeth is a long gap (diastema) devoid of other incisors and canines. The number of cheek teeth (premolars and molars) ranges from twenty-two (two premolars and three molars on each side of the upper jaws, and one premolar and three molars on each side of the lower jaws) to four (one molar in each quadrant of the jaw); they may be rooted or rootless and ever-growing, and low or high-crowned.

The configuration of the jaw articulation ensures that incisors do not meet when food is chewed, and that the cheek teeth do not occlude while the animal gnaws with its incisors. Powerful and complexly divided masseter muscles, attached to jaw and cranium in different arrangements, provide most of the power for chewing and gnawing. Incisors and cheek teeth perform different functions. The incisors cut, pry, slice, gouge, dig, stab, or delicately hold items like a pair of tweezers, and they can cut grass, open nuts, kill animal prey, excavate burrows, and fell large trees. The cheek teeth masticate (chew) the food obtained by the incisors. Chewing is crushing and grinding the food and involves the transverse and front-to-back movement of the cheek teeth in the lower jaw against the upper cheek teeth. This movement is possible because of a loose articulation between the lower jaw and cranium.

An American groundhog (USDA Forest Service)

Except for saltatorial (jumping), gliding, and fossorial species, the postcranial skeleton of rodents is relatively unspecialized. The radius and ulna (bones of the lower arm) are unfused; the elbow joint permits free movement of the forearm; and front feet have four digits in most species, with a thumb that is vestigial or reduced in size. Tibia and fibula (bones of the lower leg) are usually fused near the ankle, and the hind feet have three to five digits. Some species have internal cheek pouches (chipmunks) or external, fur-lined cheek pouches (kangaroo rats and mice, pocket gophers) that open near the angle of the mouth. Rodents exhibit a wide range of stomach morphology, from a simple sac to a complex structure resembling that of ungulate ruminants. They have a relatively unspecialized brain. There is usually a baculum in the penis, and testes are either inguinal or abdominal in position. Ears range in size from slight ridges to large flaps; eyes are minute and covered with transparent tissue in some species but large in most. Tails may be rudimentary (mountain beaver and many fossorial species) or very long relative to the length of the head and body (most squirrels and arboreal species in other families); the tail is about as long as, or only slightly longer than, the head and body in most rodents.

The range in body size between the house mouse (15 grams, body 10 cm long) and the woodchuck (6,000 grams, body 50 cm long) brackets most species of living rodents. At one extreme is the Old World harvest mouse (*Micromys minutus*), one of the smallest rodents, weighing 5 to 8 grams, with a body up to 8 cm long (the length of a person's little finger). The largest living rodent is the capybara (*Hydrochaeris hydrochaeris*) of Central and

South America, which weighs 35 to 65 kg and has a body 100 to 135 cm long, with a shoulder height up to 60 cm. Some extinct species were even larger, attaining the size of a black bear (the giant beaver, *Castoroides*, from Pliocene-Pleistocene sediments of North America) or small rhinoceros (*Telicomys*, related to the living South American pacarana, *Dinomys*, and found in Late Miocene sediments of Argentina).

Rodents may be active during the day (diurnal), only at night (nocturnal), or sometimes part of the day and night. The popular conception is that rodents are strictly herbivorous, and that is true for some species, but diets of most include vegetative and reproductive parts of plants, fungi, invertebrates, and vertebrates. Some species are opportunistic generalists; others are specialized predators of arthropods and vertebrates. Food is either eaten where gathered or carried to burrows and stored. Species living in arid habitats and on oceanic islands are able to obtain their water requirements from their food. Shelters may consist of a simple nest on the forest floor beneath cover, in tree holes, in leaf and stick structures in tree crowns, in rock crevices, or in mounds of cut vegetation built in aquatic environments or burrows. Rodents may be active all year, or enter periods of dormancy or deep hibernation. Breeding time and frequency, length of gestation, and litter size vary widely. Population size may remain stable or fluctuate, and some species migrate when populations become excessively large.

The body form of tree squirrels (Sciuridae) may be similar to that of the earliest (Paleocene and Early Eocene) and presumably generalized, rodents (species of extinct North American *Paramys*, for example). By adhering to bark with their claws, tree squirrels can adeptly scamper up tree trunks, run along branches, and leap to adjacent trees; they nest in tree holes or in stick nests constructed in the crowns (characteristics of an arboreal manner of life). Other arboreal squirrels nest and forage in trees but glide from one tree to the next (flying squirrels). Many species are equally agile on the ground, and shelter in burrow systems that they excavate (terrestrial and semifossorial ground squirrels, prairie dogs, marmots), and some are capable swimmers (occasionally amphibious). A few species utilize burrows for nesting but forage in trees (long-tailed ground squirrels).

The specialized body forms of other rodent species signal particular locomotor patterns and ecologies. Some strictly arboreal species have a prehensile tail (South American porcupines, for example); others glide from tree to tree, supported by fur-covered membranes between their extended appendages (flying squirrels and anomalures). Highly specialized fossorial rodents are basically furry cylinders with protruding, strong incisors, small eyes (sometimes not discernible externally) and ears (represented by only a low ridge in some species), and expansive front feet bearing powerful digging claws (zokors, blind mole rats, African mole rats, pocket gophers, bamboo rats, blesmols). Amphibious rodents possess specialized traits (such as thick and waterproof fur, webbing between digits, side-to-side flattened tail), allowing them to forage in aquatic habitats but den in ground burrows or stick houses (muskrat and beaver are the most familiar). Terrestrial, leaping species have short forelimbs, long and powerful hind limbs and feet, and a long tail used for balance (jerboas, kangaroo rats and mice). The body forms of some rodents converge on those in nonrodent orders, resembling shrews (Indo-Australian species of shrew mice), hares (viscachas), pikas (gundis), small pigs (pacas), miniature hippopotamus (capybaras), and small-bodied forest deer (acouchys and agoutis).

—*Mary Ellen Holden*

See also: Biogeography; Deserts and Semiarid Scrublands; Evolutionary Biodiversity; Herbivory; Lagomorpha; Mammalia; Tropical Rain Forests

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S

Salamanders

See Amphibians

Sandalwood Tree

The sandalwood tree (*Santalum fernandezianum*) from the Juan Fernandez Islands (also known as the Robinson Crusoe Islands), located off the coast of Chile, was prized for its fragrant wood and aromatic oil. Commercial demand for sandalwood resulted in overharvesting and extinction less than 400 years after the discovery of this species.

Sandalwood has been used for religious, decorative, and medicinal purposes by many cultures since antiquity. The wood is used for carvings because it retains its pleasant fragrance for many years. The oil, which is extracted by steam distillation from the heartwood and roots of mature trees thirty years of age or more, is used in traditional medicine and ceremony. Although there are several species of *Santalum*, the type formerly known from the Juan Fernandez Islands was unique, and the characteristics of its wood and oil are still being studied nearly a century after its extinction (Baeza et al., 1999; Hoenesien et al., 1998).

The Juan Fernandez Islands form a small archipelago located off the coast of Chile. As is the case on many isolated islands, the flora and fauna of the Juan Fernandez Islands demonstrated a high degree of endemism. The earliest Western explorers to reach the islands, in the sixteenth and seventeenth centuries, found lush forests full of aromatic woods and no human inhabitants. The islands became a way station where ships could be refitted and supplied. Since the only large mammals on the islands were seals, domestic goats and pigs were introduced to provide a ready source of meat for the visiting sailors. These intentionally introduced species, along with the rats that accompanied the new arrivals, were extremely destructive to the native flora and fauna. Having recognized the need to protect this fragile and unique ecosystem, the Chilean government designated this archipelago a national park in 1935; the International Union for the Conservation of Nature has made it a World Biosphere Reserve.

For *Santalum fernandezianum*, however, protected status came too late. In 1908, Carl Skottsberg, the premier naturalist authority on the Juan Fernandez Islands, wrote upon visiting the last remaining sandalwood tree: “It is a strange sensation to be at the death bed of a species; perhaps, and most probably, we are the last scientists to see it alive." When Skottsberg returned in 1918, the tree was dead ("Los apuntes," 2001).

—Julie Pomerantz

See also: Extinction, Direct Causes of

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Scaphopods

See Mollusca

Scorpions

See Arthropods, Terrestrial

Sea Kelp

See Protoctists

Sea Urchins

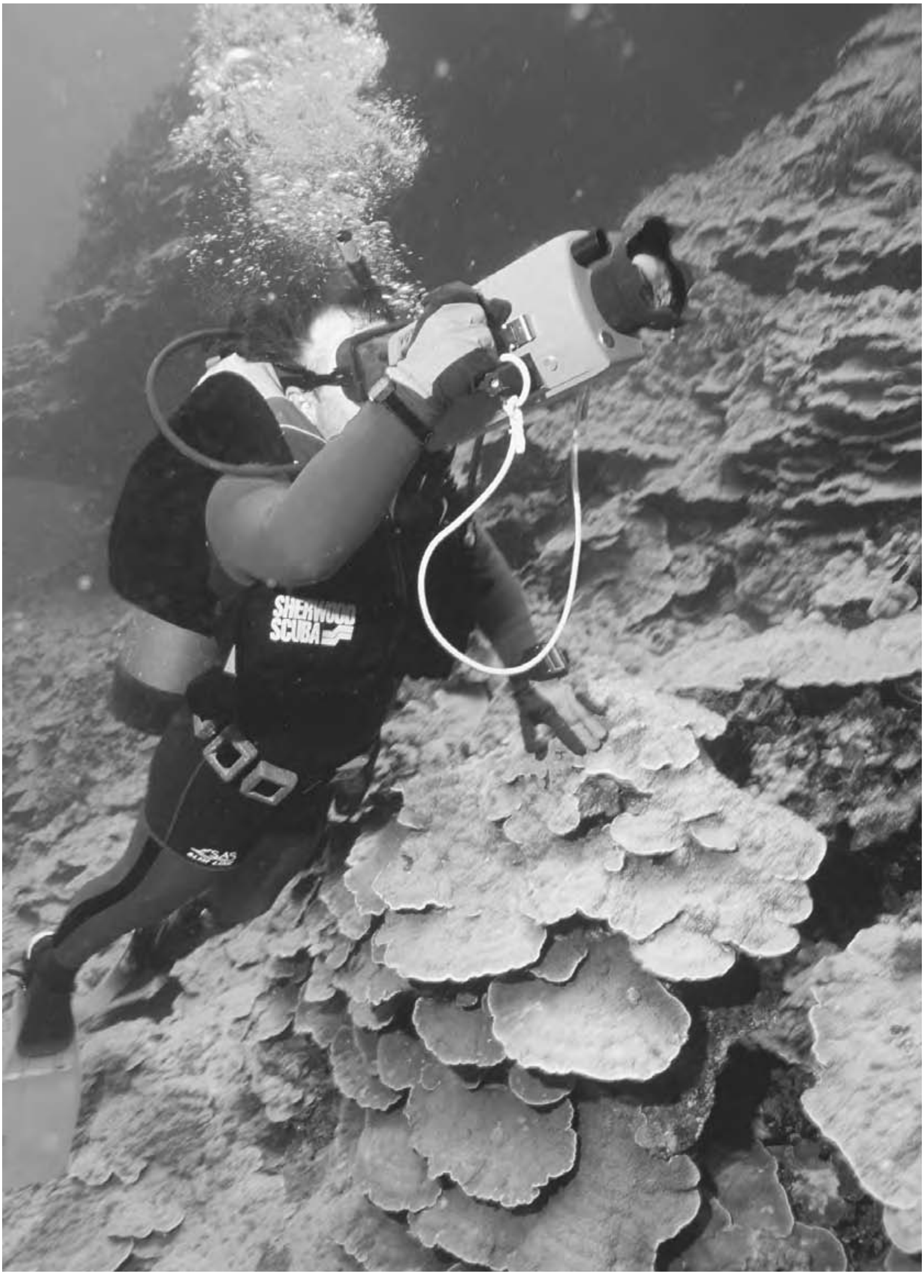
See Echinoderms

Seamounts

Seamounts are submarine volcanoes that rise more than 1,000 m above the seafloor; they occur individually, in clusters, or in lines. They are most abundant in the Pacific Ocean basin where more than 10,000 have been counted. Some of them form islands when large volumes of molten material produce volcanoes that grow above the surface of the sea. Mauna Loa on the island of Hawaii has an elevation above the seafloor of about 10,000 m and a volume of 4,000 cubic kilometers, one of the largest mountains on earth. Seamounts with flat tops are called guyots, named after the Swiss-American oceanographer Arnold Guyot. Their flat tops look like they were eroded by waves, but they are generally found 1,500 m below the sea surface, making such a theory seem implausible. However, submarine exploration of guyots has shown that many have dead coral reefs on their surfaces and have features that look like they were created by wave erosion.

A good way to explain their flat tops is to examine the Hawaiian Island chain, which contains a long string of volcanoes, many below the ocean's surface. As we trace the line of volcanoes westward from Hawaii, we find that they get smaller and older. Hawaii is active, but Kauai, 500 km to the west, is not; it is about 5 million years old. Midway Island is 2,600 km away and is 28 million years old. In between are other islands, seamounts, and guyots. At the Yuryaku seamount—3,500 km from Hawaii and 43 million years old—the chain turns northward and is now called the Emperor Seamount chain; it terminates near the Aleutian Islands, where the oldest seamount is 65 million years old. The Hawaiian-Emperor Seamount Chain is 5,500 km long.

How can such a long string of volcanoes be produced, volcanoes that are within plates, not along plate boundaries? Geologists suggest that below the lithospheric plates, "hot spots" or "plumes" are generated within the mantle and stay fixed in place for a long time. About forty plumes have been identified on the earth.



Diver near the Loihi seamount, a volcano forming in the waters off Hawaii (Robert Ressmeyer/Corbis)

The molten materials from these plumes pierce the plate and build volcanic edifices. As the plate moves, the volcano is carried away from the source of volcanic material and becomes dormant and then extinct. Today, even though Mauna Loa is still active, Hawaii is moving away from its hot spot, and a new volcano named Loihi is being formed on the seafloor to the east. Erosion eventually destroys volcanoes that are no longer being renewed by volcanism, bringing them down to sea level.

However, other factors are also involved. Over the hot spot, the plate bulges upward. As the plate moves past, not only does it move downward but, in addition, the hot rock cools, shrinks, and becomes denser and sinks. As a result, the farther that volcanoes move away from the hot spot, the lower they get, until they eventually sink into the sea; they erode and develop a growth of corals when their surface is in shallow water. Changes in the direction of the line of seamounts can show geologists how plates move over the course of time.

—*Sidney Horenstein*

See also: Geology, Geomorphology, and Geography; Plate Tectonics

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Sere

See Succession and Successionlike Processes

Sharks, Rays, and Ratfish

See Chondrichthyes

Simpson, George

See Evolution

Sixth Extinction

Extinction events have struck life throughout its entire 3.5-billion-year history on earth. Each time, life has managed to rebound. Ever since there have been complex forms of life on earth—the expanse of geologic time spanning the past 600 million years or so—five major mass extinctions, global in scale, have devastated the earth's ecosystems and sent many species to extinction: the Late Ordovician (approximately 440 million years ago); Late Devonian (approximately 360 million years ago); the Permo-Triassic crisis (245 million years ago—the largest of all so far, with perhaps as many as 96 percent of all species on life becoming extinct); Late Triassic (approximately 210 million years ago); and the Late Cretaceous (65 million years ago—the famous K-T event). Numerous less global extinction events occurred in between these major global events. All such mass extinction events were caused either by extraterrestrial impact, global climate change, or some mixture of physical factors.

We now live in what many geologists and biologists consider the Sixth Extinction (also known as the "biodiversity crisis"); according to Harvard biologist E. O. Wilson, the earth is losing more than 30,000 species a year (approximately 3 per hour)—a rate of loss equal to the great global mass extinctions of the past. The cause this time is different from any in the past: the cause this time is a single biological species, ourselves, species *Homo sapiens*. Because of the profound changes in our ecological status, brought about by the increased reliance on culture in human ecology and culminating in the origin of agriculture some

10,000 years ago, the global population of humans has recently surpassed 6 billion—and with that explosion in our numbers has come a transformation of the planet's surface through the spread of agriculture, urbanization, and other physical transformations of terrestrial habitats; the spread of alien species, including pathogens; and simple overharvesting of the world's fisheries and timberlands. Together with pollution, these factors stand out as the leading cause of death of so many species of plants, animals, fungi, and microbes each year the world over. Sustainable development, conservation, and stabilization of human population numbers seem to be the best hope of curbing this current wave of mass extinctions.

The Sixth Extinction has so far developed in two distinct phases. Phase I began when our species, *Homo sapiens,* began to spread out of our homeland of Africa just less than 100,000 years ago. By that time, humans were accomplished hunters as well as gatherers of edible plants and fungi. According to the archaeological record, wherever human beings invaded, ecosystems were profoundly disrupted, and many animals quickly succumbed to extinction. This wave of extinction accompanying the migration of *Homo sapiens* was for the most part likely caused by overhunting, especially in regions that earlier hominid species had never reached. In addition, some paleontologists have suggested that people brought disease-causing microorganisms with them as well, along with pets, and that these additional factors may well have played a role in driving native animals extinct.

Perhaps the most famous victim of *Homo sapiens*–induced extinction in this first wave of the Sixth Extinction was none other than our collateral kin, the Neanderthals (*Homo neanderthalensis)* of western Europe. Whether by direct competition, or perhaps even open warfare, Neanderthals were gone within 5,000 to 7,000 years of the appearance of modern humans in Europe, some 38,000 years ago.

Archaeologists dispute the earliest dates of the peopling of the Americas, but modern humans did not arrive in North America in any significant numbers until 12,500 B.C.E. Some archaeological finds document evidence of hunting and butchering (for example, points embedded in rib cages of extinct bison; scrapings on bones of mammoths and mastodons). It was right after humans arrived in numbers in North America that most of the great species of Ice Age mammals became extinct: wooly rhino, wooly mammoth, American mastodon, giant bison, and so forth. In the Caribbean, humans arrived about 8,000 years ago—and soon thereafter the larger mammals of the Caribbean islands, including some monkey species, became extinct. One final example—human colonization of Madagascar only 2,000 years ago—shows the correlation again working: elephant birds, a species of pygmy hippo, and some of the larger species of lemurs all succumbed to extinction immediately thereafter. Extinction of birds and other species in the Pacific also reflects the relatively recent spread of humans to the remote islands of the Pacific Ocean.

Phase II of the Sixth Extinction overlaps with Phase I, the expansion of modern humans around the globe. Phase II began with the invention of agriculture and the immediate changes that agriculture brought to the human ecological condition. Phase II started slowly, as human population growth has exploded exponentially mostly in the last few centuries. But in these past few hundred years, the explosive growth in human population numbers—together with the rapid growth of industrialization and the even newer technologies of communication—has prompted major transformations of the terrestrial landscape for agriculture and logging. Coupled with the spread of alien species, pollution, and overharvesting (all consequent on the fact that humans are no longer dependent upon the productivity of local ecosystems), these factors have combined to trigger the enormous increase in the rate of species loss that has come to be called the "Sixth Extinction."

—*Niles Eldredge*

See also: Agriculture and Biodiversity Loss: Industrial Agriculture; Agriculture, Origin of; Alien Species; Conservation, Definition and History; Ecological Status of Modern Humans; Extinction, Direct Causes of; Mass Extinction; Pollution; Population Growth, Human; Sustainable Development; Urbanization

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Sloshing Bucket (Theory of Evolution)

See Evolution

Smallpox

Smallpox (variola), a member of the orthopox genus of viruses, has been extinct in the wild since 1977, and it may have the distinction of becoming the first species to be totally extinguished by world consensus. This virus, "the most terrible of all the ministers of death" (Macaulay, 1800), has plagued humans since the beginning of civilization. Until the1960s, smallpox was still common in some parts of the developing world, and the risk of an outbreak in Europe was a source of serious concern. Smallpox was used as a biological weapon during the French and Indian Wars, when British forces distributed contaminated blankets with the intent of initiating outbreaks among the Native Americans. Persons of all ages and classes were potential victims for this indiscriminate killer. However, since 1978, the tables have been turned. Humans now control the fate of smallpox and must wrestle with ethical issues about genocide that never troubled the virus.

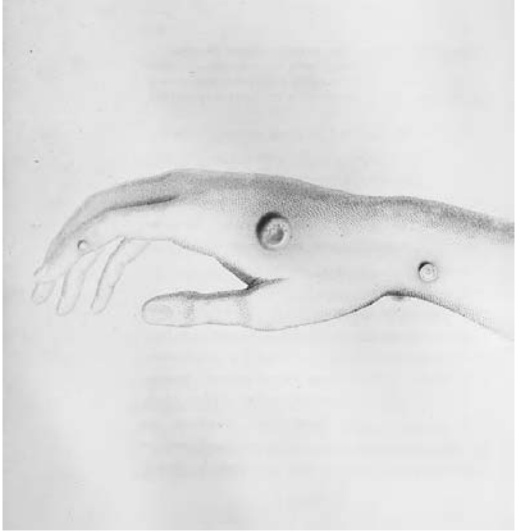
Orthopox viruses are large, complex viruses, with a characteristic brick-shaped structure measuring about 200 nm in diameter. Three naturally occurring members of the orthopox genus are known to infect humans: smallpox, monkeypox, and cowpox (also called vaccinia). Cowpox causes mild skin lesions. Outbreaks of monkeypox with occasional fatalities occur among people in Africa who have contact with the squirrels and monkeys that are the natural hosts of that virus. In contrast, smallpox is extremely contagious and has a high fatality rate.

Smallpox infection begins with inhalation or ingestion of the virus. The infectious dose is believed to be only a few virions. After a two-week incubation period, the patient develops a fever and a rash beginning on the face, arms, and in the mouth, and then spreading over the entire body. Pustules form and crust over, with scabs that fall off to leave severe pitted scarring on those who survive. Historically, 20 to 60 percent of smallpox victims died, usually during the second week of the illness. Death most likely resulted from the toxemia associated with circulating immune complexes and variola antigens. Other forms of smallpox—the hemorrhagic and malignant forms—were less common, which sometimes meant that these cases were not promptly identified and that quarantine of these patients was delayed. As is true for most viral diseases, there is no specific treatment for smallpox. All that can be done for patients is to provide supportive care.

It was long known that people who had recovered from smallpox were immune to reinfection. This led to a practice called variolation, in which people were inoculated with infectious material from patients who had had a mild case of the disease. Variolation significantly reduced the number of fatalities associated with smallpox outbreaks, but in some cases fatal smallpox infections resulted from the inoculation. Cowpox infection in humans was also known to produce immunity to smallpox, but without the risk of inducing fatal disease. In 1796, Edward Jenner was the first to demonstrate the efficacy of "vaccination" in the prevention of smallpox. The modern vaccine is a genetic hybrid between vaccinia and variola. The adoption of vaccination in Western countries eliminated the threat of massive outbreaks in those areas.

The World Health Organization (WHO), an agency of the United Nations, began a global eradication program in 1967. Massive vaccination programs coupled with disease surveillance and quick response to outbreaks facilitated its eradication. The last naturally occurring case of smallpox was reported in Somalia in 1977. However, the last recorded death by smallpox occurred because of a laboratory accident in 1978 (Kreeger, 1994). In 1979 the WHO declared the world free of smallpox, with stores of virus remaining only in two research laboratories.

The WHO Ad Hoc Committee on Orthopoxvirus Infections made a recommendation in September 1984 to destroy all remaining stores of the smallpox virus, stating that the risk of an outbreak outweighed its value for future research. Destruction was initially delayed in order to allow the viral genome to be sequenced. In May 2000 the WHO set a new deadline for destruction of virus stocks—2002—in order to allow further international research into antiviral agents, improved vaccines, and investigations of the genetic structure and pathogenesis of smallpox. The WHO did, however, reaffirm that elimination of the virus is the organization's ultimate goal.



Hand of Gloucestershire milkmaid Sarah Nelmes showing cowpox blisters from which Edward Jenner developed the smallpox vaccination technique, 1798 (From the collections of the Library of Congress)

The key reason given for the need to destroy the last stocks of the smallpox virus is the danger of accidental or intentional release. In 1999 and 2000, WHO teams inspected the Russian and U.S. facilities where smallpox is stored. They were satisfied with the biological safety and physical security of the facilities, but there is concern that other stocks of virus might remain in non-WHO laboratories. Others have raised the concern that virus preserved in the tissues of previous victims might be the source of new epidemics, or that the virus could re-emerge as a variant of monkeypox (ibid.).

Although the smallpox vaccine is very

effective, the immunity is not permanent. Vaccination of the general public was discontinued in the 1970s because the disease was no longer considered a threat. It is believed that persons who were vaccinated more than ten years ago are susceptible to the virus, although they might not be as severely affected. In addition, the prevalence of persons with compromised immune systems caused by the human immunodeficiency virus (HIV) increases the susceptibility of some populations. Increased human mobility has made intercontinental travel rapid and commonplace, and it has the potential to disseminate contagion on a scale unknown at the time of the last smallpox outbreak (Henderson et al., 1999).

For many people there is no ethical dilemma regarding the fate of the smallpox virus: It is a threat to mankind with no known redeeming characteristics, so its destruction is justified. To others the matter is more complicated. Does mankind have the right to knowingly exterminate a species? If we wish to eliminate things that are dangerous or frightening, the list will also include many creatures that we are currently striving to protect from extinction. Are we sure that there is nothing more that we can learn from the smallpox virus, or that smallpox has no possible use that would benefit mankind? How will future generations remember this decision?

