Burton Guttman

Evolution

Beginners
GUIDES

evolution

a beginner’s guide

evolution

a beginner's guide

burton s. guttman

ONEWORLD
OXFORD

evolution: a beginner's guide

Oneworld Publications
185 Banbury Road
Oxford OX2 7AR
England
www.oneworld-publications.com

Reprinted 2006

A CIP record for this title is available
from the British Library

ISBN-13: 978–1–85168–371–0
ISBN-10: 1–85168–371–2

Typeset by Jayvee, Trivandrum, India
Cover design by Two Associates
Printed and bound by Biddles Ltd, Kings Lynn

NL08

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preface

Evolution is a fascinating business, its fascination attested to by the many books on the subject now available. In addition to technical monographs for the specialist, books continue to appear that are addressed to the general reader. Some of these general books display the results of evolution over the past billion years or so, often with marvelous color paintings that show how we believe the many creatures of the past appeared in life. Books about human evolution are especially fascinating, such as those by Donald Johanson, Bryan Sykes, and Ian Tattersall listed in the References at the end of this book. Other popular books, such as Richard Dawkins' interesting series, explore the processes of evolution, often from fascinating new viewpoints. And evolution inspires the more philosophical books, like those of Daniel Dennett, for the story of how humans got to be what we are raises a number of much broader questions.

As someone who has studied evolution, and biology in general, since my teen years, I have enjoyed many of these books and have profited from reading them. But I have wondered sometimes how readers who are not professional biologists have reacted to the same books. When I have used some popular books about evolution with relatively young college students in interdisciplinary courses (where the big, fat, encyclopedic textbooks of biology were inappropriate), I haven't worried about the students lacking some basic information, because my colleagues and I could supply that information as part of the course. But what about the intelligent, interested lay reader sitting in his easy-chair of an evening and trying to digest the same information? Lacking much formal education in biology, and probably quite a few years removed from any formal education, is he getting the full impact of the book?

Hence, this book. It is part of a series called Beginner's Guides, and its purpose is to let the reader who is interested in evolution take a step backwards to bone up on some fundamental ideas about biology and evolution before plunging on into the many other books I've