—*Julie Pomerantz*

See also: Five Kingdoms of Nature; Medicine, The Benefits of Biodiversity to; Viruses

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Snails

See Mollusca

Snakes

See Reptiles

Snowball Earth

Snowball Earth is the name given to a series of extensive glaciations that took place around 600 million years ago that might have triggered the appearance of the first complex animals on earth. When life developed the ability to make creatures out of many cells rather than just one that led to the possibility of eyes, teeth, legs, arms, shells, claws—all the organs and appendages that distinguish complex animals from primordial slime. Hence, whatever caused this development in the history of life was responsible for most of the biodiversity that we see on earth today. Some researchers believe that the global "Snowball" glaciations were the trigger. Most researchers agree that this was the coldest period the earth has ever experienced. Although opinion is divided about whether the glaciations triggered the development of complex life, and if so, by what mechanism, the coincidence in timing is widely believed to be significant.

The origin of complex animals has long been a mystery. Earth first formed more than 4.5 billion years ago, and for most of its history the only living things on its surface were simple, single-celled creatures like bacteria and algae. Traces of complex animals date to around 580 million years ago. Tiny preserved embryos have been found in Guizhou Province, South China, dating to some time after 590 million years ago. Evidence of large, complex, jellylike creatures called Ediacarans has been found in South Australia, Namibia, the White Sea area, and Newfoundland (Xiao et al., 1998). The oldest of these have not been accurately dated, but they appear to be older than 575 million years. After the early embryos and Ediacarans the so-called Cambrian explosion occurred, which set the foundations for every family of complex animal living on earth today—including humans. The question that remains unanswered is this: when single-celled creatures ruled the earth for most of its history, what caused complex animals to emerge suddenly and unexpectedly from the primordial slime, and why did it happen at that particular moment in time?

Some researchers believe that the birth of complexity was triggered by the largest and most severe ice age ever to strike the earth. Rocks dating from around 700 to 600 million years ago bear the indisputable signs of ice. Ancient icebergs carried boulders far off land and then dropped them onto the silty seafloor when they melted. These so-called dropstones are now preserved in siltstones around the world. Also, ice on land slipped and slid over the surface, dragging pebbles, stones, and rocks along with it. The melange of rocks bulldozed together by the ice is also preserved in many places around the world, often bearing scrape marks where the rocks were dragged along the ground. The glaciations were extremely widespread. Evidence for them is found on every continent (apart from Antarctica, where evidence of any ancient processes is hard to come by, since most of the surface is buried under modern-day ice).

How cold was it? Over geological timescales, earth's continents shifted on its surface, and hundreds of millions of years ago the continents were in different positions. Research measuring the magnetic fields trapped in the ice deposits from the Flinders Ranges of South Australia shows that the continent was close to the equator when the ice formed (Sohl et al., 1999). Since the equator receives the highest concentration of sunlight in the world, it is the hardest part of the planet to freeze. Thus, the Snowball Earth must have been at least very heavily ice covered, if not totally frozen. There is some controversy about whether the continents were completely covered in ice, and whether the oceans froze over all the way to the equator. However, some researchers (Hoffman et al., 1998) estimate that global average temperatures then were around minus 40 degrees centigrade, compared with an average today of around plus 15 degrees centigrade. That was almost certainly the coldest the earth has ever been. This period must have delivered a severe shock to the earth's climate system, and many scientists find it at least highly suggestive that all the evidence for the emergence of complex creatures appears later than the rock horizons bearing signs of ice. There are no undisputed signs of complex animals before the ice signs.

If the ice did trigger the emergence of complex life, what mechanism was involved? Nobody really knows. One possibility is that the severity of the ice age wiped out single-celled creatures from many of the world's environmental niches. Thus, when the ice finally melted, the niches were available to be occupied by more complex animals. Another possibility is that larger, complex animals were more energy-hungry than their predecessors. Since burning oxygen is a very efficient way of providing energy, complex animals may have required a pulse of oxygen to trigger their development. Some researchers speculate that just such a pulse of oxygen may have accompanied the melting of the ice.

—*Gabrielle Walker*

See also: Evolution; Evolutionary Biodiversity; Geological Time Scale; Mass Extinction; Paleontology

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Soil

The term *soil* is used in different ways in different disciplines. To engineers, soil is any loose material above solid bedrock, a usage equivalent to the term *regolith*. Soil scientists use the term for any material capable of growing plants.

To a geologist, soil is produced by weathering and is the residual product of the chemical, physical, and biological breakdown of rock, whether bedrock or material that has been transported. Climate, topography, the composition of the material, and the length of time the processes have been working determine the type of soil.

Rocks are broken down naturally by mechanical disintegration and by chemical decomposition. Freezing water in rock fractures breaks them apart, while daily temperature fluctuations also help to disintegrate rock. The result is an increase in surface area that provides more surfaces for chemical weathering to take place. Water and gases in the atmosphere attack minerals in the rocks, chemically producing new minerals that are stable or capable of being dissolved. Limestone, for example, is made up for the most part of the white mineral calcite. If limestone has a color other than white, it contains other minerals that give it its color. As the limestone is dissolved away, it leaves a small residue of noncalcitic minerals that becomes part of the developing soil.

Feldspars, components of granite, change to clay, while some of the darker minerals, ferromangnesium silicates, also change to clay but include insoluble residues of iron oxides as well.

The mineral quartz, common in many rocks, is usually resistant to chemical attack and remains behind. Igneous rocks form from molten material; those that crystallize at high temperatures break down easily at the surface, while those that form at a lower temperature and pressure weather more slowly.

In general, the higher the temperatures and the greater the quantity of water, the greater the amount of weathering. Chemical and mechanical weathering go hand in hand, but climate determines which predominates. In cold climates mechanical weathering is dominant, while in tropical climates chemical weathering is. Biological weathering is another factor that plays an important role in the breakdown of minerals, by producing enzymes that are reactive with them.

As rocks break down the weathered product, soil forms on the surface. In newly exposed rock there is a rough succession of organisms that attack the rock. Lichens are the pioneers, succeeded by mosses and quickly by other plants that take the opportunity to grow in cracks and crevices. As the plants decay they aid in the soil-forming process. It turns out that soil is not a simple, homogenous mass but is divided vertically into distinct zones, the soil profile.

In a typical profile, the top zone, exposed to the surface, is designated the O-horizon, where newly fallen leaves and other plant parts accumulate. It is followed by the A-horizon, containing the most decayed rock and most of the organic remains. Rain percolating through the A-horizon, also called the zone of leaching, picks up any material that is soluble and transports it downward to the B-horizon, the zone of accumulation. The B-horizon rock material is not as decayed and contains some organic material. Below it is the C-horizon, which is composed of broken up bedrock that merges with the unaltered bedrock below. The boundaries between the zones may be sharp or gradational, and in well-developed profiles it is possible to subdivide the horizons. Not only do soil profiles contain subdivisions but, in addition, in some instances a horizon can be entirely missing, while others contain horizons that are transitional between A, B, and C. These variations are the result of the combination of different soil-forming factors, such as rate of formation and erosion, wind, amount of precipitation and running water, topography, and extent and kinds of human activity.

Soils were historically classified into two generalized groups based on climate: pedalfers forming in wetter climates, found in tall grass prairies, broadleaf deciduous, and needle leaf forests; and pedocals in dryer climates, such as desert shrub environments and short and medium grass steppes. Pedalfers are usually acid and subject to extensive leaching, which leaves behind oxides of aluminum and iron, and clay. The term *pedalfer* is a combination of *ped* (soil), *al* (aluminum), and *fer* (iron). A special type of pedocal is laterite soil, which often is bright red and forms in tropical climates with heavy rain and high temperature. Leaching takes place at a maximum rate, and these soils end up with insoluble aluminum and iron compounds. The iron gives laterites their red color.

Tropical rain forests have a very lush growth of vegetation, giving people the idea that the soil will make a productive farm. It comes as a great surprise that these farms do not live up to their potential. Although the forest itself contains considerable amounts of nutrients, there is little in the soil. The lushness comes from the continual accumulation and rapid decay of vegetation that has fallen to the surface, supplying new plants with nutrients. Clearing away the forest for crops clears away the nutrients.

In a matter of a few years, cleared land with laterite soil becomes increasingly unfarmable. Under natural conditions lateritic soil, while developing under the forest canopy, is shielded from the sun, and the roots keep the soil loose. Cleared of vegetation, however, the sun takes over and bakes the soil into a hard material (*laterite* comes from the Latin word for “brick”) that doesn’t allow much water to soak into it, or roots to find spaces to grow. Many buildings in tropical climates, such as the temples at Angkor Wat in Cambodia, are built of laterite. Even the application of fertilizer to such soil would not be beneficial. Farms are therefore soon abandoned, a new section of rain forest is cut down, and so on—thus the development of one farm can cause the destruction of a vast amount of rain forest. This process of deforestation also destroys the habitats of many animals and plants, ultimately causing some of them to become extinct.

Pedocal soils—*ped* for soil, *cal* for calcium carbonate—are found in drier climates; they leach less extensively, and soluble materials remain in the soil, especially in the B-horizon.

Plowing the rich prairie soil with a tractor, South Dakota, c. 1920 (From the collections of the Library of Congress)

Where calcium carbonate is present the soil is alkaline, and where it becomes dense it forms a tough cemented layer called caliche.

Objections to the above historical classification of soils centered on the notion that it did not take into account variations in bedrock composition, soil texture, and other characteristics. Many new attempts at classifying soils have been developed and adopted by different countries for their own needs, taking into account the various factors that produce soil: variations in composition and texture, and the bedrock whence it came. UNESCO uses 110 different types on its soil map of the world, while the U.S. Department of Agriculture has developed a classification that contains ten orders that are subdivided further into suborder, great group, subgroup, family, and series; there are about 12,000 soil series.

A brief look at this classification gives a good idea of the range of soil types, because it is based on appearance, nutrient status, organic content, color, and climate: entisols, soils with layering just forming and little structure; vertisols, containing clays that expand when wet and contract when dry, capable of mixing the upper layers; inceptisols, young soils with weakly developed horizons, especially the B;

aridosols, soils of deserts and semiarid regions, often saline or alkaline, with little organic matter; mollisols, grassland soils and forest soils, sometimes rich in calcium, with a thick layer of organic material; spodosols, arid soils with organic-rich A-horizon, and a B-horizon containing organic matter and iron leached from the A-horizon; alfisols, including most acid soils with clay-enriched B-horizon; ultisols, similar to alfisols but weathering is more advanced, including clay and some lateritic soils; oxisols, more weathered than ultisols, and includes most laterites; histosols, bog-type soils.

The formation of soils is complex, and they can vary over short distances even though the bedrock is similar. In a valley, for example, one valley wall may be warm and sunny and the other shady and moist, while the valley floor is wet. These conditions determine the type of vegetation that will grow, which ultimately plays an important role in determining the type of soil and the organisms within it.

—Sidney Horenstein

See also: Climatology; Deposition; Erosion; Geology, Geomorphology, and Geography; Topsoil Formation

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Source of Crops

See Agriculture, Benefits of Biodiversity to

Speciation

Speciation is the formation of one or more descendant species from an ancestral species. Species are here understood to be groups of interbreeding organisms whose members are generally incapable of breeding with members of other such groups.

Speciation is a crucial aspect of the evolutionary process. Little progress was made in understanding speciation as long as it was felt that species evolve naturally as time goes by, in a gradual progressive manner, through simple natural selection. The feeling ever since Darwin was that, were the fossil record complete and fully studied, the nature of the evolutionary process is such that it would be impossible to draw lines between ancestral and descendant species (the notion of "phyletic gradualism"; see also Punctuated Equilibria).

However, the discreteness of species finally earned the serious attention of evolutionary biologists. Geneticist Theodosius Dobzhansky developed the concept of "isolating mechanisms"—that is, a list of factors that would interrupt the reproductive process between different groups within the same species, a process he felt was the necessary first step toward forming one or more descendant species from an ancestral species.

Biologists draw a distinction between "sympatric" species (species living in the same place at the same time), and "allopatric" species—contemporaneous species that live in different places. Controversy has raged for years on whether or not it is possible to disrupt reproductive connections sufficiently in sympatry so that two fully fledged species could evolve out of a single species. The consensus for most of the twentieth century was "no"—although examples involving parasites who live on obligate hosts are among some of the categories of sympatric speciation that have begun to gain acceptance in recent years.

Allopatric speciation remains the central part of speciation theory—simply because all biologists agree that separation of parts of a single species into two or more regions such that contact is rare or impossible gives a head start to the process of establishing two sets of populations that can no longer interbreed. The further idea is that plant or animal species will evolve in isolation so that enough genetic differences accumulate that, should the geographic barriers ever break down and members of both sets of isolated populations come back into contact with each other, they will either (1) attempt to mate and be successful—forming hybrids that are perfectly normal—in which case speciation has not occurred; or they will (2) breed successfully, but the hybrids (generally recognizable as such) form a thin line along a zone of contact; whether or not full hybridization eventually occurs (and, again, speciation fails), or whether the hybrid zone eventually disappears (leaving two different, noninterbreeding species) depends on future events, and it is not certain in such instances whether speciation will succeed or fail; or they will (3) attempt to mate, but their offspring will not be viable (hardy); or they will (4) attempt to mate, but without any offspring at all, as too many genetic differences will have accumulated to allow fertilization to occur; or (5) they won't even recognize each other as appropriate mating partners in the first place. Possibilities 3 and 4 fall into Dobzhansky's "postmating isolation" categories, while possibility 5 is an example of "premating" isolation—considered an even stronger form of isolating mechanism in the speciation process.

Indeed, some biologists have pointed out that selection can simply change the normal mate recognition signals (whether visual, vocal, or chemical) when populations are physically isolated—just to keep mating going on within each of the separated populations. If these signaling systems change enough, should contact ever reoccur, the members of the two groups will simply not recognize each other as prospective mates at all.

Many paleontologists have, in recent years, come to the more controversial conclusion that much if not most anatomical change in evolution occurs during speciation events, and, further, that speciation events tend to occur in bunches within single regional ecosystems—usually following an episode of extinction of many species from physical environmental factors (see Evolution).

In any case, it is known that speciation can be exceedingly rapid. For example, Lake Victoria, home to hundreds of species of (now severely endangered) cichlid fishes, is known to have dried up almost completely only some 12,000 years ago. It is thought that the fishes living in the lake prior to the drying event all became extinct—with surviving species coming down to replenish the lake's ecosystem from the tributaries that empty into Victoria's basin. Thus biologists are forced to conclude that most of the hundreds of species now living in Lake Victoria evolved from a relatively few ancestral fish species in the scant time of 10,000 to 12,000 years! Such species "flocks" have always proven difficult to understand in terms of standard allopatric speciation theory: how does reproductive isolation occur within a single lake?

It turns out that many of the fish species currently living in Lake Victoria breed only in particular places; for example, some need a pebbly bottom, which occurs only sporadically around the margin of the lake. This has led some biologists to suggest that these local breeding populations, with the fish so closely tied to relatively small patches of substrate, are in fact miniversions of allopatric environments, where physical isolation of even a few thousand years is sufficient for behavioral, anatomical, and genetic divergence—and therefore true speciation—to occur. Other biologists prefer to imagine isolation occurring in the tributaries themselves, with periodic extinctions weeding out species living in the lakes, and new species evolving outside the system and periodically invading the waters of the lake. Other lakes of the great East African Rift System have similar flocks of cichlid fishes—and the mystery of their speciation patterns has yet to be fully resolved.

Finally, it should be noted that botanists, in particular, have suggested additional ways that speciation can occur. Polyploidy, a genetic condition much more common in plants than in animals, can result when two related species hybridize with one another. The number of chromosomes in cases of polyploidy doubles (that is, rather than having the chromosomes match up as in normal sexual reproduction); the offspring, with twice the number of chromosomes of either parent, can mate only with other polyploid individuals produced the same way. But they can, then, mate perfectly well with one another—yielding an example of speciation through hybridization.

—Niles Eldredge

See also: Evolution; Evolutionary Biodiversity; Natural Selection; Punctuated Equilibria; Species

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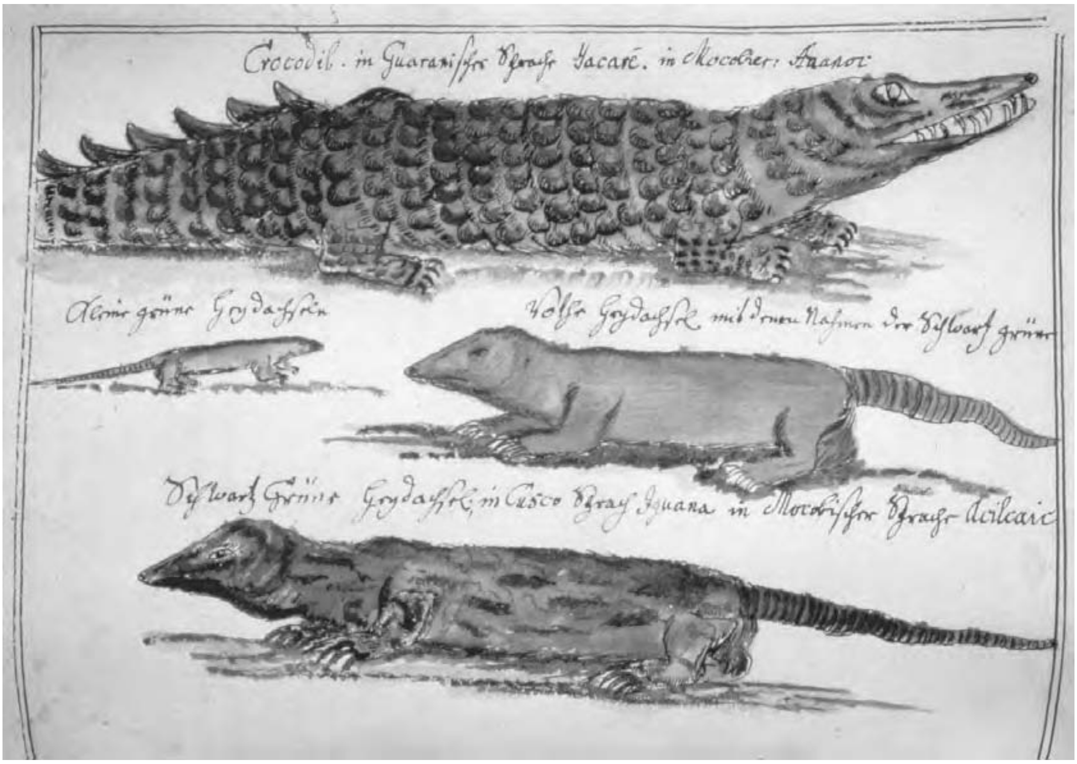
Species

The species is the lowest generally recognized division of the Linnaean hierarchy of life. Thus every species belongs to a genus, while genera are division of families, and so forth. Every species that has been discovered and named by biologists is called by both its generic and specific name: for example, our own species is called *Homo sapiens*. *Homo* is the genus to which our species "*sapiens*" belongs (along with other fossil species, such as *Homo erectus*). Generally, scientific names of species are italicized; once the name has been spelled out completely in a text, it is permissible to write it in abbreviated form—for example, *H. sapiens*.

Thus species are a category of life, and every particular example—again, such as *Homo sapiens*—is an actual historical entity, referred to as a taxon (pl.: taxa) by systematists. Taxa can be of any rank: thus a family in the Linnaean system is another category, higher than the species; Family Hominidae, to which our species belongs, is also a taxon—a particular collection of related species belonging to several different genera.

Biologists are still uncertain how many species of plants, animals, fungi, and microorganisms currently inhabit the earth. So far, just under 2 million species have been discovered and named. Although the great majority of bird and mammal species are thought to have been discovered and already named, many fishes and marine invertebrates, as well as tropical plants and insects, are thought to remain undiscovered. Bacteria and other microbes are probably the least well known of all the major divisions of life.

In view of the rapid loss of species currently underway (see Sixth Extinction), biologists have redoubled their efforts to find and name as many species as possible before they are lost to extinction. And they have tried to sharpen their estimates about the total number of species currently in existence. According to one estimate (based primarily on the rate



Drawing of various species of South American animals by Father Florian Paucke, a Jesuit missionary. Paucke (1719–1789) produced detailed drawings of flora and fauna. (Bojan Brecelj/Corbis)

of discovery, plus estimates of the number of species per hectare typically found in places like tropical rain forests and coral reefs), there are at least 10 to 12 million species on earth. Other estimates range even higher—more than 100 million. That we have traveled to the moon but still do not know within an order of magnitude how many species there are on earth is both testimony to the state of our biological ignorance and a direct signal of how much exploratory and analytic work needs to be done on species.

Most of the species that have existed on earth are already extinct—and, of course, we have no precise idea how many species have existed since the inception of life more than 3.5 billion years ago. But the process of evolution continually produces new species (through the process of speciation), and species diversity is considered to be at least as high now as it ever was during the history of life.

Species occupy a special place in evolutionary biology. Unlike the other categories of the Linnaean hierarchy, which are simply ever-larger collections of related species, species are the bottom-line division. Species are composed of organisms, not taxa, and organisms within a species are capable of interbreeding—of producing offspring with one another. Thus, from the standpoint of evolutionary biology, species can be defined as "groups of organisms capable of interbreeding." This definition (a shortened version of the so-called biological species concept) is important because it stresses the genetic connectedness that holds a species together. This species concept is most directly applicable to sexually reproducing organisms, such as most animals (for example, mammals, birds, insects) and higher plants; it is somewhat more problematic when it comes to strictly asexual organisms and microbes—perhaps especially bacteria. Yet bacteria and many forms of life that reproduce asexually are also capable of exchanging, and occasionally do exchange, genes between one another, so in an extended sense, the notion of species as the greatest collection of breeding individuals applies to all of life.

As reproductive entities, species can be thought of essentially as packages of genetic information. Like each individual organism, every species has an origin (a beginning), a history, and an end (through extinction). Species tend to be very long-lived: The average age of a marine species is between 5 and 10 million years, and some species last a lot longer than that. Life on land seems a bit more precarious, and rates of evolution (origination of species, or "speciation") and extinction are on average faster on land than in the sea. Terrestrial mammals, for example, seem to last only about 1 to 3 million years.

Yet such longevities of species came as something of a surprise to evolutionary biologists. Darwin himself originally felt that species, in a sense, do not exist as real, stable entities. Darwin's task was to convince the world that life had evolved; the biology of his day saw species as immutable—permanent entities each created separately by a Divine Creator. To show that there could be connections—evolutionary transitions—between species, Darwin essentially argued that species are transient entities: The different kinds ("species") you might see visiting the bird feeder in your backyard might look sharply different from each other, but those differences, Darwin thought, are bound to change. More closely related species resembled each other still more closely in the not-so-distant geological past, and they are bound to deviate from one another still further as time goes on and evolution keeps working.

Thus, to Darwin and most other early evolutionary biologists, species are ephemeral entities—almost like progress reports of a continual process of evolutionary transformation. However, we now understand from the fossil record that species have discrete origins and persist, usually recognizably unchanged ("stasis"), and eventually become extinct.

An important key to the puzzle of species—that is, what species are and the role they play in the evolutionary process—came in the work of the geneticist Theodosius Dobzhansky and the bird systematist Ernst Mayr (see also Evolution; Speciation). Previously, biologists looking at modern species thought of them as collections of similar organisms that happen to interbreed. They did, however, realize that sometimes females of different species, such as some American warblers and finches, look more like one another than they do the springtime males with which they pair up, occupy a territory, and produce one or more broods of offspring. Naturally, biologists were forced to keep males and females together in the same species, even though, strictly speaking, sometimes some members of a species looked more like members of other species.

Dobzhansky and Mayr, in effect, simply reversed the logic. Species, they said, are breeding communities—the largest group of animals who share adaptations allowing them to interbreed. For that reason, the individuals within a species share a pool of genetic information—and that is why the members of a species tend to resemble one another more closely than they do members of other, even closely related, species. That males from different closely related species may appear more different from one another than females, at least among some birds, simply reflects the reproductive adaptations that ensure that females will mate with appropriate males and not waste time selecting mates with which their reproductive efforts would end in failure (though occasionally between-species matings are successful—a phenomenon known as hybridization).

In addition to developing the biological species concept, Dobzhansky and Mayr thought that, ironically, Darwin never did adequately address the "origin of species" in his book of that name. Because Darwin saw species as transitory stages of a continual evolutionary stream—lineages constantly being modified gradually by natural selection—he failed to address the question of why most species most of the time do appear to be discrete (that is, noticeably different from one another). Dobzhansky thought that such discontinuities between species must be a direct result of the evolutionary process—and not, for example, simply a matter of the extinction of intermediates that once, in the past, bridged the gap between two particular species.

Thus Dobzhansky and Mayr developed the notion of allopatric speciation (see Speciation)—the idea that new species evolve essentially by budding off from their ancestral species when a portion of a species becomes physically isolated from the main section of the species. If natural selection modifies the features (and, of course, the genetic information underlying those features) far enough in the isolated population, the ability to interbreed could easily be lost, as there would now be a genetic mismatch.

Although it is still a somewhat controversial matter, the data of paleontology strongly suggest that most adaptive evolutionary change occurs in conjunction with the origin of new reproductive communities—in other words, new species. But why would the attributes of organisms in a species devoted to such things as energy procurement (for example, finding and consuming prey, in the case of a carnivore such as a lion) change at the same time as new reproductive adaptations are evolving?

One plausible explanation was given in Mayr's idea of peripheral isolates. Species have definite ranges in space as well as in time. Only a very few species are known to exist all over the earth—and even then not in absolutely all habitats. *Homo sapiens*—our own species—is one example. Most other species are restricted to portions of continents. For example, the red-bellied woodpecker is an Eastern bird species of the United States, moving up North in recent years from its ancestral southerly climes as global temperature has been on the rise. From the Rocky Mountains westward, other closely related species of woodpeckers replace the red-bellied woodpecker. The question then becomes: What restricts the ranges of species?

Two factors in general govern the geographic distribution of species. One is simply history: A species might very well be able to occupy an area, but its ancestors simply never got there. There are no bears, modern or ancient, in Africa, yet there are bears in India and many other places where habitats seem rather similar to those known in Africa. Bears simply never got there. Moreover, we know that the movements of humans, both inadvertently and deliberately, have transported species to places far from their native habitats—and many of them have thrived, often to the detriment of species native to their new homes (see Alien Species, Introduction of).

On the other hand, the map of the distribution of any modern species has boundaries—boundaries subject to change as environments change (as in the case of the red-bellied woodpecker, above; see also Habitat Tracking). The reason why those boundaries are there at any particular moment, though, is that the organisms of each species have environments to which they are adapted—in terms of available food, temperature, rainfall, and the like. Things are less lush for a species as you approach its boundaries—for the simple reason that the environment itself is marginal for a species as you observe it from its center to its edge.

Now consider Mayr's peripheral isolates, a population living near the margin of a species' range, where life is more difficult than it is for the organisms of that species living near the center of the range. If something happens—a river changes course, or a section of land becomes too arid, or the like—thus cutting off the marginal population from the members of the species nearer the center of the geographic range of the species, and if there is the appropriate genetic variation, natural selection is likely to quickly modify the adaptations of the organisms in this peripheral population, in effect "redefining" the relatively harsher conditions at the periphery of the ancestral range as the new optimum, preferred habitat. Rapid adaptive change is likely to occur in the process of budding off a new species from the ancestral species.

After their origin, and assuming that the new species survives (many newly evolved species are thought to go extinct quickly—a sort of species-level analogue to infant mortality), species are apt to remain very stable for long periods of time—contrary to Darwin's original supposition. Two factors seem to underlie this phenomenon of so-called stasis: habitat tracking, and the geographic structure of species themselves.

Habitat tracking occurs when the environment changes and, instead of natural selection constantly modifying a species to keep pace with that environmental change, the range of a species shifts as familiar habitat spreads to new locales that the species can easily reach. The recent change in the range of red-bellied woodpeckers, for example, in response to global warming is an example of such habitat tracking.

But it is the geographic structure of the internal genetics of species that seems to be most important in causing the relative lack of evolutionary change that most species exhibit throughout their multimillion-year histories. Most species are broken up into local populations that are parts of different ecosystems. Consider, for example, the American robin, the species *Turdus migratorius*, a species of thrush. This species is found throughout North America, extending its range far to the north to forage and breed in the summer months. In the Adirondack Mountains of New York state, this bird lives in dense, moist forests. It is also found in sandy, sunny coastal habitats of the Atlantic Coast—and rocky habitats of the Pacific coast. In between, it can be found in suburban gardens and in the arid, desertlike environments of the Southwest. It is as at home in high altitudes as it is at the coastal shorelines. In short, robins are ecological jacks-of-all-trades.

Imagine, then, the different sort of existence a robin leads in the moist, cool woodlands of the American Northeast—as compared, say, with life at an elevation of 6,000 feet in the arid Southwest. The conditions—amount of rainfall, foodstuffs, potential predators, even potential diseases—will be very different in those places, a reflection of the very different physical environments, hence ecologies, of those regions. Natural selection will be acting very differently in those places—and in all the other different ecological settings where robins are found. In other words, the very patchiness of species distribution—divided up as nearly all species are into local populations integrated into very different local ecosystems—virtually ensures that no species is destined to develop gradual evolutionary change all in the same direction across the entire range of a species. Rather, local populations each have their semi-independent histories, which condition is bound to lead to little or no net genetic (that is, evolutionary) change for the species as a whole.

Species also become extinct. As we have seen, the vast majority of species that have ever lived have already become extinct—died of natural causes. Although any species might independently dwindle to the brink of extinction for a variety of reasons, the kinds of environmental changes that in essence go too far too fast (so that habitat tracking, and hence survival, are impossible) are generally apt to drive a number of species living in a region to extinction at more or less the same time. The history of life as revealed in the fossil record suggests that most species come into existence with others in its regional ecosystems at about the same time (joining those already there); all of these species survive for roughly the same interval of time (often for millions of years), but then many tend to disappear at about the same time—victims of extinction as environmental change disrupts and modifies the habitat. The cycle then starts over again—in episodes that have been called "turnover pulses," or periods of "coordinated stasis." Thus species do not live in a vacuum: the evolutionary history of each species is usually closely connected to the origins, histories, and extinctions of other species living in the same general region.

—Niles Eldredge

See also: Alien Species; Evolution; Evolutionary Biodiversity; Extinction, Direct Causes of; Habitat Tracking; Human Evolution; Linnaean Hierarchy; Punctuated Equilibria; Sixth Extinction; Speciation

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Spiders

See Arthropods, Terrestrial

Sponges

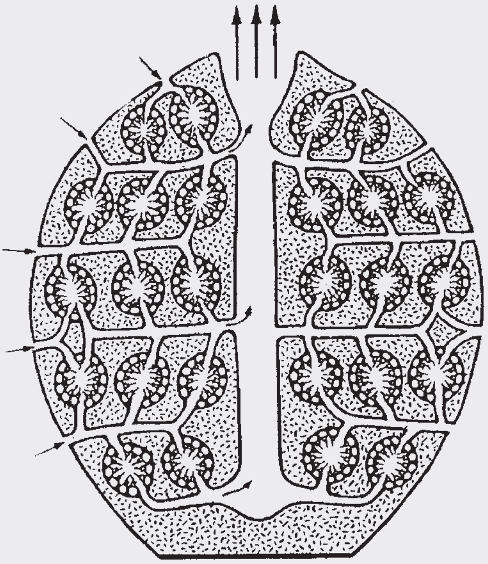
The body plan of members of the Phylum Porifera, known as sponges, is perhaps the simplest among living animals. Sponges contain few different cell types, and these are not organized into the distinct tissues that characterize members of other animal phyla. Sponges are also relatively uniform in manner of life—they are all sessile, aquatic, and feed on particles suspended in water. Despite this simplicity of form and function, sponges are an important component of animal diversity in marine and freshwater habitats (with at least 5,000 living species)—and they have been since they appeared as fossils in the late Precambrian. Sponges play vital ecological roles in many aquatic habitats, especially coral reefs, and because they are thought to be the most primitive living animals, they also play an important role in studies of animal phylogeny.

Living sponges are divided into three classes: the Calcarea, Demospongiae, and Hexactinellida. Members of the first two groups make up the vast majority of known species, and much of what follows will describe these groups. Hexactinellids are quite different and will be discussed separately.

Although some species are consistently tube- or vase-shaped, the bodies of many

Figure 1

The Internal Anatomy of a Demosponge

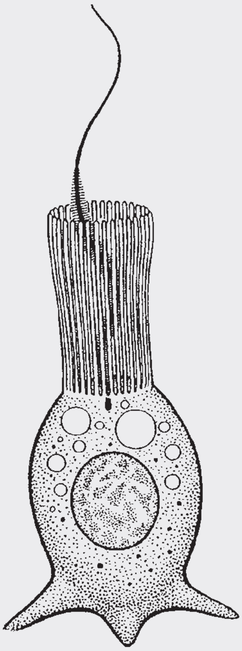


Source: Pearse, Vicki, et al. 1987. *Living Invertebrates*. Palo Alto: Blackwell Scientific Publications. p. 79. (Reprinted with permission)

Note: Arrows show water flow patterns through the body. The outer surface of the sponge is covered with pinacocytes. Water enters canals through ring-shaped pinacocytes, propelled by the flagellae of numerous choanocytes (in this sponge, the choanocytes are organized into distinct chambers). Used water is passed into the spongocoel and eventually out the osculum.

Figure 2

A Sponge Choanocyte



Source: Pearse, Vicki, et al. 1987. *Living Invertebrates*. Palo Alto: Blackwell Scientific Publications, p. 77. (Reprinted with permission)

Note: Each choanocyte has a collar of fine microvilli, from which a long flagellum protrudes. The beating flagellae of many choanacytes propel water through the canal system of a sponge.

sponges lack any obvious symmetry, taking the form of irregular encrustations or lumpy or branching masses of tissue. This irregularity masks a consistent organization at the cellular level. Sponges are organized around a system of canals through which they pump a unidirectional water current (see Figure 1). The outer surface of the body is lined by a single layer of flattened cells, the pinacocytes. Some pinacocytes are ring-shaped, with the central hole serving as a pore through which water enters the sponge's water-pumping system. The canals of this system may be lined in part with more pinacocytes, but they also include regions lined with distinctive cells called choanocytes (see Figure 2). Each choanocyte bears a collar of microvilli from which protrudes a single flagellum. These flagellae provide the motive force for pumping water through the sponge. The choanocyte-lined canals eventually lead to a central chamber, the spongocoel, which opens to the outside by one or more large openings, or oscula.

Between the outer pinacocyte and inner choanocyte layers lies a thin, gelatinous matrix, the mesohyl. The mesohyl contains mobile cells, the amoebocytes, and also structures that contribute to the shape and firmness of the

A cloud sponge. Sponges are perhaps the simplest of living animals, but they make an important contribution

sponge—for example, collagen fibers and mineralized spicules. The composition of these structural elements varies among sponges and plays an important role in their systematics. For example, members of the Class Calcarea have spicules made largely of calcium carbonate; in demosponges the spicules are siliceous. Spicules come in an astonishing array of shapes and sizes. The mesohyl of some demosponges also includes particularly robust arrays of collagen fibers that form a meshlike network, called spongin. When the body of one of these sponges is dried and cleaned, all that remains is the spongin. This material has been used for centuries by humans as "bath sponge."

Water pumped through the sponge by the choanocytes provides food and oxygen, as well as a medium for carrying out metabolic wastes. As water passes over the choanocytes, suspended particles are captured on their microvilli and taken into the cells, where they are digested. Very small particles, including bacteria, can be removed from the water in this way. Used water passes into the spongocoel and out the oscula. Because sponge canal systems may be very convoluted and contain large numbers of choanocytes, sponges can process water at enormous rates. Some sponges also take advantage of ambient currents to help drive water through their canal systems.

Unlike other animals, sponges have no internal systems for transporting food, respiratory gases, or metabolic wastes. Most cells are in direct contact with or at least very near the water passing over the sponge or through the canal system, and each cell exchanges material with this water independently.

Most sponges are hermaphroditic. Adults

typically release sperm into the seawater; sperm are captured by choanocytes of neighboring sponges and transported to the mesohyl, where they fertilize eggs. Embryos are brooded in the mesohyl until they are released as larvae that settle to the bottom and metamorphose into juvenile sponges.

The above applies to the most frequently encountered sponges, members of the Calcarea and Demospongiae. Calcareous sponges are all marine. Demosponges, which include most living sponges, occur in both marine and freshwater habitats. They are often brightly colored and may reach several meters in diameter. Some demosponges that contain substantial amounts of spongin are harvested for sale as bath sponges. A few species bore into calcareous substrates and are important eroders of coral reefs. Demosponges are also actively studied, because many contain bioactive compounds that may be useful as drugs.

A few demosponges have evolved an unusual body form—a massive calcareous basal skeleton on which rests a thin film of sponge tissue containing siliceous spicules. When living species with this body form were first discovered, in cryptic tropical marine habitats in the 1960s, they were accorded status as a separate class, the Sclerospongiae. The discovery of living "sclerosponges" allowed paleontologists to recognize previously problematic fossil taxa—archeocyaths, chaetitids, sphinctozoans, and stromatoporoids—as sponges. Members of these groups were extremely important reef-building organisms in the Paleozoic and Mesozoic eras.

Hexactinellid sponges are so peculiar that some argue they merit placement in a separate phylum. Their spicules are characteristically six-pointed and siliceous, and they are sometimes fused to form a rigid internal skeleton. Spicules are mostly surrounded by a few large syncitia—multinucleate cells—rather than the typical sponge construction of layers of mononucleate cells. Even the choanocytes, otherwise characteristic of all sponges, are unique in form. Although mostly separate from the rest of the syncitial body, they contain no nuclei. Hexactinellids are exclusively marine in habitat.

Sponges are thought to have evolved from protists called choanoflagellates, which closely resemble choanocytes. Phylogenetic analyses suggest that sponges share a common ancestor with the rest of the metazoans. Relationships among the three living classes of sponges are not well resolved.

—*Bruno Pernet*

See also: Evolutionary Biodiversity; Protoctists

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Starfish and Brittle Stars

See Echinoderms

Stasis

See Habitat Tracking; Punctuated Equilibria; Species

Subsistence

At the most fundamental level, subsistence means survival: eating food, drinking water, obtaining clothing and shelter, and reproducing. The term generally denotes a mode of life in which production is engaged in for the primary purpose of consumption. The Alaska state legislature, in the 1978 Subsistence Act, defined subsistence as "customary and traditional uses" of fish and game for food, clothing, and other specific needs. Whether the term is used in the broad or narrow sense, the fruits of subsistence labor go to meet the needs of the family or community, rather than entering a local trade or larger market economy. Continued access to territory for the purpose of acquiring foods, medicines, raw materials, and other goods is necessary in order for a community to maintain a subsistence way of life. Hunter-gatherer societies past and present have lived off the land by tracking wild herds, picking berries, and catching fish. Shifting cultivation, also known as swidden or slash-and-burn agriculture, is a principal means of subsistence in many parts of the world: clearing and burning fields, planting genetically diversified crops in rotation, and allowing fields to lie fallow in rotation, in order for the soil to replenish its fertility. The increasing pressures of population, agriculture, and development threaten surviving traditional modes of economic life whose sustainability remains dependent on ecological factors.

The term *hunter-gatherers* describes societies in which the principal modes of sustenance are hunting, fishing, or collecting wild plant foods and fungi. Few African peoples survive today as hunter-gatherers compared with the ancient past, when for millennia hunter-gatherers lived over much of the African continent. Much of our information about African hunter-gatherer societies of the remote past is based on observing the activities of more recent practitioners. In southern Africa, hunting and gathering were virtually the only means of subsistence until about 3,000 years ago. Nomads tracked game animals and fresh sources of food, carrying their mobile settlements with them. Subsistence producers eventually, however, had nearly all of their land and livelihood co-opted by pastoralists, gardeners, and agriculturalists. Those bands who remained were gradually assimilated into neighboring peoples. The Khoisan people in the arid Kalahari region are the largest African group still practicing a hunter-gatherer way of life. They are the heirs to an ecosystem that has provided continuous subsistence for at least 9,000 years. What is today a desertlike environment went through wetter periods over the past 11,000 years, and pockets of water moisture remain below the surface of the sand. Drought-resistant grasses, fruit trees, and thorn bushes draw on this moisture and provide fodder for herds of large game. In the Okavango swamplands of the northern Kalahari, fishing rather than game hunting was the principal subsistence activity.

By 10,000 years ago African hunter-gatherers had successfully developed tools and microlithic blade technology for acquiring food. Axes, projectile points, and traps were used in forest areas in the Middle and Later Stone Ages. In the savanna, Later Stone Age hunters were expert at lethal weaponry, killing animals with bow and arrow, finely carved multipronged spears, and poisons. Small, roving bands of hunters tracked and felled large prey species of hoofed mammals. Small game was caught in snares and traps or hunted with dogs and clubs, and reptiles and bird eggs provided a dietary supplement. Bones were used to make tools, ornaments, and weapons, while hides were fashioned into clothing and carrying bags. Contemporary hunter-gatherers obtain more than half of their nutrition from gathered foods. Even though plants are subject to seasonal unavailability and climatic cycles, they are more reliable and plentiful food sources than game animals. Men probably covered great distances on hunting trips, while women were the primary gatherers and caregivers for children. They used carrying bags to

A hunter from the G/wi clan, hunting springhares in the Ghanzi District of Botswana. The hunter-gatherer culture of the Kalahari has been largely destroyed by loss of territory, reductions of wild plants and game, and assimilation of hunter-gather clans into cultures established by colonial settlers. (Peter Johnson/CORBIS)

collect fruits, and sharpened sticks to dig up tubers and roots; they also caught highly nourishing termites, caterpillars, and locusts.

Early bands of hunter-gatherers lived in small, mobile groups of kin, allowing them to survive by adapting to environmental conditions. Khoisan hunter-gatherers have lived in the Kalahari Desert for thousands of years, coming in contact with herders and farmers for the past two millennia. They hunted antelopes, birds, and small game, but meat was only a small part of their diet; the principal foods were gathered plants such as the sour plum and baobab fruit, or the mongongo nut in areas where the !Kung lived. In the dry south, water was extracted from groundroots and melons, and sucked from the earth through a straw during the winter drought season. Meat was divided and distributed to the community by the hunter making the kill, who gained prestige and status through his successful actions. The more abundant edible plants were shared with close kin.

The hunter-gatherer culture in the Kalahari has been largely destroyed by the loss of territory to outsiders, colonial settlers hunting natives like animals, assimilation and dependency, poverty, and disease. Only a small number of Khoisan continue to subsist principally through hunting and gathering; about 95 percent of modern Khoisan people are herders or farmers. Small land parcels in Namibia and Botswana are reserved for Khoisan hunter-gatherers, although the future of their territory remains very much uncertain.

Assessments of the socioeconomic value of biodiversity have tended to focus on three aspects of interactions between human societies and the ecosystems of which they are a part: ecological functions such as conservation and climate regulation, commercial use such as resource extraction, and subsistence values—the provision of goods for local consumption, independent of translocal market economies. The latter has been the most undervalued and ignored by researchers and policy-makers alike. Although the role of subsistence production in industrialized society is economically and nutritionally marginal or even negligible, for local and indigenous populations in tropical rain forests, Arctic and sub-Arctic tundra, and other rural ecosystems it remains an important part of the regular diet, small-scale, nonmarket-oriented economy, medicinal healing practices, and traditional ways of life. One study in the 1980s found that hunting remained an indispensable source of protein for people living in sixty-two developing countries (Secrett, 1986, cited in Shiva et al., 1991, p. 26). In some places such as areas of the Russian north, subsistence production has actually increased in the past decade as a crucial supplemental source of provision in economies of scarcity. Many other people remain dependent to a large extent on the continued ability to produce food, firewood or other fuels, and medicines for their own use. The rights and resources of sustainable practices are threatened by shrinking habitat, species loss, fluctuating yields and harvests attributable to global climate change, governmental regulation of land use and hunting and fishing rights, large-scale development projects imported by multinational corporations and transnational organizations, and the rise of intellectual property laws that define genetic diversity as a patentable laboratory process but exclude or fail to recognize the contributions of farmers, growers, and breeders over the centuries.

The preservation of indigenous knowledge for subsistence cultivators to build on an existing base of diversified agricultural production is known as extension. The goal is to create alternatives to eliminating diversified agricultural production and replacing it, either with cash crops or with monoculture varieties of high-yield grains that deplete the soil's fertility and whose genetic uniformity renders them susceptible to insects and disease. Agronomists and commercial technicians often look at small-scale subsistence producers as obstacles to development. Clashes in cultural value systems, and asymmetrical socieconomic power and control over resources, lead to conflicts over policy matters when the economic projects of modernization may be at odds with the way of life and environmental practices of marginalized rural indigenous minorities.

Scientists and aid workers are finding that local indigenous knowledge is often the most valuable resource for improving subsistence techniques. Sharland (in Warren et al., 1995), for example, reports that before civil war disrupted local subsistence patterns in the 1990s, the Moru people of southern Sudan practiced shifting cultivation, farming a staple crop of sorghum mixed with other grains to provide the mainstay of their diet, selling or bartering surplus produce and vegetables. They also raised some livestock, keeping poultry at the household level, and supplemented their intake with wild foods (from tubers to insects), hunting, fishing, and gathering honey in the bush. The local cultivation repertoire included traditional techniques of preparing mild poisons from forest fruits and bulbs to repel termite infestations, and protecting groundnuts from marauding foxes with bitter infusions of mahogany bark. The particular environmental knowledge and plant terminology of women, who are the primary agriculturalists in Moru society, helped outside scientific advisors identify pests and crop diseases, as well as effective countermeasures. Data from India and South America similarly show a wealth of ecological information in local practices, beyond those identified by outside scientists and researchers.

In Alaska the discovery of oil on the North Slope led to a push for the settlement of native land claims, so that the Alaska pipeline could be built. Under the 1971 Alaska Native Claims Settlement Act, Alaska native people were organized into regional and village corporations holding title to more than 44 million acres; in exchange all aboriginal land claims were extinguished, including hunting and fishing rights. The 1978 Subsistence Act established the priority of hunting and fishing by rural, mostly native residents over sport hunting and other uses of wildlife. The distinction between management for subsistence and sustainability, and potential depletion through commercial development and the unregulated activities of tourists and sportsmen, is a contested point in Alaska today. There is a need for supplementary cash income to drive the subsistence mechanism in the present age. In order to live a subsistence way of life successfully in modern Alaska, people need to buy snowmobiles and kerosene. The Alaska National Interest Lands Conservation Act defined subsistence uses to include handicraft production using nonedible wildlife products, if the animals were hunted for consumption, for barter and customary trade. The act made provisions allowing for a federal takeover of wildlife management. This possibility, which would remove state control over local subsistence activities, is opposed by many native Alaskans on the grounds that it would leave the native corporations without a voice in the management of fish and game on traditional lands, threatening the survival of the rural subsistence way of life.

—*Thomas R. Miller*

See also: Conservation, Definition and History; Cultural Survival, Revival, and Preservation; Ethnoscience; Indigenous Conservation; Land Use

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Succession and Successionlike Processes

Directional changes in the composition and organization of ecologic communities over time are collectively known as succession. The process of succession is usually associated with a single local community: the initiation of a new community at an unoccupied site is referred to as primary succession; recovery following a disturbance is termed *secondary succession*. Secondary succession is one of the most thoroughly studied developmental phenomena in ecology, most of the studies having been carried out in temperate forests that featured localized disturbances and subsequent recoveries. The best-known descriptions are of "old field successions," in which plant communities recover from farming activity, involving abandonment of cleared patches and serial recolonization from a regional species pool. Despite the level of interest in succession, however, there is a continuing debate about deterministic versus probabilistic factors involved in the processes of change, the relative importance of internal biotic control ("autogenic succession") compared with abiotic external forcing ("allogenic succession"), and whether only local communities undergo succession or if the process can be generalized to larger, more inclusive systems. All true succession and successionlike processes make up the developmental properties of ecologic systems collected under the term *temporal dynamics*. The study of these directional changes in ecologic systems has led ecologists to speculate about general, lawlike characterizations of nature since the late nineteenth century, and the level of interest has never abated.

The temptation to extrapolate and overgeneralize has been irresistible in studies of temporal dynamics. The urge to identify general processes that are like physical laws has usually led ecology into dead ends, because in many cases scaling considerations have been ignored. Some ecologists would use the term *succession* to refer to any directional changes occurring in various kinds of ecologic systems at any position in the so-called ecologic hierarchy: communities or local ecosystems, regional ecosystems, even the entire biosphere—all have been characterized as undergoing succession. Succession also is used to describe both biologically controlled transitions and those paced by outside, environmental changes. This has caused much confusion and is related to the inability of ecologists to settle on definitive concepts for the fundamental units of ecologic organization. In this summary, succession will be regarded as a developmental process restricted to local ecosystems and involving mostly internal dynamics.

Temporal Dynamics in General

Different kinds of developmental processes are associated with different kinds of ecologic systems; are controlled by either dominantly extrinsic or intrinsic adjustments or turnovers in composition; and may occur within the lifespan of one system or involve replacement of a previous system by a newly organized system. Smaller, more localized systems are associated with faster process rates; larger systems that contain such systems have more sluggish behavior and processes that encompass longer time spans. The important points are: different temporal dynamics characterize different levels in the ecologic hierarchy, and succession is only one of several kinds of changes that ecologic systems may undergo.

Primary succession—The initiation of a new local ecosystem at an unoccupied site. Earliest colonists have adaptations for broad dispersal, utilization of abundant resources, and rapid growth rates and high fecundities. As the system develops, these organisms are displaced or replaced by other organisms that were present from the beginning or that arrive subsequently, having weaker dispersal ability, resource specializations, and comparatively slow growth rates and low fecundities. Late arrivals are often superior competitors. The buildup of species in a local system produces spatial heterogeneity and ameliorates physical-chemical factors, potentially making way for the addition of other species. Species richness and diversity are low at first, then increase rapidly; if the system remains disturbance-free, supercompetitors will eventually dominate the system, producing low diversity again, but for different reasons. In this view of primary succession, the embedded processes result in the initiation of a new local ecosystem largely by means of colonization and internal interactions. Some ecologists refer to the end-product of succession as an equilibrium system known as the climax (better known as developmental maturity). The developmental stages are called seres. Biomass increases, nutrients are conserved more efficiently, and productivity declines in the course of succession (see Table 1). This entire process takes on the order of one to ten years in most aquatic environments, and ten to a thousand years in terrestrial systems, with much variation. A well-documented example is the reestablishment of terrestrial ecosystems now taking place on the slopes of Mt. St. Helens, a volcano that erupted in 1980 in Washington state.

Table 1
Immature versus Mature Stages of Succession of Ecosystem Properties

System Properties	*Immature*	*Mature*
Ecosystem energy flow		
Production/system respiration	>1 or <1	≈1
Production/biomass	Relatively high	Relatively low
Net system production	High	Low
Food web geometry	Simple	Complex
Nutrient cycling		
Mineral cycles	Open	Closed
Exchange rates	Fast	Slow
Importance of detritus	Little recycling	Efficient recycling
System structure		
Species diversity	Low	High
Heterogeneity	Disorganized	Organized
Symbiosis	Relatively rare	More common
System stability		
Overall stability	Relatively low	Relatively high
"Information" content	Low	High
Entropy	High	Low
Nutrient conservation	Low	High
Properties of organisms		
Habitat/resource specialization	Low	High
Body sizes	Often small	Relatively large
Life cycles	Often short	Long
Population growth	Rapid, unbounded	Resource-constrained
Competitive strategies	Colonization	Competitive exclusion

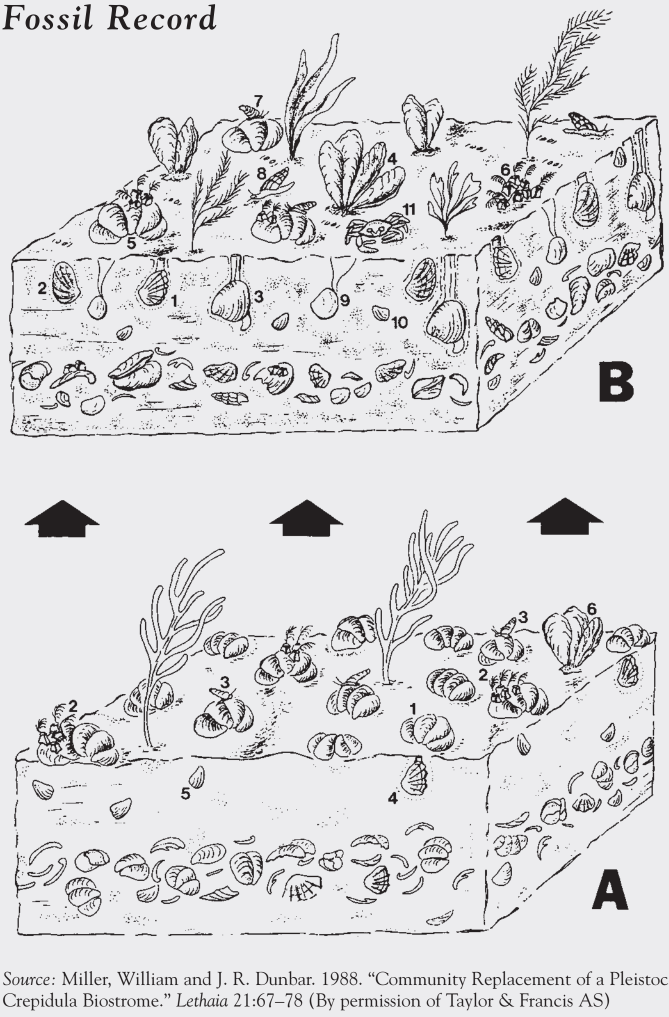
Source: Based on Odum, Eugene P. 1969. "The Strategy of Ecosystem Development." Science 164: 262–270.

Note: More recent work on succession shows the process to be less predictable than characterized here and to be subject to continual "resets," with few systems ever attaining idealized maturity or successional "climax."

Secondary succession—Recovery from a disturbance that is primarily controlled by internal dynamics and does not involve total collapse of the system. Many of the generalizations about primary succession apply. The internal dynamics consist of a changing network of population components and their interactions involving what are called facilitation (early arrivals modify a site to make survival of later arrivals more likely); tolerance (accumulation of species able to tolerate the developing conditions at a site, primarily reduced availability of resources); or inhibition (adding species with specialized survival strategies in the crowded neighborhood of populations undergoing gradual turnover). Secondary succession probably takes about the same amount of time as primary succession; it may occur repeatedly and often is reinitiated before a system has reached a dynamic equilibrium. Because of this, some ecologists think that the climax is an idealization, a condition rarely achieved in local ecosystems consisting of spatial mosaics at different stages of succession at any one time. In other words, ecosystems are almost always recovering from the last disturbance. An example is the patchwork of benthic marine ecosystems in Long Island Sound, each recovering from a different episode of dumping of dredged sediments.

Community response—Temporal changes in a local ecosystem paced by external environmental factors, such as seasonal fluctuation in climate or aperiodic habitat changes, not leading to a complete collapse of the system. This would include many examples of so-called allogenic succession; it occurs in stressful environments, settings characterized by frequent shifts in the environment, or locations that experience strong, unpredictable disturbances. An example would be the annual changes in species composition and community organization in a high-latitude lake controlled by high-amplitude seasonal cycles of temperature, runoff from the adjacent landscape, and chemical concentrations.

Figure 1. **Community Replacement Documented in the Marine Fossil Record**



Source: Miller, William and J. R. Dunbar. 1988. "Community Replacement of a Pleistocene Crepidula Biostrome." *Lethaia* 21:67–78 (By permission of Taylor & Francis AS)

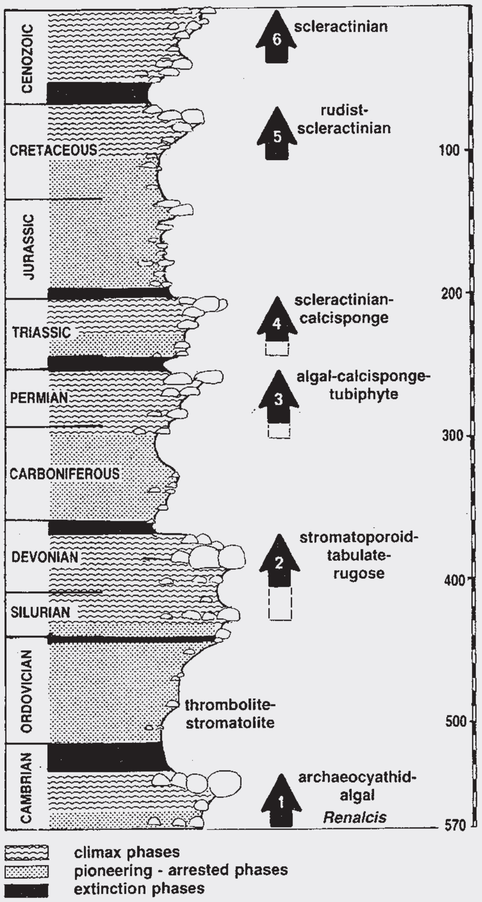
Note: This example from a Pleistocene embayment in what is now the outer coastal plain of North Carolina involved the replacement of a bottom community dominated by the slipper snail *Crepidula* with a more diverse community dominated by the clams *Anadara* and *Ostrea*. Patterns such as this one are common in shelly fossil beds deposited in low-energy environments and were once thought to be examples of ancient succession.

Community replacement—When interaction networks are disrupted and environmental tolerances of the component organisms are approached or exceeded, local ecosystems degrade and collapse. Collapse could be incremental when local extinction removes "hub" populations that have retinues of associated species depending on them for resources or habitat structure. Weakly interacting populations would disappear independently as the tolerance limits of different species are reached. A catastrophic collapse, eradicating all local populations in an ecosystem, could eliminate all of the organisms rapidly without regard for individual adaptations or interaction partnerships. Subsequently, a new assemblage of organisms could invade the area and establish a new ecosystem having a different composition, internal organization, and functional identity. Such transitions involve more than one local ecosystem and may take longer (perhaps on the order of 10 to 10,000 years) to take place than succession and response. Directional eutrophication and in-filling of lakes is usually cited as an example of allogenic succession. Because a series of distinctively different ecosystems are involved, replacing one another as the environment changes from deep water to bog, this is really a form of community replacement. In paleontology, many well-preserved vertical transitions observed in localized assemblages of marine fossils are also examples of replacement, not succession (see Figure 1). Reorganization of plant assemblages paced by climate change over the last 10,000 years, when viewed at a particular locality, is another form of community replacement.

Regional transitions and turnover pulses—Regional ecosystems undergo processes that resemble succession and replacement but that are unique to the larger, more inclusive scale of such systems. This is the level of organization at which ecologic and species-level evolutionary processes intersect in many crucial ways. When a significant proportion of local ecosystems collapse, the regional system will be reorganized or replaced by a new system. The most important processes include interregional migrations, local and species-lineage extinctions, and speciation events. In terms of establishment of new regional systems, immigrants and newly evolved species may be swept into interaction networks in the early stages, with some species becoming the dominant players in the new regional economy; others, however, develop only minor roles, which may explain both abundant versus rare differences and the subsequent durable structure of such large systems. Regional transitions are largely forced by major changes in the surrounding environment, such as climate fluctuation in terrestrial settings and sea level changes in marine settings. Many coincident regional transitions take place during mass extinctions. Such patterns probably encompass 1,000 to 100,000 years and are as yet poorly understood. In the Devonian marine formations of New York state, groups of related fossil assemblages that probably record regional ecosystems, having durations of several million years, replace one another as a result of environmental changes that caused extinction and faunal turnover at the regional scale.

Larger transitions—Some paleontologists have claimed that local and regional ecosystem turnovers are examples of a kind of scaled-up succession, not unique processes involving

Figure 2. Reef-building Episodes over 500 million years



Source: Copper, Paul. "Ecological Succession in Phanerozoic Reef Ecosystems: Is It Real?" *Palaios* 3: 136–152, fig. 4, p. 147. (Reprinted with permission)

Note: Some authors claim that these patterns in the fossil record are examples of succession. Clearly, the largest patterns of evolution and extinction are reflected in the waxing and waning of reefs at this scale of resolution, not the local processes involved in succession.

larger, more inclusive systems. Some have gone even further and described major transitional patterns at the provincial to global scale as instances of succession, such as the waxing and waning of reef-building episodes in marine environments through the Phanerozoic Eon (see Figure 2). Reefs disappear during mass extinctions and eventually reappear during intervening periods, consisting of generally similar "guilds" (functional groups) but of different taxonomic components. Other workers have referred to such patterns as "community evolution," occurring over time spans of 1,000,000 to 100,000,000 years. Clearly, the processes involved in these major transitions in the history of life are completely different from succession occurring in a local ecosystem. Recklessly using the terminology in this way has not only caused confusion but has also retarded efforts (especially in paleontology) to understand the true nature of evolutionary and ecologic processes occurring at such grand scales. Some of these very large transitions have occurred only once (the emergence and deployment of complex marine ecosystems at the beginning of the Cambrian Period), while others appear to reflect recurrent ecologic patterns involving different kinds of organisms and probably different causes (for example, mass extinctions in the Phanerozoic Eon, all of which seem to include extinction, survival, and recovery phases; see Mass Extinction).

Succession in Particular

Most ecologists would now regard succession as a community or local ecosystem process, and consider the general processes to include autogenic mechanisms constrained or mediated by allogenic environmental contexts. They would agree that organisms occurring in early stages are generally unsuited for the later stages of development (for various reasons specific to the different organisms involved), that much depends on availability of colonists, that organizational complexity of local systems increases during succession, and that systems left undisturbed for long periods of time usually come to be dominated by one or a few supercompetitors. At least small-scale disturbance is needed to open space or relinquish resources to less successful competitors and thereby bolster diversity. This means that the most diverse ecosystems are those experiencing intermediate levels of disturbance or small-scale disruptions, allowing coexistence of many species.

There are two modern ways of thinking about true succession. Ecosystem ecologists tend to see it as involving an orderly process of development of the trophic (food) relationships from simple pathways to more complicated weblike interactions, change from rapid to slow flow rates of nutrients, and increase in homeostasis (self-regulated stability) over time. The maturation of systems appears to be mostly a manifestation of the thermodynamic properties of interacting population systems. Systems are predicted to self-organize to increase efficiency of energy and chemical transfers, build up pools of biomass and nutrients, and reduce entropy. This model stresses deterministic themes. By comparison, population ecologists are inclined to see succession as an organism-by-organism replacement process. Some outcomes are more likely than others, depending on several variables: potential for recruitment from adjacent patches; properties of component populations, including tradeoffs between reproductive biology, growth rates, competitive abilities, and methods of resource capture and utilization; and the importance of chance events like spatial patterning of disruptions, the timing of those disruptions, and previous conditions in the ecosystem. The population approach is strongly influenced by probabilistic considerations. In both approaches, communities or local ecosystems are now seen as successional mosaics, often consisting of neighboring patches at different stages of recovery at the same time.

—William Miller III

See also: Benthos; Climatology; Coevolution; Communities; Conservation Biology; Ecological Niches; Ecology; Ecosystems; Evolution; Extinction, Direct Causes of; Food Webs and Food Pyramids; Geological Time Scale; Global Climate Change; Habitat Tracking; Mass Extinction; Paleontology; Positive Interactions

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Sustainable Development

Sustainable development provides a commonly used framework within which the often conflicting goals of economic growth, human welfare, environmental sustainability, and biodiversity conservation (among many others) are discussed and resolved. The scale of the problems addressed varies from local land use decisions by villagers to global agreements on international marine fisheries. Regardless of the size of the groups or regions involved, achieving the goal of sustainable development requires a consensus on the definitions of both "sustainability" and "development" and a clarification of the relationship and potential for reconciliation between the two. Biodiversity has been incorporated into the formula in a number of ways, from a fundamental necessity for economic growth to an aesthetic component critical to continued human welfare.

Until approximately 10,000 years ago, human populations lived in small, often nomadic groups as hunter-gatherers without causing significant harm to the environment. Although this may be an example of the sustainable use of resources, it is important to note that it is a subsistence system and not one in which development or transformation is occurring in any significant way. Subsistence such as this can continue as long as resources are readily available, population levels remain low, and exploitation does not exceed the environment's capacity to regenerate. This subsistence system is fundamentally different from one in the process of development; in addition, very few subsistence-based societies exist today. From the beginning of agricultural practices and settlement, humans have embarked on a path toward development that today drives and is driven by a global economy. In this system, of many types growth is fundamental: growing economies, human populations, and demands on the natural resource base, and increasing negative impacts on the environment in the form of degradation, pollution, and climate change.

The origins of the concept of sustainable development reside in the integration of two sets of concerns raised separately by developed and developing countries. In the late 1960s, an awareness of environmental problems resulting from pollution and other side effects of economic growth emerged in Europe and North America. Concerns arose among developing nations in the Southern Hemisphere that policies reducing environmental degradation adopted by developed countries would place limitations on their own pressing needs to increase development and standards of human welfare. The preparatory Founex Report (1971) and the UN Conference on Human Development in Stockholm (1972) integrated both these environmental and development concerns into a global conservation framework. The environment-development connection was strengthened by the World Conservation Strategy (1980), which stated that not only were conservation and development compatible, they were linked as mutually necessary prerequisites.

The term *sustainable development*, already in use, was codified and broadly incorporated into environmental and growth strategies in *Our Common Future* (also referred to as the Brundtland Commission Report), produced by the World Commission on Environment and Development in 1987: "Sustainable development is development that meets the needs of the present without compromising the ability of future generations to meet their own needs." The preservation of biological diversity, implicit in the preceding discussions of environmental conservation, was explicitly stated as a goal of sustainable development in Agenda 21, the strategic document produced in 1992 at the Rio Earth Summit (officially known as the UN Conference on Environment and Development).

How do we work toward this ideal of sustainable development? First, we have to define the two, often competing terms composing the goal. Sustainable development, as advanced in both *Our Common Future* and Agenda 21, generally re-enforces a traditional economic definition of development as economic growth, and identifies technology and social organization as critical in mitigating environmental impacts and the limits they set to growth. This view emphasizes an equivalency (or at least lack of conflict) between classical economic production growth, evaluated by measures such as gross national product (GNP), and the conservation of biodiversity, and implies that such growth is a necessary component of sustainable development. Clearly, this equivalency of economic growth and development can create priorities that are at odds with the goals of biodiversity conservation and environmental protection.

Both economists and conservationists have expanded this circumscribed framework to include additional definitions of development. First, the environment itself contributes quantifiable "products" directly to development in the form of renewable resources (for example, timber for harvesting) and raw materials for industry (such as plant compounds for medicine), or by providing environmental services (such as water filtration, pollination). This economic valuation makes it possible to measure both biodiversity's contributions to growth as well as the economic costs of its degradation or loss. Second, a broader definition of development emphasizing qualitative increases in human welfare and living conditions has been proposed, which decouples quantitative GNP growth (which may or may not increase welfare) from development. If development's goals are to improve the daily living experiences of all humans on the planet, then the incorporation of aesthetic, spiritual, ethical, and intrinsic values of biodiversity into growth frameworks is not only possible but necessary. This confers to the natural world a concrete role in the qualitative advancement of human welfare independent of an economically defined utility or function.

What then is sustainable development, or sustainability? From the classic perspective of natural resource management, environmental resources can be broadly divided into two categories—renewable and nonrenewable. To meet the criterion of sustainability, any use of renewable resources must be at a level that allows natural renewal of the resources, and all overexploited systems must be given a chance to regenerate. This approach is closely linked to the concept of maximum sustainable yield commonly employed in fisheries and other harvested resources. In addition, sustainable use requires the maintenance of valuable ecological functions and services (mentioned above), which can be degraded both directly and indirectly by extraction and development (for example, logging in watersheds).

Nonrenewable resources must be preserved and used in a manner that does not result in their permanent and irreversible depletion. By definition, however, these resources—including both genetic and phenotypic biodiversity and ecosystem integrity—are irreplaceable, making absolute preservation unachievable. This logical quandary is usually managed by placing the time frame for exhaustion at some distant time (at least beyond our grandchildren's deaths) and by invoking technological innovations and undefined social actions to attenuate the effects. The conflict between preservation and use is an example of the tensions causing many to turn away from sustainable development as an effective framework for biodiversity conservation.

Is it possible to reconcile these two goals? As we see above, economic concepts of production-oriented growth invariably shortchange an environment that is highly devalued in the model, while scientists and preservationists generally view so-called sustainable development as an oxymoron. The process of putting sustainable development into practice requires a clear understanding of what is to be sustained, at what scale, and over what time period. In addition, we must consider necessary social actions and trade-offs against other social goals. Making these determinations involves a combination of value judgments, knowledge, and perspectives; a resulting sustainable development strategy for a particular situation may not contribute to sustainable development if the parameters are defined differently. For example, within a particular community it may appear that resource use is sustainable such that the resource base within that system will be available into the future, while also supporting local development. Within this small system it is possible to measure resources extracted, waste recycling and disposal, environmental impacts, and human welfare. However, the community is not a closed system, so that when looking to regional, national, and international levels, it is much more difficult to measure resource use and impacts—and particularly hard to predict how these will play out over time. Actions taken in a particular time and place will have consequences elsewhere, often involving unanticipated trade-offs.

There have been many efforts to devise indicators measuring progress toward sustainable development. Indicators of the progress or current status of systems are commonly used (for example, gas gauges, blood pressure readings, and the Dow Jones Industrial Average). Indices use selected criteria to measure relative progress toward sustainable development. Scientific knowledge does not allow us to determine levels of performance that will be sustainable, much less predict how various economic, social, and environmental factors may interact, and to do this on a global scale. Indicators are constrained by the limited availability of information over time and by the inconsistent way it is collected in various countries. In addition to these gaps in knowledge, comparisons are further hampered by political suspicions.

Traditional indictors of development and economic growth include GNP, worker productivity, and the unemployment rate. These measure changes in one part of the community—in the case of GNP, income from production—as if they were independent of the others. Such indicators are growth-oriented and based on national averages, and they consider neither the natural resource supply on which development is in large part dependent nor how economic growth may affect human well-being. The UN Human Development Index (HDI) was developed to better measure the status of human welfare and well-being throughout the world. The HDI is a composite of indicators of human longevity, knowledge (for example, adult literacy), and standard of living (a measure of individual purchasing power adjusted for the local cost of living). This approach offers an alternative to GNP for measuring the relative socioeconomic progress of countries toward increasing human welfare. One drawback of averaged indicators such as the HDI is that a country's overall index can conceal different levels of development within different groups, such as women, ethnic minorities, or the urban poor.

Indicators of sustainable development need to consider not only the economy and society but also the environment and links among all of these components. The Brundtland Commission (1987) and the Earth Summit (1992) both recognized the importance of indicators of sustainable development. The Commission on Sustainable Development (CSD) developed these interests, and in 1996 a working list of indicators in social, economic, environmental, and institutional categories was published and distributed to countries for testing. *Indicators of Sustainable Development: Guidelines and Methodologies*, based on the experiences of twenty-two countries, was published by the United Nations in 2001. Additional efforts have been made to develop indicators specific to sustainable development. The Consultative Group on Sustainable Development Indicators is developing a small number of new indices to supplement traditional growth measures (for example, GNP), with the ultimate goal of producing a composite, internationally accepted sustainable development index. The U.S. government established the U.S. Interagency Working Group on Sustainable Development Indicators in 1996, to assist policy formulation. These indicators are statistical analyses designed to collectively measure national capacity to meet both present and future needs.

Other indicators focus more explicitly on measuring the current and future status of the environment. These include the Environmental Sustainability Index (ESI), which measures five components:

- The state of environmental systems, including soil, water, air, and ecosystems.
- Stresses placed on these systems by exploitation and pollution.
- Human vulnerability to environmental change in the form of reduced food resources or increased environmental disease exposure.
- Social and institutional capacity to cope with environmental challenges.
- Ability to respond to global challenges by cooperating to conserve international resources (for example, the atmosphere).

The ESI integrates a large amount of information (twenty-two core indicators and sixty-seven underlying variables) to measure progress toward environmental sustainability for 122 countries. The goal is to allow national comparisons of environmental progress and to foster a more analytical approach to environmental decision making.

The twin tasks of defining and implementing sustainable development are complicated by disagreements over definitions, measurements, and even the possibility of accomplishing this ideal. It is clear, however, that achieving sustainable development is as much about changing human behavior as it is about defining and resolving biological and technological problems.

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See also: Conservation, Definition and History; Economics; Ecosystems; Ethics of Conservation; Extinction, Direct Causes of; Organizations in Biodiversity, The Role of

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Systematics

Systematics is the study of the diversity of organisms and the relationships among these organisms. Systematics is a natural outgrowth of the need for humans to characterize and categorize the world around them. It is one of the oldest scientific disciplines, with roots in antiquity and a formal scientific literature reaching back to Aristotle. It is the basic comparative science of biology. Comparative sciences such as systematics and astronomy use the similarities and differences among the things studied in an effort to comprehend them and their behavior. This is in contrast to the experimental sciences, in which the outcomes of controlled experiments are used to acquire understanding.

The products of systematic study are used in many other branches of biology in two major ways. First, a biologist may need some knowledge of the kinds, identities, numbers, distribution of species, and populations within species in order to conduct research. For example, do the specimens studied represent one species or several species? If several, what are their identities? Second, the same biologist may need to know the relationships among these entities in order to fully understand the comparative data she has collected. For example, are the similarities in the ecology of two species the result of convergence in a similar environment (the species are not closely related), or common history (the species are closely related)?

This kind of comparative biology is not restricted to systematics. For example, David

Hillis and colleagues at the University of Texas studied an outbreak of the AIDS virus and showed that the affected individuals were infected from a common source. This conclusion was reached by demonstrating that the AIDS viruses in each patient were all related to a common virus ancestor, and that the source of that ancestor was an infected dentist who deliberately infected the unfortunate individuals. So the uses of systematics can span from the highest level of biological organization, such as the study of the origin of entire continents, to very small levels, such as a study of a small group of AIDS patients. Systematics can be divided into four discrete but overlapping activities: discovery, description, taxonomic scholarship, and synthesis.

The discovery activity consists of the search for new kinds of organisms. Much of this activity takes the form of field expeditions, in which a variety of special techniques are employed to collect organisms and preserve specimens in a manner that allows for future study. Rare or endangered organisms are usually not collected, but are rather documented with photographs or other means. Preserved specimens are placed in collections, usually at recognized natural history museums or other research institutions where they are made available for study by experts. The community of systematic scholars is truly international, and experts on particular groups of organisms regularly visit these collections or request loans of specimens to study. A considerable amount of discovery activity also takes place in the collections themselves, when experts examine specimens and discover new organisms "hidden" among previously known organisms. This requires careful attention to the care and maintenance of natural history collections, a specialty that systematists are expected to learn in addition to their research skills.

Descriptive activities are centered on documenting diversity through scientific publication. One basic activity is the description of newly discovered species. The systematist will describe a newly discovered species by examining collected specimens, characterizing their physical appearance, summarizing variation of individuals within and between populations, documenting the species' geographic range, and comparing the species to other species. Another basic activity is to publish a revision of a particular group. The systematist will attempt to examine specimens of all the species in a genus, family, or other group, study the history of names that have been applied to these specimens, adjust the classification as necessary, describe new species, and redescribe known species. Each species account would be similar to a basic species description. Yet another common activity is to publish a flora or fauna, a work that covers all the plant or animal species for a given region of the world. Such works may contain descriptions much like a revision but be directed toward information about each species within the particular region. Or they may be more informal, as in many field guides whose major purpose is to assist the systematist and layperson in identifying specimens. Another basic activity is the generation of identification keys that allow nonspecialists to identify the specimens they observe or collect without having to take them to specialists. Frequently revisions, floras, faunas, and field guides will contain keys.

Systematists who publish species descriptions, revisions, keys, and other descriptive publications are expected to observe good taxonomic scholarship. Our present systems of classification and nomenclature date back to the late eighteenth century (see Linnaean Hierarchy), and it is common for the same species or group to have several different names. Three Codes of Nomenclature (plant, animal, and bacterial) have been adopted to ensure that all scientists use only one name for a particular species and for certain other taxa, such as genera and families. One of the main goals of the revision of a group is to sort out this history of names and use only the correct names for the species studied. This requires a thorough familiarity with the appropriate code and the correct application of the Rules of Nomenclature to the names of the group that is being revised. It is important to note that these codes do not demand that research and synthesis be conducted in a particular manner—only that names are used correctly. This ensures that systematists from different countries can communicate clearly.

Synthetic activities use the information gained from discovery and description to form hypotheses concerning the animals and plants studied. Syntheses are found as part of works that are mostly descriptive. The very act of comparing a newly discovered species to other known species is a synthetic activity. The revision of a particular group may be based on synthetic activities such as an analysis of the phylogeny of the group. A flora for a particular region might contain a detailed biogeographic analysis that attempts to account for the origin of the entire flora by studying the relationships of its members to species living in other areas. Synthetic activities require a particular philosophical approach to problem-solving, and it is little wonder that this is the area of systematics in which controversy is rife. What, exactly, do we mean when we state that two species are closely related? What principles do we use to form a biological classification? Even if we acknowledge that evolution has produced a Tree of Life, should we base revisions and classifications on phylogeny? Most of the controversy revolves around the role of phylogeny and the Tree of Life and its relationships with biological classification.

Three dominant approaches to systematics emerged in the second half of the twentieth century. "Phenetics" holds that phylogenies are largely not recoverable and that the best approach is to estimate the overall similarity of species and classify on that basis. Its adherents are called pheneticists. "Phylogenetic Systematics" holds that there is a method for recovering phylogenies that is rigorous and testable and that classifications should be based strictly on the recovered phylogenies. Adherents are called phylogeneticists. "Evolutionary taxonomy" holds that reconstructing phylogenies is an important activity but that classifications should be based on both similarity and genealogical relationships, and adherents of this approach seek to balance the two; they are called evolutionary taxonomists.

Phenetics began as a reaction by its proponents, such as Robert R. Sokal of the United States and R. James Sneath of Great Britain, to what they perceived as a lack of rigor in biological systematics. Systematics seemed to these early pheneticists more an art than a science, with little justification for how systematists made their decisions. They proposed to replace this "art form" with rigorous procedures for determining the overall similarity of organisms, using mostly measurements and other means of quantification. Computer programs were used to summarize the data and organize them into repeatable (for the same measures) indices of similarity. Species that were more similar were grouped into genera, similar genera into families, and so on.

Evolutionary taxonomy is actually the oldest of the three modern approaches; it grew out of the Evolutionary Synthesis (1920–1950). Its proponents, such as Ernst Mayr, G. G., Simpson, and Julian Huxley, wished to incorporate the rejuvenation of Darwinian evolution into systematics. Thus there was a heavy emphasis on the nature of species, integration of population phenomena, and recognition of levels of biological organization in theoretical works. The distinctive features of this approach emerged only with the rise of its competitors, phenetics and phylogenetic systematics. By the late 1970s the differences were apparent. Evolutionary taxonomists adopted methods introduced by the phylogeneticists for reconstructing phylogenies but advocated a dual approach to classification in which some groups were classified according to strict genealogical relationships and others were classified according to similarity relationships. The adoption of certain theoretical concepts such as a dual concept of relationship and a concept of "minimum monophyly" (see below) were the theoretical underpinnings of this approach.

The German entomologist Willi Hennig formalized phylogenetic systematics based on earlier German influences. Hennig adopted what he considered a strictly Darwinian concept of "relationship": genealogical relationship. Species were not necessarily closely related because they are similar, but because they shared a unique common ancestor. They might, indeed, be very similar, but in some cases they might not. For example, crocodiles and birds are not very similar, but they share a common ancestor not shared with lizards and snakes. (Dinosaurs share the same ancestor.) Hennig would classify birds and crocodiles together, and not classify crocodiles with snakes and lizards, because he rejected the pre-Darwinian concept of "relationship" as "similarity relationship."

One of Hennig's central insights, also adopted by later evolutionary taxonomists, was his conclusion that only certain kinds of homologous similarities were evidence of common ancestry relationships among organisms. This led him to conclude that overall similarity could not possibly unravel evolutionary relationships. These special homologies, termed synapomorphies, were the homologies thought to have evolved only in the unique common ancestor of the related organisms and not in earlier ancestors. For example, birds and crocodiles (and probably most dinosaurs) build nests and take care of their young; these characteristics are thought to have arisen in the common ancestor of the group. Thus, these characteristics would be synapomorphic homologies, and they would imply a group composed of crocodiles and birds. In contrast, a body covered with scales is certainly a homologous similarity shared by crocodiles and lizards, but this homology is thought to have evolved in the common ancestor of birds, crocodiles, and lizards and thus does not suggest a unique relationship between crocodiles and lizards that excludes birds. Instead, it implies a larger group composed of all vertebrates ("reptiles," mammals, and birds) descended from an ancestor that had epidermal scales. Thus this homology is not "discarded"; it is simply used at a different level of analysis.

Since evolution was not thought to involve large steps during descent, the number of characteristics that supported any particular common ancestry relationship was necessarily small compared with the total number of homologous similarities shared by any two organisms or species (or genera, and so forth). Thus, to work out a phylogeny of a large group, many characteristics would have to be employed, only a few of which would be applicable for any pair of relationships to be tested. Since Hennig's concept of relationship was strictly genealogical, he insisted that natural groups be strictly monophyletic, groups that arose from single ancestral species and that included the species and all its descendants. These groups are termed monophyletic groups, or clades (hence "cladist" is an alternative label for phylogeneticist).

Phenetics and phylogenetic systematics caught the general attention of the systematic community in the 1960s, and the clash between these newer paradigms and evolutionary taxonomy became the dominant theme of theoretical systematics for some twenty years. Phenetics and phylogenetic systematics were associated with distinctly different empirical methods. Pheneticists produced "dendrograms"—tree graphs linking species by estimates of overall similarity. Phylogeneticists produced phylogenetic trees—tree graphs linking taxa by common ancestry as shown by synapomorphies. Both pheneticists and phylogeneticists rejected overall similarity as a method for discovering phylogenies, but pheneticists abandoned the search for phylogeny, while phylogeneticists continued the search as a necessary step to achieve their concept of "relationship" as genealogical relationship through the discovery of synapomorphic homologies.

There is no doubt that the pheneticists were at least partly justified; systematics did seemingly lack a rigorous and testable set of methods. But phenetics, after an initial popularity, failed. There were many reasons for the failure, but three stand out. First, the results were rarely repeatable for the same specimens using different systems of measures and different indices of similarity. If the phenetics community could have settled on one method of collecting traits and one method of linking organisms into similarity relationships, they might have developed an internally consistent system. However, that was never accomplished. Second, the similarity measures contained information from both homologous and convergent traits. But evolutionary biologists wanted to know which traits were homologous and which were convergent. Evolutionary biologists needed phylogenetic trees to obtain that information; similarity dendrograms did not provide it. Third, phylogenetic systematics demonstrated that phylogenies were, indeed, recoverable in a rigorous and testable manner. The recovery of historical information did not need to be an art form. Phylogenies (or, more properly, hypotheses of phylogeny) are much more interesting to evolutionary biologists than similarity measures, even when measures of similarity were organized into dendrograms that look like phylogenies.

Evolutionary taxonomists did not have an explicit method for discovering phylogenetic trees. They adopted the methods of phylogenetic systematics. In the clash of paradigms, evolutionary taxonomists attempted to reach a middle ground on the issue of classification by adopting a dual concept of relationship. In some cases groups should be classified genealogically, but in other cases they should be classified by similarity. The justification for grouping by similarity grew out of an interpretation of the evolutionary synthesis that levels of organization were significant evolutionary phenomena that denoted so-called adaptive zones. In reality, this amounted to a justification that certain "important" and long-recognized groups should be retained in classifications, even though their continued recognition violated the concept that organisms should be classified strictly on the basis of common ancestry relationships (that is, the concept of strict monophyly).

The position of the evolutionary taxonomists is best evaluated by a contrasting example of how an evolutionary taxonomist and a phylogeneticist might classify birds. Evolutionary taxonomists recognize Aves (birds) as a class of vertebrates. There is a historical precedence for this, as systematists have long recognized birds as one of the major classes of vertebrates. There was a supposed theoretical justification as well. Birds have departed so strongly from the level of organization represented by reptiles that they now occupy an adaptive zone worthy of class recognition. Although this might sound very reasonable, there is a problem. The decision also requires recognition of Class Reptilia, which includes the closest living relatives of birds, dinosaurs, and other archosaurs such as crocodiles and alligators, along with more distantly related organisms such as snakes and lizards. This seemed a reasonable conclusion, because Reptilia also is a long-recognized group, but it leads to the conclusion that the common ancestor of birds, dinosaurs, and crocodiles is a reptile. That, then, leads to the idea that Reptilia is somehow ancestral to Aves, a shorthand notion that if the ancestor of archosaurs were found it would be classified as a reptile rather than classified in a group that included all of its descendants, dinosaurs, crocodiles, and birds. This concept has been termed minimum monophyly. Aves is classified on the basis of genealogical relationships; Reptilia is classified on the basis of similarity relationships (dinosaurs and crocodiles are similar to lizards and snakes); and the system was justified by appealing to the concept of minimum monophyly, which allows groups (Reptilia) to be ancestors of other groups (Aves).

Phylogenetic systematists reacted sharply to the concept of minimum monophyly and grouping by similarity. Their paradigm demanded strict monophyly and grouping by genealogy. Phylogeneticists argued that species are the highest level of biological organization capable of being ancestors, and that Aves should be placed within the group Archosauria along with all other descendants of the ancestor of archosaurs, such as dinosaurs and crocodiles. In other words, Reptilia would disappear from classifications altogether and would be replaced by Archosauria (birds, crocodiles, dinosaurs, and so forth) and Lepidosauria (snakes, lizards, and so forth).

Hennig and his colleagues saw phylogenetic systematics as the systematic culmination of the Darwinian Revolution, rejecting the pre-evolutionary idea of similarity as the basis for classification and embracing Darwin's idea that classifications that reflect genealogy should be adopted whenever possible. However, they faced several political problems. For one thing, strictly phylogenetic classifications would lead to the abandonment of many familiar groups, such as Reptilia and the ape Family Pongidae. (Chimpanzees and gorillas are more closely related to humans than to gibbons.) And, it would lead to lowering the hierarchical ranks of other groups that are monophyletic, such as classifying Aves as an order of Archosauria rather than one of the classes of vertebrates.

In spite of the political difficulties, and in spite of the fact that popular classifications found in school texts still have not changed, phylogenetic systematics has established itself as the dominant paradigm of systematics. There are several reasons for its success. First, the phylogenetic method of discovering phylogenies has proven a boon to evolutionary biologists who require information about the genealogies of species to do critical research in evolutionary biology. What is the correlation between geologic history and the history of the origin of species? Are certain modes of speciation more common than others? Are newly evolved species more genetically conservative or genetically diverse than older species? One needs a phylogeny to answer all of these questions.

The issue of classification has become clear. As it turns out, the claim by phylogeneticists that species are the highest possible level of biological organization capable of being ancestors is widely accepted. Those who disagree argue that only populations and individual organisms can be ancestors; no one argues that higher taxa, such as genera or classes, can be ancestors. Thus, while most biologists accept speciation as a natural process, there are no recognized natural processes that allow groups of species such as Reptilia to give rise to entire other groups, such as Aves. This conclusion undermines the major assumption underlying the concept of minimum monophyly. There is another problem with evolutionary taxonomy. The philosopher David Hull pointed out more than thirty years ago that classifications containing a mix of groups formed on the basis of similarity and genealogy will always be logically inconsistent with the phylogeny as a whole if they contain "similarity groups" such as Reptilia along with "genealogy groups" such as Aves. In spite of the fact that inclusion of such groups as Reptilia seems a good accommodation to the world of practical taxonomy, a classification that included such groups would be illogical relative to the Tree of Life. It seems that if biological classification is to fulfill Darwin's paradigm, it will have to be phylogenetic and adhere to the concept of strict monophyly. Evolutionary biologists not only need phylogenies to answer critical evolutionary questions, they also need biological classifications that organize this information in a manner that is logical relative to the phylogeny itself.

—*E. O. Wiley*

See also: Classification, Biological; Linnaean Hierarchy; Phylogeny

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Termites

See Arthropods, Terrestrial

Thylacine

The image of the Thylacine (*Thylacinus cynocephalus*) occupies a place of honor in the Tasmanian coat of arms, but in life, fear and ignorance allowed the species to be driven to extinction (Dixon, 1991). Otherwise known as the Tasmanian tiger or Tasmanian wolf, the thylacine was the largest carnivorous marsupial to have existed in historic times. The thylacine ranged over much of Australia, Tasmania, and Papua New Guinea, and it was the top predator in those areas before the arrival of humans. The combined effects of competition, habitat destruction, and relentless persecution by humans led to the demise of this species less than a century ago. The story of the thylacine is a classic example of mankind's love-hate attitude toward other predators. Although they are admired for their strength and untamed nature, predators are generally feared and often resented as competitors for resources.

The thylacine superficially resembled a large dog. It was a sleek animal, weighing 15 to 30 kg, with short, dense, yellowish-brown fur marked by distinct black stripes across the back and rump. The tail was long, broad-based, and somewhat rigid. Although the head was doglike in appearance, the jaws were capable of an unusually wide gape. Like all marsupial mammals, the thylacine gave birth to its young at a very immature stage. After birth, a litter of two to four young completed their development in their mother's pouch, until they were mature enough to follow their mother or stay in the den by themselves (Smith, 1982).

The thylacine's closest surviving relatives are other carnivorous marsupials of Australia, such as the Tasmanian devil (*Sarcophilus harrisii*) and the quolls (*Dasyurus spp.*). The extinct carnivorous marsupials from South America were more distant cousins (Nowak, 1999). Thylacine fossils have been found on mainland Australia, Tasmania, and Papua New Guinea, and aboriginal rock art confirms that the species existed in Australia during the time of the first human inhabitants. But by the time Europeans arrived, the thylacine's range had already been reduced to the island of Tasmania. Competition with dogs (*Canis familiaris dingo*) introduced by the Aborigines was probably a significant factor in reducing the thylacine's range, and the species may have survived longer in Tasmania in part because dingoes were not introduced there.

European settlers, who arrived in Tasmania at the beginning of the nineteenth century, set out to tame the wilderness and reshape the landscape in the image of their homelands. The thylacine was perceived as a wolf among their sheep, and it acquired a notorious reputation as a killer of livestock, despite the fact that dogs were much more destructive. There was no room for predators in the pastoral paradise envisioned by these settlers, and therefore a bounty was set for their extermination. The peak of the killing occurred in 1900 (Smith, 1982). Indiscriminate killing coupled with population fragmentation and habitat loss caused the thylacine population to decline rapidly. Disease may also have contributed to the demise of this decimated, fragmented population. A few naturalists recognized the precipitous decline of the species, but the concerns of ranchers took precedence. The last shooting of a wild thylacine occurred in 1930, and the species was granted protected status in 1936—a little late.

Much of what has been recorded about the habits and ecology of the thylacine has come from the observations of trappers, hunters, and ranchers, and there may be a certain lack of objectivity in their accounts (Jones and Stoddart, 1998). It is thought that the thylacine was primarily a nocturnal, solitary hunter. Pairs or small family groups were occasionally observed, and lairs were found in rock crevices and hollow logs. In Tasmania, the thylacine's range appears to have extended from the mountaintops to the coast (Dixon, 1991). Grasslands and open woodlands were probably favored as habitat rather than dense forest.

From examination of the anatomical evidence, Jones and Stoddart (1998) and Jones (1997) concluded that the thylacine's reputation as a sheep killer was significantly overstated. The thylacine's teeth and limbs suggest that its prey was most likely to have been small relative to its body size. It probably hunted its prey in a pounce-pursuit manner in fairly open habitats, and it killed with a crushing, penetrating bite. The remains of small- to medium-size herbivores (less than 5 kg) have been found in cave deposits along with thylacine remains. Hunters reported that thylacine stomach contents included kangaroo and even echidna (*Tachyglossus spp.*) remains (Smith, 1982; Dixon, 1991).

Individual animals survived in zoos for up to nine years, but they never bred in captivity. The last known thylacine, a female named Benjamin, died in a private Hobart zoo in 1936 (Dixon, 1991). The fact that even the sex of the world's last thylacine was misidentified is telling of the ignorance regarding this species. Expeditions have been mounted in search of the thylacine, and many alleged sightings have been reported, but there have been no substantiated observations of the species for more than sixty years (Rounsevell and Smith, 1982; Smith, 1982).

Now, in what might become one of the most intricate (and costly) biological feats ever attempted, scientists at the Australian Museum have proposed a plan to resurrect the thylacine. DNA will be extracted from museum specimens; the genome will be sequenced and used to create a living thylacine. The project has thus far been successful in DNA extraction, but the challenges of reconstructing chromosomes and a surrogate pregnancy still lie ahead. The project plan also stipulates that habitat preservation must be a priority in order to provide for a new thylacine population. Critics abound. Although the scientists are optimistic, they themselves acknowledge that it is likely to be decades before the project is completed (Colgan and Archer, 2000).

—Julie Pomerantz

See also: Agriculture and Biodiversity Loss: Industrial Agriculture; Alien Species; Carnivora; Convergence and Parallelism; Extinction, Direct Causes of; Mammalia; Preservation of Species

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Tides

The ocean tides are generated by the gravitational pulls of the moon and sun. However, most of the tidal effect results from the gravitational pull of the moon, which tugs at the side of the earth facing it, causing the earth to bulge slightly in that direction. Because water is less dense than the solid earth it bulges out more, forming a tidal crest on the side facing the moon. On the opposite side, the earth is pulled toward the moon more than the ocean, leaving a bulge or crest of water on the opposite side.

Inasmuch as the moon is the controlling body, the tidal crest moves at the same rate as the moon's orbit—about 1,000 miles per hour at the equator. For any given place there are two high and two low tides during a complete rotation. Because the moon and earth's rotation are not synchronous, the time difference between the two high tides is about 12 hours and 25 minutes, not 12 hours. Since the relative positions of the sun, moon, and earth are known with precision, tidal charts can be produced in advance to show the exact times of high and low tide at any given place.

Other factors, such as the eccentricity and inclination of the moon's orbit in relation to the earth's, the irregular configuration of the ocean basin, the Coriolis force (caused by the rotation of the earth), friction as water moves, and the influence of the sun, complicate tidal rates and fluctuations.

For example, in deep water the tidal range is about 1.5 m. As the tide approaches the continental shelf it slows down because of friction, resulting in a higher tide. When the earth, sun, and moon are aligned in a row, a so-called spring tide occurs—that is, higher than normal tides caused by the enhanced combination of their gravitational pulls.

However, when the three bodies are at right angles to one another, the tidal effects of the sun and moon tend to cancel each other, producing a low, or neap, tide.

A rising tide is often called a flood tide; it lasts for 6 hours and 13 minutes, the time it takes to reach its maximum height. For a short time the water may seem motionless or slack; then the tide reverses and the water level drops, forming an ebb tide lasting the same amount of time—6 hours and 13 minutes.

In estuaries, such as the Hudson, for example, the flow of the ebb tide is strengthened by the addition of river water that also diminishes the strength of the flood tide as it flows against the incoming water. As tides move up and down and flow back and forth in bays, estuaries, and the shallow continental shelf, they often transport a considerable amount of sediment.

In the open ocean the tidal current travels at about a quarter of a knot. But when it reaches land, the resulting tidal currents increase in speed, in some cases to 10 knots, especially in estuaries, bays, and straits where they become restricted. Along coastlines that become progressively more narrow, water is squeezed together causing the incoming tide to rise higher and higher. In the Bay of Fundy, between Nova Scotia and New Brunswick, Canada, this funneling effect produces tides up to 20 m in height.

However, the height of a tide is not as easily predictable as its timing, because it is controlled, in part, by meteorological conditions. For example, wind as well as atmospheric pressure cause substantial rises and falls in predicated height.

Both the solid part of the earth and the atmosphere respond to the same tidal forces as the ocean. As would be expected, the effect of tides on the denser solid earth is much less than in the ocean, while it is greater than in the atmosphere, where it is manifested as small changes in atmospheric pressure in any given place.

Tides also affect animals, such as some molluscs and arthropods that live along the shoreline, where their life activities are adjusted to the tidal cycles. Alternating fluctuations in temperature, changes in food supply, salinity, possible predation, and movement of sand—all these mold their behavior and physiological responses. These animals have adapted to a constantly changing environment, and it has been shown that their tidal rhythms continue even after the organism is put into a laboratory. A good example is the fiddler crab, commonly found scavenging and mating during low tide. As high tide approaches the crabs retreat into their burrows until the next low tide approaches, when their internal clocks tell them to begin to leave their burrows.

—*Sidney Horenstein*

See also: Beaches; Coral Reefs; Lagoons; Oceans

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Toadstools

See Fungi

Topsoil Formation

Topsoil is the upper layer of the soil profile. It is composed of minerals and rock particles, humus, dead and decaying organic matter, water, and an array of living creatures. The kinds of animals are specific to the location, but in general they include rodents, earthworms, insects, fungi, bacteria, protozoans, and viruses. It is these life forms that digest and decompose the organic matter by feeding on their dead and dying tissues, creating humus. These organisms leave their waste behind as well as their dead bodies, thereby contributing again to the soil by becoming part of its organic matter. Proteins are changed to usable nitrogen compounds, and minerals such as phosphorus, potassium, and calcium are changed to soluble compounds.

As decomposition takes place, sugars, starches, and organic acids are destroyed quickly; fats, cellulose, proteins, waxes, and lignins take longer. Because lignins are resistant to breakdown, they become more abundant as the process of humification takes place. Carbohydrates are attacked by a variety of bacteria and fungi when the humus is well aerated. Cellulose, a fibrous structure in many plants, is decomposed more slowly than sugars and starches, and by a limited number of types of bacteria and fungi. These organisms require nitrogen to accomplish their cellulose decomposition, depriving living plants of nitrogen while the process is going on if an excess of cellulose material is present. Proteins are decomposed by numerous kinds of fungi and bacteria into amino acids and then ammonia, and finally into nitrate.

Rodents and earthworms move through the topsoil, mixing it and allowing air and water to easily permeate the material. The chemistry of the water in the soil varies in composition and concentration, and thus in the chemical changes effected. These conditions, in turn, determine the variety and abundance of living organisms that in turn influence the development and properties of the soil.

Topsoil is distinguishable from the other horizons in the soil profile because of its position and because humus usually is much darker, because organic matter coats the mineral particles. The thickness of topsoil depends on the rate of erosion and the rate of accumulation of organic matter, as well as the level of nutrient demand. It may be an inch thick, or several feet, but, in general, it is thicker on flat surfaces and thinner on slopes. The uppermost part of topsoil consists of fresh or partially decomposed litter and other plant parts that have recently fallen onto the surface. It is most conspicuous in forests but not so in grasslands, where it seldom occurs. When it does, cultivation destroys it. On grasslands the organic material dies annually, adding to the soil humus, including the root systems of perennial grasses that are replaced every few years.

The decomposition of fallen leaves and needles in forests produces organic acids, which increase the leaching power of percolating water and hasten the removal of soluble materials. As a result, grassland soils are neutral to basic, while most forest soils are acidic.

—Sidney Horenstein

See also: Deposition; Erosion; Geology, Geomorphology, and Geography; Soil

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Topsoil, Loss of

When soil is exposed, it is removed by wind and rain. For example, rain pounding on the surface of soil breaks it apart, making it easy for running water to carry it away. At first, erosion may be sheets of water running down a slope. However, as time goes on, flowing water may become concentrated in tiny channels, or rills. With time these may enlarge to gullies, making the fields unusable because equipment can't get around. As the gullies enlarge and widen by lateral erosion, the stream banks are undercut, eating into adjacent land.

The question of how much soil is lost is uppermost in the minds of farmers, soil scientists, and other scientists interested in rates of erosion. Although the answer is difficult to determine, a clue is the amount of sediment that is being transported by streams. The material in streams includes not only dissolved minerals but also rock material from nonsoil sediments as well as soil, so that it becomes a task to assess how much is actually soil. In the United States alone, the Department of Agriculture has estimated that more than 4 billion tons of soil are lost each year. .

After soil dries it is often loose, allowing wind to carry it off, the amount being determined by wind speed. The rate of wind erosion of soils is difficult to determine, but it is thought to be usually less than that of water erosion except during times of drought.

A good example of wind erosion occurred in the Dust Bowl area of the United States during the 1930s, where 100 million acres of land centered on parts of Oklahoma, Texas, New Mexico, Kansas, and Colorado were affected by severe loss of soil. It resulted from a combination of factors, including the clearing of land of natural vegetation, drought, constant wind, and poor farming practices. Dust storms began in 1932 and carried dust eastward on the prevailing winds, dimming the sun and producing rain loaded with dust in distant places such as New York.

By the end of the decade increased rainfall and improved farming techniques had substantially reduced the problem. However, drought returned several times, each event producing substantial wind erosion of the remaining soil. One of the techniques developed to counter the problem of wind erosion is keeping the soil wet with irrigated water; that method can continue as long as the local aquifer contains adequate water. In May 2002 newspaper articles related that in Montana more than a thousand wheat farmers abandoned their farms because drought had once again resulted in failed crops and blinding dust storms—reminding many people of the Dust Bowl days of the 1930s. Worldwide, dust storms have substantially increased as a result of deforestation and the conversion of naturally vegetated land to farms.

Another type of soil destruction does not necessarily involve its loss, but rather heavy nutrient depletion by crops such as corn, cotton, and tobacco. In these cases the soil has to be substantially fertilized, which can indirectly cause streams and groundwater to become polluted.

Irrigation in desert areas where evaporation is high has deleterious effects on the usefulness of soil. For example, in Egypt irrigation water from the Nile is spread over fields. As the water evaporates it leaves behind dissolved salts in the open spaces of the soil. With time the soils become so salinized that they can no longer supports crops. In ancient Egypt, when the Nile flooded it removed the salt and deposited a new layer of silt. With the building of dams across the Nile, however, this process no longer occurs, because sediments are trapped in the reservoir.

Cultivation of soils for agriculture, deforestation, overgrazing, and other intrusions such as grading for highways, urban land use, and bulldozing areas for large-scale engineering works have caused the loss of natural vegetative cover and increased soil losses. This is a direct consequence of the growth of world population and improvements in technology upsetting the balance of nature.

Although it is hard to estimate how much soil is being formed today, it seems safe to say that erosion far exceeds soil production. For example, in the New York City area, glaciated bedrock still retains its smooth surface with no sign of soil formation even after 18,000 years. Researchers estimate that in California it takes as much as 2,000 years for one inch of soil to form, and that topsoil in various parts of the world is being lost at rates up to eighty times faster than it is being created.

On farms, as elsewhere, the roots of plants hold soil together. Farming practices that leave the remains of plants in fields after the crops have been harvested, and planting crops between the cash crops, help reduce erosion. These plants also protect the soil from erosion by wind and rain. Windbreaks using rows of trees, fences, and contour plowing are all techniques that have been introduced to reduce soil loss.

—Sidney Horenstein

See also: Erosion; Geology, Geomorphology, and Geography; Soil; Topsoil Formation

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Tourism, Ecotourism, and Biodiversity

Leisure travel is big business. Its many niches, including holiday resorts, theme parks, package tours, independent travel, and budget tours have a collective influence on local ecologies and economies in destinations all over the world. Tourists travel for a variety of reasons—rest and relaxation, sightseeing, pleasure, adventure, education, and the broadening experience of other lands and cultures. The ecological impact and resource demands of a steady influx of large numbers of humans significantly transform destination locations. A dramatic increase in tourism in recent decades is placing new strains on coastal, mountain, and desert ecosystems. Poor Third World nations often lack resources to develop

A group of tourists photographing in the Galapagos Islands, Ecuador. As the number of tourists flocking to fragile ecosystems increases, the proclamation "Take only pictures, leave only footprints" provides limited protection from the cumulative impact of thousands of footprints. (Galen Rowell/Corbis)

a tourism infrastructure and to increase the capacity for visitors and the income they generate, while at the same time preserving the fragile environments and habitats that are often the principal attraction in the first place. Ecotourism is growing in popularity, and the development of conservationist tourist programs in tropical biodiversity hot spots like Costa Rica and Belize are models for other countries to follow.

Growth and Impact of Tourism

By the mid-1990s, tourism had become the largest industry in the world. Each year, more than half a billion people spend some time as international tourists, while uncounted millions more travel domestically. The advance of tourism has reached farther and deeper into more isolated areas of the planet than all the invasions and migrations of history. Many areas are becoming dependent on the tourism sector as their primary source of income. The infrastructure built to facilitate this transnational flow of people, goods, services, and currency includes air, rail, land, and sea carriers, roads and airports, hotels, restaurants, and resort complexes. Tourist ministries, international agencies, and entrepreneurs also restore heritage sites, promote commercial handicraft enterprises, and commodify nature and culture for mass consumption.

Tourism is one of the world's largest export industries, but instead of exporting raw materials for production or finished goods for consumption, the tourism sector of the economy "imports visitors to consume goods and services locally" (Kirshenblatt-Gimblett, 1998, p. 153). The environmental impact of mass tourism on natural sites and fragile ecosystems can degrade the resources upon which it depends. The development of economic infrastructure with a large carrying capacity for visitors is a virtual prerequisite for countries to create and maintain successful tourism sectors. The commercial transformation of sites, which may have been attractive primarily for their unspoiled beauty, tends to increase proportionately with the carrying capacity of roads, hotels, and sewage facilities for visitors. Thus for optimal benefit to residents, regional interests, and tourists, development must proceed by balancing growth with limits.

These issues are matters of concern for those in charge of formulating and implementing global north-south policy. In the Third World, long-term protection of the environment and a fair share of profits for impoverished local residents can be difficult to attain. The transfer of wealth from First World guests directly to the multinational corporations of the travel industry often fails to generate enough income for local workers, sales to regional consumer businesses, and taxes to state governments, to benefit the community. International organizations have a role to play in establishing and monitoring a framework in which ecological priorities are weighed against economic issues to promote equitable and sustainable development and conservation solutions.

Before the Industrial Revolution, leisure travel was reserved mainly for the wealthy few. During the nineteenth and early twentieth centuries, workers' occupations became automated, their mechanized tasks grew tedious and repetitive, and their hours were strictly regimented. There arose a recognized need for relaxation and stress reduction, but few public outlets for recreation were available. For the first time organized leisure activities, promoted for their beneficial effects on health, fitness, and psychology, became a regular part of life for the great masses of working people. City parks and nature preserves were established, and travel by steamer or rail steadily expanded throughout the first half of the twentieth century. With the inauguration and increasing affordability of jet travel during the postwar era, vacationers from the United States, Japan, Germany, and all corners of the industrialized world have taken to roaming abroad in ever greater numbers. Today, with millions of people taking annual holidays, the travel and leisure business has expanded to become the largest of all global industries.

Natural scenery and warm climates are attractive to sight-seers, adventurers, pleasure-seekers, and package vacationers. The tourist industry as a whole is vertically integrated, largely controlled by the apparatus of state governments and large multinational corporations—principally hotel chains and airlines. At the same time, destination locations undergo extra strain placed on local resources for goods and services to satisfy the crowds of consumers. The appeal of many Third World destinations to tourists depends on keeping the natural environment relatively pristine while accommodating pleasure-seeking visitors accustomed to First World lifestyles.

Case Studies: The Caribbean, Hawaii, and Nepal

The environmental and economic impacts of tourism in the Caribbean Sea varies as widely as the highly uneven development of the industry and its facilities throughout the region. The rapidly expanding tourist industry is highly seasonal, and its fluctuating supply and demand are heavily subject to unpredictable boom-and-bust cycles. A sudden downturn in business because of hurricanes or tropical storms, rising airline prices, recession, unfavorable exchange rates, or uncertain political events can mean a sharp drop in local fortunes, leading to layoffs and closures and devastating island economies. Several small island countries including Anguilla, Antigua and Barbuda, Bahamas, St. Kitts and Nevis, St. Lucia, Turks and Caicos, and the U.S. Virgin Islands depend on tourism for between 50 and 90 percent of their annual gross domestic product.

Environmental problems stemming from tourism tend to be small-scale, intensive, multiple, and scattered among distant sites. Even localized problems, however, can cause disruptions to the wider marine and land ecosystem. Loss of mangrove swamps—dense biomass that naturally regulates atmospheric carbon levels—to overdevelopment may have far-reaching consequences for global warming. Degradation of coastlines from erosion and sedimentation, caused by overbuilding and construction of solid waste or sewage facilities, is a major contributor to water pollution in tourist hot spots like Aruba, Barbados, Jamaica, and Puerto Rico. Runoff from cruise ships, yachts, and passenger ferries is the main source of oil and fertilizer pollution in some of the relatively wealthier playgrounds, including the U.S. Virgin Islands.

In many places, the main attractions are land- and marine-based activities such as reef snorkeling, scuba diving, and fishing. In those areas the protection of fragile coral reefs from overexposure to manmade pollution, erosion, and overharvesting of seafood (including conch, lobster, and grouper) is crucial to maintaining a viable marine habitat for fish and aquatic wildlife. Living coral reefs provide vital feeding grounds and shelter for a wide variety of tropical fish species. Corals are killed off or have their growth slowed down by cooling waters affected by global climate change, as well as by sediment and fertilizer running off of deforested slopes. Corals are also damaged and destroyed by pleasure boats and commercial ships dropping anchor and trawling the seafloor for seafood, or they are worn down by currents and contact from boating and diving activity. They are silt-laden by increased runoff in storms because of construction or the loss of buffer zones such as estuaries, salt ponds, and mangrove swamps. Finally, corals succumb to cooling ocean temperatures and diseases associated with environmental stressors. The loss of reef areas also removes an important protective barrier from shorelines in the Caribbean region, which suffers annual tropical storms and devastating hurricanes.

Hawaii's economy depends heavily on the state's promotion to tourists as an island paradise. As fewer and fewer sugar and fruit plantations remain in operation, a steady influx of visitors is more important than ever to its economic health. Hawaii ranks first among the U.S. states in number of species on the endangered and threatened list, with 317 animal and plant species, more than 25 percent of the U.S. total. The humpbacked whale, monk seal, and green sea turtle are among the larger aquatic creatures whose habitats are being adversely affected by shoreline development (especially of hotel and resort complexes) and marine pollution. Numerous bird species disappeared from Hawaii's forests during the twentieth century, including the Hawaii 'O'o, a long-tailed forest-dwelling bird. The short-tailed albatross, Newell's shearwater, Hawaiian crow, and common moorhen are on the list of endangered or threatened birds. Through strict fishing regulations, the state is charged with ensuring the maintenance of viable populations of near-shore fish, including the bonito, mullet, red snapper, yellow-fin tuna, and other food species that are popular menu items at restaurants and resorts.

Since the late 1970s the Himalayan mountain kingdom of Nepal, one of the world's poorest countries, has become a major destination for its spectacular mountain ranges and semipermanent urban colonies of international travelers and trekkers. Once far off the beaten trail, the small nation now plays host to hundreds of thousands of European, American, Australian, New Zealander, and Japanese guests each year. Tourism is an important source of foreign exchange; yet rural Nepali villagers see scant revenue from trekkers passing through, while urban businesses catering to more than 300,000 travelers per year face a high overhead in imported goods and make little profit. Drug trafficking, corruption, and political turmoil are destabilizing factors accompanying the uneven development of the tourism-dependent Nepalese economy.

In the Himalayas, the world's tallest mountain range, trekking and mountaineering spur development in the form of agricultural production, lodging houses, trails, and jobs. However, most of the currency spent by trekkers goes to pay for costly imports, with less than 2 percent going to local communities, according to a World Wildlife Fund estimate. These modest gains at the village level are being offset by the environmental damage of human and non-biodegradable waste disposal, increased firewood consumption, forest clearing and accelerated erosion on the slopes, and the need for foraging land. The country is heavily dependent on gathered firewood, which provides 83 percent of fuel in urban areas and 98 percent in rural areas (Sattaur, 1996, p. 54), and it is severely lacking in adequate public health facilities and clean drinking water. Even though local practices generally remain at an appropriately modest scale, the heavy influx of foreign visitors can place a heavy strain on the ecosystem. Deforestation of the slopes is an urgent concern. A traveler taking hot showers, having relatively elaborate meals cooked, and burning bonfires for warmth uses as much firewood in a day as a typical Nepali uses in a week. Voluntary efforts to tie conservation into development in the Annapurna area are now getting trekkers organizing expeditions to pack in their own kerosene for fuel.

Endangered animal species in Nepal include tigers in the southern Tarai plains, red panda in the hill country, and snow leopards in the high mountains. Pollution generated by visitors is a growing threat to Nepalese biodiversity. The Mount Everest base camp has become home to a large amount of litter left by international climbing expeditions, with as much as 50 tons of garbage dumped over the past four decades, although the effects so far have been limited mostly to the immediate area. Conservation surcharges, replanting of trees, legislation facilitating community forest management, and restricted tourist access to the most fragile areas have helped to ease the environmental strain of tourism somewhat in Nepal. As elsewhere, sustainable tourism planning requires the cooperation of government, international agencies, local communities, travelers and sportsmen, and the travel industry to boost local benefits while minimizing environmental impact.

Ecotourism

Two of the fastest growing sectors of the tourism industry are ecotourism and ethnic tourism. Ethnic tour packages cater to customers seeking encounters with authenticity in the form of native peoples, cultures, and arts. Some travel in groups to local villages, while others attend showcases, official performances, and other arranged events. Ecological tourism or ecotourism, which depends on the universal appeal of the wonders of nature, is potentially a more lucrative sector than ethnic tourism. Both ecotourism and ethnic tourism share a basic mindset: combining access with preservation.

Generally upscale consumers in search of nature and wildlife constitute a tempting market for packagers, agencies, and government managers of national parks, bird sanctuaries, game parks, and biosphere reserves. Demand is particularly high in the tropics and in biodiversity hot spots like the Central American rain forests. The business practices of ecotourism reflect its customers' concern with bioethics while inevitably making inroads of its own into fragile ecosystems with (at a minimum) vehicles, food and water consumption, and problems of waste disposal. Costa Rica, Belize, and Venezuela are among the states that have implemented successful ecotourism programs to date, offering limited access to sites while promoting preservation and sustainable development of the wilderness.

Some of the world's most spectacular megadiversity sites are among its most endangered, places where a wealth of species have evolved without defenses against man or other predators. In the isolated ecosystem of the Galapagos Islands, made famous by Charles Darwin's observations of rare endemic species, trained guides escort visitors on low-impact nature tours. Although the flightless dodo went extinct in Mauritius soon after human colonization, birds without fear of humans can still be seen up close in remote ocean archipelagoes like the Galapagos and Seychelles. Human access to their nesting grounds must be strictly controlled, as the inadvertent importation of even the smallest predatory animal into their sanctuaries could spell rapid extinction for these rare oceanic bird species.

Big-game safaris and trophy hunting are major businesses in eastern and southern Africa. Game parks, wildlife reservations, and nature preserves attract substantial foreign currency. Africans are building more lodges and modern guest facilities, in a delicate balancing act between preservation and overuse of land and water. The endangered large mammals of Africa are at the mercy of governments, local needs, tourists, and the travel industry. Collaboration and cooperative planning among the various stakeholders need to support set-asides of land and water, conservation activities, research by wildlife biologists, and captive breeding programs. An especially important factor is the training of local people as rangers and guides, to prevent poaching as well as to provide economic alternatives to the environmentally damaging encroachment of subsistence activities onto protected lands.

In South Africa there is increasing local involvement in big-game safaris and expanding economic development in parks and wildlife habitat preserves. Game parks and nature reserves are popular destinations for tourists, and ecotourism is the most rapidly expanding tourism category in South Africa. Tourism now accounts for an estimated 5 to 10 percent of the country's gross domestic product and employs more than 500,000 workers. More than 2.5 million foreign visitors are expected per year, nearly twice the number of guests a decade ago. One of the major tourist areas, Kruger National Park, reports more than 1 million bed-nights occupied annually. Visitors based in bush lodges or beach houses snorkel and scuba, hike and climb, fish and hunt game, take photographs of animals, watch whales and birds, and travel in jeeps, boats, and all-terrain vehicles.

More than 5 percent of the land in South Africa is held in public preserves, and most of the country's biodiversity is represented within the boundaries of those protected zones. However, the protected areas are disproportionately savanna zones, while other ecosystems are more seriously threatened. Nature tours, attracting millions of visitors annually, have become the leading use of endangered resources. In the past, safaris and big-game hunting were for the privileged few who represented the country's elite and their First World international clientele. Changes in official and popular notions of who the stakeholders are in postapartheid South African wildlife conservation have led to rural development initiatives. Local communities are becoming more active in joint management and conservation of lands and resources with park and reserve authorities. The South African state has recently come to regard the traditional knowledge of indigenous caretakers itself as a valuable resource for ethnic and ecological tourism, and a legitimate preservation priority in its function as a potential magnet for the travel sector's continued growth.

Even an ethos proclaiming "Take only pictures, leave only footprints" has inherent limits, as thousands of footprints have a cumulative impact on the fragile ecosystems of rain forests, deserts, volcanic deposits, montane peaks, hidden valleys, and scrublands. In heavily trafficked destinations like Yellowstone National Park or the Hawaiian Islands, the question of how many footprints are too many is reaching a critical juncture. Land and marine preserves presently generate and depend upon the financial support of tourist dollars in a delicate balancing act between commercial exploitation, indigenous stewardship, preservation, and despoliation of scarce or nonrenewable natural resources. The linkage of endangered species conservation with the travel industry, governmental support, and public promotion of wildlife conservation activities is crucial. Plans for developing infrastructure, transportation, and lodgings must include the training of local people as paid caretakers, and the provision of incentives to prevent poaching. If this is not done, the imperatives of survival for expanding populations on a shrinking resource base will render the administrative protection of arable lands and endangered animals moot.

Kenya provides a model of development, with its well-established scientific research community working closely with the managers of game parks and the tourism bureau.

But many other potential tourist destinations lack the spectacular big game animals found in Kenya, as well as financial and institutional resources, political influence, roads and facilities for transportation, and accommodations. Eldredge, writing of the Okavango Delta, observes that ecotourism can be both an economic savior and an ecological destroyer for small communities: "With tourists come speed boats, airplanes, helicopters, four-wheel drive vehicles—not to mention water usage, disposal of human and solid wastes, clearings for buildings and airstrips, and so on." Although the indigenous San people were an integral part of the local Kalahari ecosystem, he points out that "ecotourists are not . . . no postagricultural, let alone postindustrial, people are part of any local ecosystem whatsoever, not even the systems in which each of us lives" (Eldredge, 1998). No matter how passive, respectful, light of foot, and environmentally aware outside visitors may be, they will inevitably affect a system simply by their presence. Finding a sustainable balance between preservation and access is one of the greatest challenges facing the tourism industry in the twenty-first century.

—Thomas R. Miller

See also: Beauty of Nature, Biophilia and Ethics; Coral Reefs; Cultural Survival, Revival, and Preservation; Erosion; Extinction, Direct Causes of; Indigenous Conservation; Organizations in Biodiversity, The Role of; Sustainable Development; Valuing Biodiversity

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Tree of Life of Living Species (Cladogram)

See Evolutionary Biodiversity

Tropical Rain Forests

Tropical rain forests are complex communities of plants and animals that occur in equatorial regions with year-round warmth and abundant rainfall. They grow over large areas of Africa, Asia, and Central and South America. Tropical rain forests occupy only 6 to 7 percent of the earth's surface, yet they contain more than half of the world's plant and animal species. These forests are also home to millions of native people, such as the Kayapo and Yanomami in Brazil, the Dayak of Borneo, and the Mbuti pygmies of Zaire, who have lived in rain forests for several centuries. Tropical rain forests provide us with many goods and also serve important environmental functions. Numerous products of importance in our daily lives, such as chocolate, black pepper, rubber, and coffee come from rain forest plants. Rain forests help regulate the earth's climate, maintain air quality, reduce erosion, and provide habitat for plants and animals. In spite of these benefits, rain forests are being cut at an alarming rate. Some scientists believe that we are losing 40,000 square kilometers of rain forest—an area about the size of Pennsylvania—each year. There is growing concern that the destruction of tropical rain forests will

Tropical jungle forest, the Cameroons. Tropical rain forests occupy 6 to 7 percent of the earth's surface, yet they contain more than half of the world's plant and animal species. (UN photo)

lead to the elimination of thousands of species of plants and animals.

What are Tropical Rain Forests?

Tropical rain forests are woodlands of tall trees that occur in tropical climates. The temperature in a rain forest rarely rises above 93 degrees Fahrenheit or drops below 68 degrees Fahrenheit. An average of four to twenty-one feet of rain fall in a rain forest, and thundershowers may occur more than 200 days a year. Because of the continual moisture and warmth, rain forests stay green throughout the year. Only a few species lose all of their leaves for a brief period. The production of flowers and fruits in the rain forest is not seasonal; it varies from species to species. Some species produce fruits every year, others fruit several times a year, and a large group of trees in southeast Asia, the dipterocarps, produce fruit at unpredictable intervals of from two to five years.

Rain forests contain more different kinds of plants than any other forest in the world. Scientists have counted more than 250 species of trees in small tracts of rain forest in South America and southeast Asia. A similar plot of forest in northern New York would contain only about 10 to 15 tree species. In addition to trees, rain forests contain a great variety of herbs, small palms, bamboos, climbing vines, ferns, and epiphytes such as orchids, bromeliads, and mosses that grow directly on the trunks and branches of large trees. Recent findings suggest that about 45 percent of the world's plant species occur in tropical rain forests.

A large percentage of the animals that live in tropical rain forests are insects. A single rain forest tree in Peru yielded 43 species of ants—about the same number as in all of the British Isles or Canada. A sample of nineteen tree crowns in Panama yielded more than 900 species of beetles. Birds, amphibians, reptiles, and mammals are also common in rain forests. Many animals such as bats, gibbons, monkeys, sloths, frogs, lizards, and snakes may spend their entire lives in the trees and never descend to the ground. Forest deer, hogs, tapirs, and many kinds of rodents roam the forest floor. Chimpanzees, coatis, and several members of the cat family live on the ground and in the trees.

Rain Forests around the World

Tropical rain forests occur in all three of the world's tropical regions: Central and South America, Asia, and Africa. The forests in each region resemble one another, but each contains a distinctive group of plant and animal species.

The Americas

About half of all the rain forests in the world are found in the American tropics (neotropics). The largest expanse of forest—more than 2.6 million square miles—is in the Amazon basin. Rain forests also extend from the Pacific coast of Ecuador and Colombia through Central America to southern Mexico and along the Atlantic coast of Brazil.

Neotropical rain forests contain a rich assortment of plant species. A survey of five acres of forest in the Brazilian Amazon recorded 502 species of plants. Twenty of these species were new to science. Important timber trees such as mahogany, rosewood, and tropical cedar are found in neotropical rain forest, and rubber, cocoa, Brazil nuts, cashews, heart of palm, vanilla, and avocados are also native here.

The rain forests of tropical America are known to contain about 300 to 400 species of birds, 50 to 100 species of mammals, and more than 500 species are butterflies. There are more bats here than anywhere else in the world. Toucans, parrots, sloths, and monkeys feed in the forest canopy. Capybaras, coatis, tapirs, and ocelots forage along the forest floor. The Amazon River contains about half of all the known species of freshwater fish, the piranha being the most notorious example. Neotropical rain forests are home to a variety of native peoples. The Yanomami of northern Brazil, the Shibipo of Peru, the Kuna of Panama, and the Lacandon Maya of southern Mexico all depend on the rain forest for their livelihood.

Asia

Rain forests cover about 1.2 million square miles in the Asian tropics. They grow in western and southern India and extend eastward through Burma, Thailand, Vietnam, and the Philippines. Large blocks of forest occur in Indonesia, particularly in Kalimantan (Indonesian Borneo) and Irian Jaya, Malaysia, and Papua New Guinea. There is also a narrow belt of rain forest along the northeastern coast of Australia.

Asian rain forests are unique in that a single family of trees, the dipterocarps, forms a dominant part of the canopy on many sites. Dipterocarp trees produce valuable timber (meranti) and resins useful for varnish and caulking (damar). The seeds of some species contain an edible fat that is similar to chocolate (illipe butter). Pitcher plants, rattan, gutta percha (a latex used in dentistry), and numerous edible fruits such as durian, rambutan, mango, litchi, and banana are native to the rain forests of Asia. The world's largest flower, the parasitic *Rafflesia*, is also found here.

These forests are home to hornbills, flying foxes, orangutans, gibbons, wild pigs, tigers, elephants, and rhinoceroses. The island of Borneo alone has more than 200 mammal species, 500 resident and visiting bird species, 166 species of snakes, and 183 species of amphibians. There are tens of thousands of species of beetles in Asian rain forests.

The nomadic Penan of interior Borneo rely exclusively on the rain forest for subsistence and rarely practice agriculture. They are one of the last remaining groups of hunter-gatherers in the world. Another Bornean group, the Lun Dayeh of Sarawak, are excellent rice farmers. The Lua people of Thailand harvest more than 200 wild plant species from the rain forest for food and other purposes.

Africa

The African tropics contain about 810,000 square miles of rain forest. The forested area centers on the Zaire basin and extends westward through the Congo, Cameroon, and Gabon to the Atlantic Ocean. Small patches of rain forest also occur on the east coast of Madagascar.

African rain forests are not as rich in plant species as are the rain forests of South America or Asia. Only 50 species of palm grow here, as compared with 1,300 species in the Asian tropics. There are only 4 species of bamboo, and bromeliads are absent. Small tracts of African rain forest contain from 50 to 100 species of trees. A number of excellent timber species, such as African mahogany and ebony, are native to the African tropics. Other well-known plant resources from the region include cola nuts, the oil palm, and coffee.

The rain forests of tropical Africa contain gorillas, mandrills, and chimpanzees. Gorillas and chimpanzees forage on the ground as well as in the trees. Mandrills, with their brightly colored faces, confine themselves to the forest understory. Squirrels and monkeys share the canopy with more than 300 species of birds, lorises, bush-babies, and golden pottos. The okapi, a half-deer, half-zebralike animal, roams the forest floor. Bush pigs and peafowl are also ground-dwellers in these forests.

Forest-dwelling people in the African tropics are collectively known as pygmies. The Mbuti pygmies live in the Ituri forest in northern Zaire. They are partly nomadic and live in groups in simple huts. To the west, the Baka inhabit the rain forests of southern Cameroon, and the Aka are found in the northern Congo.

The Importance of Rain Forests

Rain forests are important to human societies because they contain a high diversity of species and perform a variety of key ecological functions. Rain forests have economic value, scientific and health value, and environmental value. Rain forests are also valuable for recreation. These qualities are maintained only, however, if the rain forest remains intact.

The major economic value of rain forests comes from the production of timber. About 60 billion cubic feet of wood valued at more than $7 billion are harvested each year from rain forests. Nontimber resources such as fruits, nuts, oils, fibers, and resins are also very valuable. Indonesia exports about $300 million of rattan products each year, and more than 50,000 tons of Brazil nuts, 6,000 tons of carnauba wax, and 18,000 tons of rubber are harvested annually from Amazonian rain forests.

Scientific knowledge about tropical rain forests is very incomplete. Of the 3 to 4 million types of organisms that are estimated to live in these forests, only about a sixth of them are known to science. Very little is known about how rain forests function as ecosystems, and how these ecological processes vary from region to region. The complex relationships between plants and animals that have evolved in tropical rain forests are also very much in need of study. Learning how rain forests function can greatly enhance efforts to manage and conserve these ecosystems.

Tropical rain forests contain many undiscovered foods and medicines of direct importance to human health. A survey in Kalimantan revealed more than 400 different plant species used for food. Several important medicines—quinine (used to treat malaria), tubocurarine (a muscle relaxant used in heart surgery), and pilocarpine (used to treat glaucoma)—are derived from rain forest plants. The rosy periwinkle from Madagascar is the source of the vincristine and vinblastine alkaloids used to treat childhood leukemia and Hodgkin's disease.

Rain forests provide several key environmental benefits. They absorb an enormous quantity of rainfall, use it, and then recycle much of it back to the atmosphere as fresh water. They regulate local climate, control soil erosion, and reduce the severity of floods and droughts. Rain forest trees absorb and store massive amounts of carbon dioxide as they grow, thus preventing the build-up of

CO_2 in the atmosphere. This helps to slow global warming, which is triggered by the accumulation of carbon dioxide and other greenhouse gases.

Finally, rain forests are places of great beauty. The lush vegetation, unique fauna, and abundant water resources offer a wealth of recreational opportunities for local residents and foreign visitors. A growing number of "ecotourists" visit rain forests each year. People of all nationalities are learning that the best way to understand the beauty and value of the rain forest is to visit one.

The Future of Tropical Rain Forests

Rain forests are rapidly disappearing. Commercial logging activities and the expansion of agriculture have damaged or destroyed extensive areas of forest in the tropics. Huge mining projects, the construction of hydroelectric dams, and government resettlement programs have also taken their toll on the rain forest. According to the best estimates, the world lost 1.1 billion acres (450 million hectares) of rain forest between 1960 and 1990. This is equal to an area about half the size of the United States. Over the past thirty years, Asia lost almost one-third of its rain forest, and Africa and Latin America each lost about 20 percent. Deforestation is particularly severe in regions like the Atlantic coastal forest of Brazil, Madagascar, and Sumatra, where only very small tracts of forest are left. Less than half of the original extent of the world's rain forest remains. It is estimated that we are losing one plant species and a minimum of 20 animal species every day (7,500 species per year) as a result of tropical deforestation. If this rate of biodiversity loss continues, one-quarter of the world's species may be extinct before the middle of the twenty-first century.

—Charles M. Peters

See also: Agriculture and Biodiversity Loss: Genetic Engineering and the Second Agricultural Revolution; Biogeography; Carbon Cycle; Coevolution; Ecological Niches; Global Climate Change; Pollination

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Turnover Pulse (Coordinated Stasis)

See Evolution

Turtles

See Reptiles

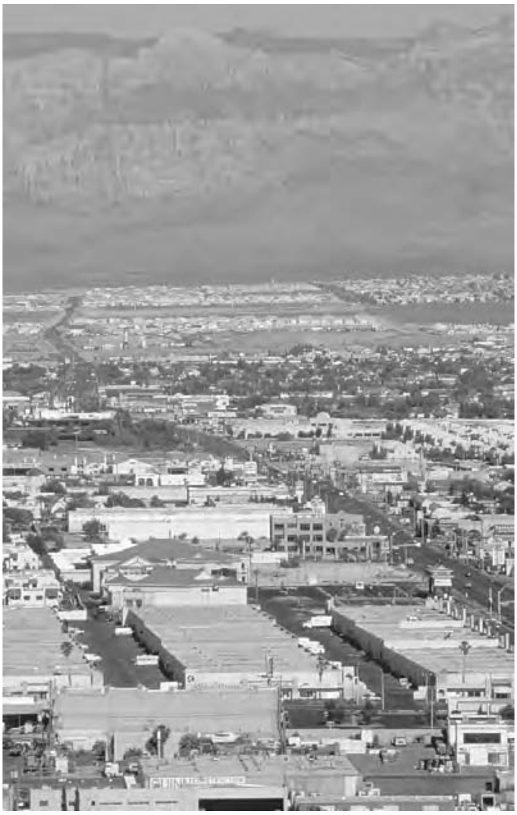
Urbanization

Urbanization—the origin, growth, and spread of cities—has been of great importance to the social and economic history of humanity over the past 6,000 years or more. Urbanization is also of major importance in considering humanity's relation to the natural world—both in terms of the factors that are actively destroying the world's ecosystems and species in the current "biodiversity crisis" (see Sixth Extinction), as well as the positive aspects of organizing and implementing solutions to the world's environmental problems.

Damascus, in Syria, is generally regarded as the world's oldest city; archaeologists are confident that there were people living at the present site of Damascus as long ago as 6000 B.C.; some think that the city might be as old as 10,000 years—reaching back as far as the very beginnings of agriculture. And the link between cities and agriculture is crucial to understanding how and why people have come to live in the densely localized concentrations that we call cities. Prior to the invention of agriculture, some 10,000 years ago, there were no cities—because there could be no cities.

Prior to the invention of agriculture, all humanity existed as hunter-gatherers: people would hunt the animals (game and fish) and gather the plants (fruits, nuts, tubers, leaves, grains, and so forth) that occurred locally. Bands of hunter-gatherers rarely exceeded seventy people and were often smaller; their numbers were limited by the "carrying capacity" of the environment—that is, the amount of food available to sustain a population of humans. Eventually, all the readily hunted game and easily collected plants would be exhausted, and the band would have to move on. Sometimes they would follow migrating herds of game, but all hunter-gatherers were either fully, or at least partially, nomadic. There simply was not enough food available year-round, or for many years running, to allow people to have a completely settled existence.

Agriculture changed all that. When agriculture was invented (independently, in several places, but perhaps earliest in the Middle East around 10,000 years ago), people learned to transform the grasslands and forests of their native regions into cleared fields, in which they planted one or more crop species (from seeds they had formerly collected growing wild). Although history is full of examples of crop failure and episodes of starvation—from ancient Egypt right up to the present day—it is nevertheless true that, for the most part,



Suburbs and developments stretch out from central Las Vegas to the hills beyond. (James Marshall/Corbis)

many more people can be sustained by agricultural productivity than by hunting for meat and foraging for edible plants. The simple proof of that statement is that there were only some 5 to 6 million people on earth at the dawn of agriculture, but now, a scant 10,000 years since human sustenance switched to agriculture and the animal husbandry that goes along with farming, our population has exceeded 6 billion.

But farming requires open land—just the opposite of cities. Flying over the central regions of the United States in the modern era confirms that cities are scattered, often quite far from one another, almost as islands in a sea of farmland. So agriculture doesn't cause cities to grow. But agriculture does require that people remain in one place in order to tend the fields and animals—almost always a year-round proposition. It can supply the food resources that, along with adequate water supplies, are the bare essentials for large concentrations of human beings to develop. And, crucially, agriculture eliminates the necessity for everyone living in a localized region to be engaged in food procurement (in hunter-gatherer societies, women usually gather the edible plants, while men usually do the hunting; all able-bodied adults take part in hunting and gathering food). With the division of labor made possible by agriculture, people began to specialize: for example, some wove, or made pots, or shoes, or bread—which could then be bartered for meats and grains.

As population numbers began to grow in the early days of agriculture, local towns developed. Early agriculture occurred predominantly along fertile river valleys, such as the Indus (India), Tigris and Euphrates (the "Fertile Crescent" of Mesopotamia), and the Nile in Egypt. City-states began to emerge along these waterways as political control of water resources (for example, for irrigation and navigation) began to be important. Towns grew into cities, often with walls for protection from raids from neighboring cities and nations.

Although cities are often full of parks and gardens, most cities—from ancient Egypt up to the present—are dense concentrations of roads and buildings. The streets of modern cities are paved in concrete and macadam, with large stone, steel, glass, and concrete buildings lining their sides. From this perspective there can seem to be no more thoroughly environmentally destructive human activity than the construction of a city. And with their need to feed and supply safe water to ever-larger numbers (some cities have populations as high as 15 to 20 million—all of which produce large amounts of waste each day), cities must reach out far afield for their supplies. Around 1900, Brooklyn (itself then considered the third largest city in the United States) was the principal supplier of fruits and vegetables to New York City (then only Manhattan). Nowadays, New York gets its fruits and vegetables, not only from neighboring communities (no longer Brooklyn, but Long Island and New Jersey), and also from Florida and California. But that's not all: countries as far from New York as Israel and Chile send produce to New York every day. And the very act of consuming what is produced elsewhere around the globe contributes to the drain on the world's environment.

If, however, cities put a tremendous strain on the natural world, contributing greatly to the degradation of the world's ecosystems and the loss of species both near and far, they also present a very positive hope for the future. For it is cities that contain the greatest concentration of knowledge—in universities, for example, as well as in research institutes and museums (see Museums and Biodiversity). Political institutions, as well, are focused in cities (for example, the UN headquarters are in New York), and the solutions to the world's problems always involve political institutions. The news media are concentrated in cities—important sources of information that underlie discussion and decision-making on environmental and other problems. And wealth: cities are sometimes heavily populated by desperately poor people, but most of any nation's wealth is controlled by corporations and individuals that are located for the most part in cities. And if wealth and international trade contribute to the environmental difficulties the world is facing, they also are necessary ingredients of a rational approach to sustainable development that we shall have to achieve to put the utilization of global resources on a sounder, more environmentally friendly footing.

—Niles Eldredge

See also: Agriculture, Origin of; Economics; Ecosystems; Museums and Biodiversity; Sixth Extinction; Species

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Valuing Biodiversity

The question of value has a long and turbulent history in economics, and nowhere is the nature of value more contentious than in the case of biological diversity. We know, of course, that all living organisms, including humans, depend on the rest of nature to survive—so ultimately, its value is infinite. But the value question becomes blurred when we begin to look at specific ecosystems and specific species. A basic difference exists between the way most biologists and most economists view biodiversity. Among biologists there is a consensus that biodiversity is critical to the health of ecosystems and to the long-run survival of the human species, and that biodiversity should be preserved even if its economic value is minimal. By contrast, economists generally view biodiversity as just one among many types of goods available for human use. We may value the species present in a tract of rain forest, for example, but we also value the income that might be generated from cutting the rain forest down and selling the timber. If the income generated from cutting down the rain forest is higher than the income generated by preserving it, then (with some qualifications) most economists would argue that society is better off cutting it down.

Some of the differences between the biological and economic views can be resolved by a better appreciation on the part of economists of the narrowness of estimates of value based on market (or pseudomarket) prices, and a better understanding on the part of biologists of the logic behind the market allocation of scarce resources. The debate may be put into perspective by considering the value of biodiversity at three hierarchical levels. At the most narrow level is the so-called market value of biodiversity; next is its social value, including nonmarket or extramarket values; and finally is its ecosystem value to the total web of life on planet earth. Emphasis will be given here to market value and how it is estimated, but this is in no way meant to diminish the fact that biodiversity is different from other market goods. Markets work by substituting one good for another according to their relative scarcity as measured by market prices. For market goods, relative price is an indicator of relative scarcity. As prices rise for one good, substitutes become more attractive. However, there are no substitutes for many of the services provided by the biological world, and therefore the ability of the market system to ensure biodiversity preservation is limited. Also, a scarcity of most market goods can be corrected by producing more of these goods. Biodiversity loss, by contrast, is irreversible on any time frame relevant to the human species.

The Market Value of Biodiversity

Market value is the monetary worth of a commodity relative to other commodities available to individual consumers. The value of a commodity is determined by how much consumers want it (demand) and how much of it is available (supply). Of course the total value of all biodiversity on the planet is infinite, since without it we could not survive. But its direct market value is limited, because most of the essential features of biodiversity are not traded in markets. Things like ecological resilience, evolutionary potential, or the oxygen produced by photosynthesis, do not have direct market value, even though they are essential to the survival of the human species. Consumers cannot express a "market demand" for these and many other features of biodiversity.

The modern market economy has served us well in guiding the use of natural and human resources and has provided a dazzling array of consumer goods to much of the world's population. Markets have proven to be so successful as a way of allocating scarce resources that it is sometimes difficult to accept any alternative. There is a real danger, however, in using monetary values to determine the proper use of the essential features of nature upon which all life depends.

Using market values, estimates have been made of the economic value of specific plants and animals. For example, wild plant species are an important source of pharmaceuticals. A frequently mentioned example of biodiversity value is the rosy periwinkle of Madagascar, which is used to produce drugs to treat Hodgkin's disease and leukemia. The income from the sale of these drugs is estimated to be around $200 million per year. The market value of yet-to-be-discovered drugs from rain forest species has been estimated to be between $3 and $4 billion.

Another important market value of biodiversity is tourism. For example, it is estimated that the direct economic benefit of Wyoming's big game animals, from tourism and hunting, is about $1 billion, or $1,000 for every large animal. The total value to the tourism industry of wildlife in all North American national parks is estimated at more than $70 billion. Estimates of the value of biodiversity may be made using survey techniques or by what is called hedonic pricing. Hedonic pricing imputes the value of an attribute by comparing cases in which it is and is not present. For example, a house on a lake without loons may be valued at $200,000, and a similar house on a similar lake with loons may be valued at $210,000. The presence of loons on the lake, then, adds $10,000 to the value of the second house. Economists can use this and other such hedonic values to piece together an estimate of the economic value of loons on that lake.

Nonmarket Values of Biodiversity: Humans in the Web of Life

All humans share a common ancestor with all the other species on planet earth. We coevolved with other species within complex ecosystems, and many scientists argue that these origins are reflected in our biological makeup and even our social institutions. We are complex mammals that need some regular contact with nature and other species for our mental health and well-being. The biologist E. O. Wilson coined the term *biophilia* to describe the affinity humans have with other species. Evidence for the need humans have for some contact with the natural world has been found in numerous psychological studies and even in economic studies seeking to determine the value of particular species. Questionnaires are sometimes used by economists to elicit nonmarket values, using a technique called contingent valuation. In these studies a significant number of respondents state that a particular species (blue whales, eagles, or coyotes, for example) should be preserved no matter what the cost—a singularly noneconomic response.

Economists recognize that not all values are captured in market prices. Sometimes people want to preserve nature not to use immediately but to keep open the option of using it sometime in the future. This is called option value. In other cases people get some satisfaction just by knowing that particular living things exist—blue whales or giant squid, for example—even though there is a small chance that they will ever see them. This is called existence value, and surveys show that it may be the most important aspect of the value that humans place on biodiversity.

The Value of Biodiversity to Ecosystems

It is generally accepted that biodiversity plays an important role in contributing to the stability and resilience of ecosystems, but that role is very complex. Some studies show that ecosystems with greater biodiversity are more resistant to disturbances such as drought. Biodiversity may also play a role in water and nutrient retention, plant productivity, and decomposition. An important finding of ecosystem studies is that the adverse effects of biodiversity loss are frequently nonlinear—that is, no serious effect may occur at first as species are lost, but then a threshold is reached at which serious consequences occur suddenly. An important issue here is the contribution of biodiversity to evolutionary potential. Seemingly redundant species may assume a key role in ecosystems when environmental conditions change or when other species can no longer play a keystone role. So yet another value of biodiversity to humans is as an insurance policy against the effects of environmental change. A change in climate, an invasive species, or human disturbance, may be less damaging to an ecosystem if it has the evolutionary potential to respond to change.

What Can Be Done to Stem the Tide of Biodiversity Loss?

There are essentially two different world views of the proper policies to be taken to protect biodiversity. Environmental economists see the loss of biodiversity as an example of what they call market failure—that is, market prices fail to capture the true economic value of biodiversity. Ecological economists, on the other hand, see biodiversity loss as a failure of markets—that is, an unregulated market economy with its emphasis on short-term individual gain cannot be expected to preserve ecological integrity. If market failure is the problem, the proper policy response is to “get the prices right” by using taxes and subsidies to ensure that all the economic benefits of biodiversity are included in its price. If market prices are inherently incapable of reflecting all the benefits of biodiversity, stronger governmental action is called for.

In spite of the inherent conflict between market valuation and biodiversity preservation, a number of steps can be taken to minimize this conflict. These include the following:

1. Stop subsidizing the destruction of biodiversity. In many cases governments subsidize the destruction of biodiversity by supporting environmentally unsound practices that would not take place under free market conditions. Examples are massive subsidies by governments around the world to the fishing industry, which has led to overharvesting of fisheries worldwide; and subsidies to the tim-

ber industry, encouraging the destruction of old-growth forests. Direct and indirect subsidies to the fossil fuel industry encourage the exploitation of pristine habitats.

2. Use the market system where possible to protect biodiversity. For the market system to function properly, the prices of commodities must reflect their true value. When market failure occurs it is a legitimate function of government to ensure that unregulated markets do not harm the social good. Biodiversity is generally undervalued since it is not traded in the market. In some cases it is possible to partially correct this shortcoming by giving consumers information, for example, through eco-labeling—labeling tuna as "dolphin friendly" or lumber products as being from "sustainable forests."
3. Exploit win-win situations. In some cases jobs and income may be generated from biodiversity protection. Eco-tourism may generate more income than the exploitation of natural areas. Preserving natural areas for natural regeneration may increase income by more than enough to offset the loss created by the reserve. For example, it has been shown that marine reserves may increase the number of fish outside the reserves. More money may be made by whale watching than can be made by whale hunting.
4. Create and protect large contiguous wild areas. Ecosystems function in ways that we are only beginning to understand, and we are losing them before we know exactly how they work. As Aldo Leopold, one of the founders of the American conservation movement, put it: A basic rule of intelligent tinkering is to save all the parts. The more wild areas we protect, the greater the chance that we will survive the population and resource use bottlenecks of this new century.

Economics is fundamentally about choice. Choices should include not only those concerning what to consume but also those concerning what to preserve. Biodiversity loss is irreversible, and the current loss of biodiversity limits our future choices. Humans are now triggering unpredictable but most likely negative changes in the environment. The effect of climate change on agriculture could put tremendous pressure on the ability of technology to cope with feeding the 6 billion-plus people on the planet. With biodiversity loss comes a loss of responses to this adverse change. In the twenty-first century we will need all the flexibility at our disposal to meet the challenges that may threaten the very existence of our species.

—*John Gowdy*

See also: Economics; Industrial Revolution/Industrialization; Sustainable Development; Why Is Biodiversity Important?

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Vertebrates

See Amphibians; Birds; Mammalia; Reptiles

Viruses

Viruses are replicative bits of DNA or RNA within a protein coat; sometimes they are also enveloped in a lipid bilayer that comes from the host cell. Viral nucleic acids code for proteins that assemble viruses within host cells. Although often called organisms, viruses are not true organisms but rather obligate molecular parasites that in principle lack the full complement of cellular machinery necessary to reproduce on their own. The biggest taxonomic division in living beings is that between prokaryotes, bacteria with no nuclei in their cells, and eukaryotes, all other nonbacterial cells, which as a rule possess nuclei in their cells (there are a few exceptions, such as the blood cells of mammals, which lack nuclei).

The five-kingdom classification scheme divides all life into bacteria (prokaryotes) and their evolutionary descendants—protoctists, plants, animals, and fungi. Notice that viruses do not appear within these kingdoms. Viruses do not grow bigger and split in two as microorganisms do. They can reproduce prodigiously, but not on their own. Viruses are so small that thousands of them can fit in the nucleus of a eukaryotic cell; whereas an animal cell consists of 10,000 genes coding for specific proteins, some viruses have as few as four genes. Lacking the chemistry of self-maintenance called metabolism, they are much smaller than cells. Outside of cells viruses are inert—they cannot reproduce, feed, or grow. Little more than pieces of DNA or RNA, viruses are best grouped with plasmids, replicons, naked DNA, and other movable bits of nucleic acid that are sometimes integrated into the cyclical functioning of cells, thereby reproducing themselves. An extracellular virus particle, called a virion, may be nothing other than a package of nucleic acid surrounded by many repeat copies of an encasing protein.

Viruses are usually shaped as helical rods or icosahedral spheres. Some are differentiated into rocket ship and hypodermic shapes, with a head full of nucleic acid and a tail to attach to the host cell and inject the viral genes. Some symmetrical viruses have been crystallized using X-ray diffraction crystallography. Advances in electron microscopy and computer imaging improve our understanding of these quasi-beings.

Viruses' Role in Disease

The word *virus* comes from the Latin meaning "poison," the result of the pathological and sometimes lethal outcomes of viral infections. Although microbiology has been dominated by the attempt to root out disease, healthy organisms are characterized not by their biological purity but by the ecological harmony of the cells that compose them. Organisms that invade and kill their hosts also ruin their environment, and are thus selected against in evolution. The same logic applies to viruses: although infamous for their role in diseases such as colds, herpes, measles, mumps, influenza, polio, smallpox, hepatitis, and human papilloma viruses (HPVs) and AIDS (HIV), most viruses go unnoticed because they cause no harm. A virus that multiplies too rapidly—say, by killing its hosts before they can reproduce—also destroys itself. Thus, over the vast reaches of evolutionary time, viruses that either do no damage, or less-than-fatal damage, have been the ones to survive. Because a given virus makes more of itself only under specific conditions, it may be stable within a population until that population itself overgrows, providing the virus with new opportunities for replication.

Thus the crowded conditions of modern humanity have been ideal for the spread of viruses, as has our tendency to replace biodiverse environments with agricultural monocrops. As frightening as they seem, the blind replication of a given virus that is afforded opportunities for growth helps keep ecosystems diverse, by tending to attack species components that become disproportionate. Viruses can also mutate to attack new hosts. The immune system recognizes as foreign to the body those strange proteins produced by viral growth. The immune response involves a variety of cells that recognize and destroy the replicating intruders. One of the frightening things about HIV is that it attacks the immune system itself, like a peremptory military strike against a missile defense system. However, again, we should not get too carried away with such militaristic medical metaphors, as parasites actually need the hosts that they are attacking to live.

History of Viruses and Virology

French-Canadian microbiologist Felix d'Herelle of the Institute Pasteur in Paris and later of the Université de Montreal discovered viruses in bacteria in 1917. Calling them bacteriophages (literally, "bacteria eaters"), d'Herelle inferred their existence when he found that infectious agents passed through filters with pores too small to admit passage by bacteria. His work followed on that of British bacteriologist F. W. Twort, who found Staphylococcus bacteria that were infected. Although subvisible agents causing infection in plants and animals had previously been known and named viruses or virus pathogens, not until the work of Twort and d'Herelle was it understood that they required host cells to reproduce.

Viruses come in two basic varieties, DNA viruses and RNA viruses. A DNA virus transcribes its DNA into RNA, which uses the host cell to make viral proteins instead of the cell's own proteins. Interfering with the normal functioning of cells, these new proteins at worst can destroy the cells whose machinery they borrow to promote themselves. When a DNA virus attacks a eukaryotic cell, it uses the mitochondria of the host cell to gain energy to rearrange its amino acids into the new proteins, some of which are enzymes that cut and splice pieces of the virus's protein and DNA to make new proteins and DNA. In extreme cases the entire cell is converted into viruses and the viruses burst out, rupturing and destroying the host cell. This process is called lysis. Less violent DNA viruses are not as dangerous to their hosts. For example, thirty different sorts of adenoviruses are commonly found in humans, and their only effect is the minor respiratory aliments we call colds; these same viruses, however, can produce cancer if transmitted to rodents—a less stable environment with which they share no evolutionary history. DNA viruses are further classified into whether their genome is single- or double-stranded.

RNA viruses do not even possess their own genes. They are, rather, tiny chemical bundles that mimic the host's messenger RNA, the RNA that translates the "code" (nucleotide sequence) of DNA into the amino acid sequence of proteins in live cells. Intercepting cell reproduction at the protein-building level, RNA viruses are responsible for yellow fever, Colorado tick fever, mumps, AIDS, and foot-and-mouth disease in livestock. Tumor-forming or oncogenic viruses are also known from this group.

The Bittner virus is an RNA virus that causes cancer in mice; the virus, transmitted through the mother's milk, may reach concentrations as high as 50 billion viral particles per drop. Such oncogenic viruses were first discovered in chickens with symptoms of the blood disease leukemia. At first most of the cells invaded by a tumor-forming virus die. The remaining cells, however, turn cancerous. They reproduce without respect for the normal taboo on tissue growth. The growth of the cancer cells, ultimately fatal to the animal body as a whole, in the short term helps replicate the virus by forming tumors. RNA viruses are subdivided into two types of single-strand RNA and one type of double-strand RNA. Still other viruses, retroviruses (such as HIV) and hepadnaviruses, are known and classified according to the intricacies of their genetic integration into host cells. Exposed to ultraviolet radiation, some bacteria lyse, releasing hoards of viruses. Because they are small and mobile, viruses play a role in evolution, by spreading bits of DNA and RNA from one species to another; although more likely to cause malfunction and disease, occasionally such transferences may be useful. Evolutionarily, the first viruses are thought to have been pieces of nucleic acid that became dislodged, perhaps under the influence of solar ultraviolet radiation, from the genes of bacteria. The lack of an ozone layer on the early earth exposed cells to relatively high levels of radiation. Because of their role in disease, the study of viruses, virology, is a well-funded and vibrant subdiscipline of medical microbiology.

—Dorion Sagan and Lynn Margulis

See also: Bacteria; Classification, Biological; Coevolution; Five Kingdoms of Nature; Microbiology; Natural Selection; Population, Human, Curbs to Growth; Protoctists

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Volcanoes

Volcanoes are landforms that are made of molten material, gas, and rock that rise through a conduit from the earth's mantle and erupt onto the surface. Molten rock that flows out on the surface is called lava. The shape and size of a volcano is determined by the volume of material, its composition and viscosity, the amount of gas, and in some cases the wind direction. Eruptions are hard to predict, and they can vary in eruptive style during the same episode and in subsequent eruptions.

Eruption of Mount St. Helens, Washington, 1980 (USGS/MSH-Rosenbaum J.)

Shield volcanoes are typical of intraplate eruption, where the lava is fluid and produces low-profile structures that in many instances are quite large because of the huge volume of material. They are the least violent volcanoes. A good example of a shield volcano is Mauna Loa on the island of Hawaii, which is produced by a mantle plume or hot spot on the ocean floor.

Composite or stratovolcanoes are among the most violent and are usually found adjacent to subduction zones. It is there that the sinking plate melts because of friction and being jammed down into hotter parts of the earth. The resultant molten rock rises upward through the continent, changing its composition as it dissolves some of the rock it passes through. Mount St. Helens in Washington, and many of the volcanoes found in the Andes Mountains of South America, are typical examples of composite volcanoes. Cinder cones are built up of molten material blasted into the atmosphere, where it cools and then falls to the surface around the vent, forming a volcanic edifice. If a strong wind is blowing during the eruption, more material may be blown to one side, forming an asymmetric cone. Often, huge volumes of lava flow out onto the surface through long cracks, forming flood lavas. Good examples of these are found in Idaho, India, and Scotland.

Resurgent volcanoes are the most violent. They are located over hot spots beneath continents, and when they erupt so much material is ejected that the entire volcanic structure collapses, leaving a huge caldera. The floor of the caldera, often containing a lake, lifts upward after the main eruptive phase, and hence its name. Lake Toba in Sumatra and the partially covered volcano that encircles most of Yellowstone National Park are examples of resurgent calderas.

Geologists are interested in volcanic eruptions because the molten material and gases are direct windows into the interior of the earth. Eruptions of these materials have been going on ever since the earth melted, during the early part of its history. Gases released from the interior during this time have made major contributions to the formation of the earth's atmosphere and oceans. Periods of intense volcanic eruption in subsequent periods of geologic history have thrown large amounts of ash and gas into the atmosphere, blocking sunlight and resulting in the alteration of climate, and possibly affecting life.

There are more than 500 active volcanoes on the earth that have erupted during recorded history. If a volcano has not erupted during recorded history but geologists think that there is a good chance that it will, it is said to be dormant. If a volcano will not erupt again, it is called extinct.

—*Sidney Horenstein*

See also: Geology, Geomorphology, and Geography; Oceans; Plate Tectonics

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Wallace, Alfred Russel

Born in 1823, in Usk, England, a small town near the Welsh border, Alfred Russel Wallace was raised in genteel poverty. His first employment was helping his brother John survey land parcels for a railroad. While still in his twenties, he taught school in Leicester, where he met young Henry Walter Bates, who shared his passion for natural history. On weekend bug-collecting jaunts, the would-be adventurers discussed such favorite books as Darwin's *Voyage of the H.M.S. Beagle* (1845) and dreamed of exploring the lush Amazon rain forests.

They were also inspired by Robert Chambers's anonymously published *Vestiges of Creation* (1844), a controversial popular treatise on evolution. Scorned by scientists, *Vestiges* championed the idea that new species originate though ordinary sexual reproduction rather than by spontaneous creation. Wallace and Bates decided that they would comb the exotic jungles to collect evidence that might prove or disprove this exciting "development hypothesis" (later known as evolution).

Bates and Wallace reached Pará, at the mouth of the Amazon, in May 1848; they collected and explored the surrounding regions for several months, then decided to split up. Wallace went up the unknown Rio Negro, leaving Bates to the upper Amazon regions. From 1848 until 1852, Wallace collected specimens and made numerous discoveries despite malaria, fatigue, and the most meager supplies. Wallace had to finance his expeditions by selling thousands of natural history specimens, mainly insects, for a few cents apiece, to the British Museum.

When he finally returned to rejoin Bates downriver, he found that his beloved younger brother Herbert had traveled across the world to join the adventure and had just died of yellow fever in Bates's camp. Grief-stricken, exhausted, and suffering from malaria himself, Wallace boarded the next ship for England. With him went his precious notebooks and sketches, an immense collection of preserved insects, birds, and reptiles, and a menagerie of live parrots, monkeys, and other jungle creatures. As Wallace was suffering a new attack of malaria at sea, the ship suddenly burst into flames off Bermuda. He was able to grab only a few notebooks as he dragged himself into a lifeboat. Everything else burned or sank beneath the waves, but he was rescued after a few days by a passing ship.

The measure of Wallace's enormous courage and resilience showed itself shortly after his

Portrait of Alfred Russel Wallace (Bettmann/Corbis)

return to England. With the insurance money he received for part of his lost collections, he immediately set out on a new expedition (1854–1862), this time to the Malay Archipelago. Before he reached thirty, Wallace had established a solid reputation as an explorer, zoologist, botanist, geologist, and anthropologist. He is also known for having discovered thousands of new tropical species, as the first European to study apes in the wild (orangutans in Borneo), and as a pioneer in zoogeography (the distribution of animals) and author *of Travels on the Amazons* (1869) and *The Malay Archipelago* (1872).

Wallace's studies of animal populations led him to recognize the "Wallace's Line," a natural faunal boundary in Malaysia that separates Asian-derived animals from those evolved in Australia. More than a century after he deduced its existence by mapping animal populations, the existence of the boundary was found to coincide with the edges of ancient tectonic plates that now lie under the sea.

His greatest claim to fame, however, is that he was the coauthor, with Charles Darwin, of the theory of evolution by natural selection, which he invented independently of Darwin. In 1855, while in Sarawak, Wallace wrote an important paper about when and where species originate. ("The how," he wrote, "was still a secret only to be penetrated some years later.") His paper, "On the Law which has Regulated the Introduction of New Species," stated: "Every species has come into existence coincident both in space and time with a preexisting, closely-allied species." This preliminary conclusion, he knew, "clearly pointed to some kind of evolution." Darwin was greatly impressed by Wallace's paper, as he had seen fossils of extinct giant sloths and armadillos in South America, and had realized that smaller, related living species still inhabit the same areas.

In February 1858, Wallace was living in a forest hut on an island near Borneo, and suffering from attacks of malarial fever. "It was during one of these [malarial] fits," he later recalled, while thinking about how species may have originated, that "somehow my thoughts turned to the 'positive checks' to increase among savages and others described . . . in the celebrated 'Essay on Population' by Malthus." Then, Wallace later recalled, the idea of survival of the fittest came to him "in a flash": in every generation those that were less well adapted to their environment would perish without leaving descendants, and the superior would remain to breed individuals like themselves. Wallace became convinced that he had found the long-sought-for law of nature that solved the problem of the origin of species, wrote it out carefully on succeeding evenings, and sent to Darwin in England.

It was this article, "On the Tendency of Varieties to Depart Indefinitely from the Original Type" (1858), that sent Darwin into a panic, for he had not yet published the evolution theory that he had been working on for twenty years. Darwin's friends, the geologist Charles Lyell and the botanist Joseph Hooker, arranged to have Wallace's paper read along with some of Darwin's early drafts on July 1, 1858, at a meeting of the Linnean Society of London. The following year Darwin raced to finish the *Origin of Species* and rushed it into print.

Wallace was informed of these developments and received a copy of Darwin's book while still in Malaysia. When he returned to England in 1862, Darwin was anxious about Wallace's reaction, and he was relieved to discover his "noble and generous disposition." Later Wallace maintained that even if his only contribution was in getting Darwin to write his book, he would be content.

After publication of the *Origin* in 1859, evolution by natural selection, biology's great unifying concept, became famous as "Darwin's theory." Since, however, it was first announced jointly with Wallace the previous year, it should actually be called "the Darwin-Wallace Theory." Wallace carried modesty to extremes, however, even calling his own book on evolution *Darwinism* (1889). Had he been more ambitious and less generous, evolutionary science might have become known as Wallaceism.

In addition to the chronicles of his travels, Wallace turned out a remarkable series of books, all landmark contributions to evolutionary biology: *Contributions to the Theory of Natural Selection* (1870), *Geographical Distribution of Animals* (1876), *Island Life* (1882), and *Darwinism* (1889). His somewhat mystical idea of the earth as a complex living system (or perhaps even a composite organism) seems, in some sense, to have foreshadowed James Lovelock's controversial Gaia hypothesis by a century.

—*Richard Milner*

See also: Biogeography; Darwin, Charles; Evolution; Evolutionary Biodiversity

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Whales

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Xenarthrans (Edentates)

Living and extinct xenarthrans are endemic to the New World and distinguished from all other living and extinct mammals by their extra joint articulations (xenarthrous articulation) bracing the lumbar vertebrae (*xenarthra* means “strange joints”). In most mammals, the vertebrae articulate with each other by two dorsal bony processes (zygapophyses), but xenarthran vertebrae also have lateral vertebral articular processes with dorsal and ventral arms. Some xenarthrans, primarily anteaters and armadillos, play an important ecological role in insect control.

The most current classification of mammals arranges the twenty-nine living species of Magnorder Xenarthra into thirteen genera, four families, and two orders. Order Cingulata contains the eight genera and twenty living species of armadillos (Dasypodidae). Order Pilosa consists of Suborder Vermilingua, containing the giant anteater, the two species of tamanduas, and silky anteater (Myrmecophagidae); and Suborder Phyllophaga for the two species of two-toed tree sloths (Megalonychidae) and the three species of three-toed tree sloths (Bradypodidae). Pangolins were once thought to be closely related to xenarthrans, but that association has been rejected.

Xenarthrans are highly specialized and are morphologically isolated from all other placental mammals. They likely separated from ancestral placental stock before the divergence of other modern placental orders. The modern xenarthran fauna represent but a small fraction of the rich xenarthran evolutionary diversity. Fossils dating from the Late Paleocene up to the Late Pleistocene and even prehistoric times have been described representing 108 extinct genera and 1 extinct family in Order Cingulata, and 96 extinct genera and 6 extinct families of Order Pilosa. The earliest fossils are from Late Paleocene strata in South America and consist of bony plates that once formed the armor of an extinct armadillo (Dasypodidae). That recognizable armadillos existed at that early period of the Cenozoic suggests that xenarthrans originated much earlier, possibly in the Cretaceous. The greatest evolutionary diversity of xenarthrans occurred between Late Paleocene and Pliocene times, when South America was an island continent; it included evolutionary lines of armadillos, huge armadillolike glyptodonts, anteaters, ground sloths, arboreal sloths, and even sloths exploiting aquatic habitats. The origin and evolutionary history of xenarthrans was confined to South America between Late Paleocene and Pliocene times, with secondary centers of radiations in Central American, North America, and Caribbean Islands after the Pliocene, when North and South America were tectonically connected.

Xenarthrans share other features besides their specialized lumbar vertebrae. In many species, especially armadillos, lumbar and caudal vertebrae are fused to the pelvis (ilium and ischium), some cervical (neck) vertebrae are fused to the axis forming a single vertebralike structure, and in some glyptodonts all backbone elements, from the pelvis to the neck, are fused. An extra cranial bone (septomaxilla) occurs in some species and is found elsewhere among living mammals only in monotremes. Scapular processes are prominent, and a clavicle is present. All living species lack incisors and canines (two-toed sloths have caninelike teeth, but no true canines; a few extinct forms had true canines). Cheek teeth lack enamel, and each has an open root, allowing continuous growth throughout the life of the animal. The number of teeth varies in armadillos and sloths (the giant armadillo has up to 100 small teeth), but anteaters lack teeth.

Most species have five clawed hind digits and three to five front digits with two or three of them bearing very long, sharp, and strong claws. A double vena cava (returning blood from posterior body regions to the heart) is common; this is a large single vein in most other placental mammals.

Living armadillos range from the Strait of Magellan at the southern tip of South America north through Central America and Mexico into the southeastern United States. The twenty species are found in a broad range of habitats: deserts, savannas, pampas (grasslands), temperate deciduous forests, and tropical evergreen rain forests. Their most conspicuous and unique trait is the protective, jointed, armorlike covering (carapace) over the head and body that is formed by bony scutes covered by horny epidermis. The scutes are arranged into a rigid plate on the head, and bands on the body connected by flexible skin. Sparse hair projects between the bands and covers the limbs and undersurface of the body. The tail of most species is also covered by bony scutes. Because the armor covering is sufficiently flexible in some species, they can roll into a ball, protecting their vulnerable soft underparts. Leathery ears range from small to large. The snout is usually elongate, and all armadillos have a long, protrusible tongue. Upper cheek teeth occur in the maxillary bone only, except for one species that also has premaxillary teeth. Sections of the vertebral column are fused (some cervical vertebrae are fused; lumbar and caudal vertebrae are fused with the pelvis), producing a rigid vertebral column that braces the carapace. The front limbs are powerful, and the digits are armed with long, strong digging claws. Armadillos walk on the tips of the front digits but on the soles of the hind feet (plantigrade).

There is a great range in body size among armadillos. The smallest are the two species of pichiciegos (*Chlamyphorus*), which are about the size of a small rat, with a head and body up to 117 mm long, tail up to 35 mm, and weight about 85 gm. The giant armadillo (*Priodontes maximus*) is the largest (about the size of a large dog), with a head and body up to 100 cm long, a tail up to 50 cm, and weighing up to 32 kg (zoo animals may reach 60 kg). All armadillos are terrestrial, some are nocturnal, others diurnal. They use their powerful front limbs and claws to dig for food and excavate burrows, where they stay when not active. Most species eat insects, but other invertebrates, small vertebrates, plants, and sometimes carrion are also sought. Armadillos may be solitary, travel in pairs, or sometimes form small bands, depending upon the species. After a gestation period extended by delayed implantation, armadillos bear a litter (up to twelve, usually two to four) of identical young produced from a single egg.

The armadillo traits reflected in the fused vertebrae and carapace reached their greatest specialization in members of the extinct Glyptodontidae, the other family in Order Cingulata. This group reached its greatest diversity between the Miocene and Pleistocene, perhaps in response to the spread of pampas in South America during that time. The largest was 2.5 to 3 m long and had a huge, turtlelike, inflexible carapace supported by an arched backbone in which the pelvis and all the sacral, lumbar, and thoracic vertebrae were fused into a single, immobile unit. The very heavy carapace was also supported by massive limbs. These ponderous animals were probably herbivores and grazed slowly over the pampas.

Living anteaters range from southern Mexico through Central America and into South America as far as Paraguay and northern Argentina. Habitat includes savannas, pampas, and tropical forests. The specializations of these xenarthrans reflect their ability to capture and eat social insects, primarily ants, termites, and bees. The skull consists of an elongate cranium, long and tapered rostrum, and a long, delicate mandible. The mouth is tubular. All anteaters lack teeth. Jaw musculature is reduced, but muscles controlling the tongue are well developed and strong. The highly specialized tongue is long, slender, covered with backward-directed, spinelike papillae, protrusible, and attaches by muscles to the sternum (breastbone), rather than to the hyoid bones in the throat (the site in almost all other mammals). Salivary glands secrete a sticky saliva that covers the tongue. Powerful front limbs end in four digits, three of them bearing large, robust, and recurved claws (the fourth digit has a small claw).

Tamanduas (*Tamandua*) and silky anteaters (*Cyclopes*) walk on the side of the front foot, with the digits and claws pointing inward; the giant anteater (*Myrmecophaga*) walks on its knuckles, with its digits partly flexed (the claws are protected in both stances). The four or five hind digits bear small claws, and the animals walk on the soles of the hind feet. The strong front limbs are used to tear apart ant and termite nests. Eggs, larvae, and adults are picked up by the sticky tongue and swallowed whole. Giant anteaters are terrestrial and mostly diurnal; tamanduas are arboreal and terrestrial and active during day and night; and the silky anteater is strictly nocturnal and terrestrial, rarely descending from tree crowns. Tamanduas and the silky anteater have strongly prehensile tails. The giant anteater does not construct burrows, but rests curled up in tall grass and forest underbrush; tamanduas shelter in large tree holes; and the silky anteater rests during the day in vine tangles or on branches in the tree crown. The silky anteater, about the size of a tree squirrel, is the smallest living anteater, with a head and body up to 230 mm long, tail up to 295 mm long, and weighing up to 295 gm. The largest is the giant anteater, about the size of a wolf, with a head and body up to 120 cm long, a tail up to 90 cm, and weighing up to 60 kg. Anteaters are solitary or go about in pairs; a female and her young may form a small band. All living anteaters bear a single young; gestation ranges from 130 to 190 days.

The five species of living tree sloths occur only in tropical evergreen rain forests from Honduras in Central America south to northern Argentina. About the size of monkeys, these animals are highly specialized for arboreal life and a folivorous diet (young leaves, tender twigs, and buds). For most of their lives they hang from limbs in the crowns of trees, a position they maintain while eating, sleeping, mating, and giving birth. They descend to the ground once or twice a week to urinate and defecate, and will occasionally descend and move awkwardly along the ground to another tree. Two-toed sloths (*Choloepus*) have long limbs, with the front limbs being only slightly longer than the hind limbs. Their feet are narrow and curved, with two digits on the front feet and three on the hind. All digits of each foot are bound together by skin. The claws are very long, laterally compressed, and recurved. Three-toed sloths (*Bradypus*) have three digits on both front and hind feet, and each digit bears a long, recurved claw. The front limbs are much longer than the hind. Both kinds of sloths hang from branches by their long limbs and grappling claws. The tail is absent or vestigial in *Choloepus* but short and blunt in *Bradypus*. Tree sloths have shaggy, coarse fur consisting of long overhairs and short underfur. The overhairs are roughened by transverse cracks or longitudinal fluting, providing habitat for green algae and cyanobacteria in the fur of *Choloepus* and algae in the fur of *Bradypus*—giving the sloths a greenish cast if the algae is prolific. The coat of *Bradypus* also provides refuge for some species of moths and beetles. Like other strictly herbivorous mammals, tree sloths have a chambered stomach in which digestion is enhanced by micro-organisms that break down cellulose. Cervical vertebrae vary from five to nine (seven is usual in nearly all other mammals), and allow a greater range of head movement, which is important to a sedentary, hanging animal. Tree sloths bear a single young after gestation of about 11 months in *Choloepus* and up to 106 days in *Bradypus*.

Living tree sloths appear very similar, but aspects of their morphology, physiology, and ecology are convergent. The two species of two-toed tree sloths are the only survivors of the Megalonychidae, which reached its greatest diversity during the Miocene-Pleistocene (more than twenty-five extinct genera) in South America, and included arboreal and giant terrestrial species. One of these ground sloths, *Megalonyx*, was the size of a large cow, evolved in North America, and once occurred as far north as Alaska. The Family Bradypodidae contains only three-toed tree sloths and is not represented by fossils. Anatomy of the living species indicates a very distant relationship to both Megalonychidae and the extinct Megatheriidae.

—Mary Ellen Holden

See also: Arthropods, Terrestrial; Bacteria; Mammalia; Protoctists

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Z

Zebra Mussels

See Alien Species

Zoology

Zoology is the subdivision of biology (the scientific study of living systems) that deals specifically with animals. Animals belong to the Kingdom Animalia (see Evolutionary Biodiversity). Animals are multicellular eukaryotic organisms—meaning that animal bodies are composed of many cells that have most of their genetic information located in a distinct, double-walled nucleus within the cell.

Animals are heterotrophs—meaning that they derive the energy they need to develop, grow, and stay alive through the consumption of other animals, plants, or fungi. Most animals are capable of movement (locomotion) during at least some phases of their life cycle; for example, though barnacles (crustaceans) are rooted to the sea bottom, they develop from free-swimming larvae.

Animals have developed a wide range of feeding and locomotion mechanisms that determine in large measure the role that each species of animal plays in its ecosystem. Although the variety of feeding and locomotion types among mammals, birds, reptiles, amphibians, and fishes are familiar, marine invertebrates are less so. Feeding mechanisms among marine invertebrates include filter feeding—mostly in groups that are attached to the seafloor, such as corals and sea anemones (coelenterates), bryozoans, tunicates (sea squirts), and sedentary polychaete worms. Filter feeding involves the use of a straining device (tentacles of various sorts, sometimes lined with cilia) to remove very small particles of biological material (bacteria, eukaryotic microbes, as well as particles of decaying tissue) from the water (along with chemical nutrients and oxygen). The term *deposit feeding* refers to the actions of some clams and snails that derive their nourishment from removing small food particles that are trapped in muds or stuck to the sides of sand grains.

The original subdivisions of zoology reflected the development of laboratory instrumentation. For example, Antoni van Leeuwenhoek was the first to reveal the existence of the microbial world, using a microscope in the seventeenth century. Microscopic examination of animal tissues became the subject of the science of cytology. Similarly, when the science of genetics was founded at around 1900, the famous "fly room" of Thomas Hunt Morgan's Zoology Department of Columbia University became the locus where the very notion of genes and chromosomes was first developed, through careful experimentation and observations on fruit flies.

Physiology, study of the way animal bodies function, is another early and important branch of zoology. Anatomy, too, was an early subfield of zoology; anatomy continues to be an important field especially in medicine, for which all entering graduate students are required to complete a rigorous course specifically in human anatomy. "Comparative anatomy" involves the study of how the same parts of an animal's body takes different forms: for example, the forelegs of some animals are modified (through the course of evolution) into wings for flying, or fins or paddles for swimming. Embryology is the study of how animals develop from a fertilized egg.

Modern biology tends to be divided up differently from these older subdivisions of zoology (and botany and microbiology). Separate zoology and botany departments for the most part no longer exist. For example, the advent of the serious study of evolution in the mid–nineteenth century, and ecology somewhat later, has led, in modern times, to university departments of ecology and evolution that are separate from departments of molecular biology. These divisions maintain the older interests in the anatomy, physiology and embryology of animals (and plants), but do so as unified subject areas utilizing similar analytic techniques. Today's embryology, for example, is usually called developmental biology, and it is associated most closely with molecular biology because the central goal has become the explanation of the development of the adult form from the underlying genetic instructions—which can now be read in molecular terms. A laboratory studying mouse development is thus likely to be next door to one in which the development of ferns from spores is being analyzed, all with the techniques of molecular biology.

Although there has been a natural tendency in the history of biology to delve deeper and deeper into the smaller anatomical and, ultimately, chemical workings of the bodies of organisms (to the point where molecular biology now receives the majority of the attention and funding in modern biological science), none of the prior interest in larger-scale phenomena—such as anatomy, evolution, and ecology—has been lost. That zoology is usually no longer taught as a subject distinct from botany or the other traditional fields of biology reflects a growing realization that there is a unity to all life—from the molecular processes of the genes, the biochemical workings of energy production and development, on up through the behavior of organisms and the organization of such larger-scale biological systems as ecosystems and species.

—Niles Eldredge

See also: Ecology; Ecosystems; Evolutionary Biodiversity; Food Webs and Food Pyramids; Systematics

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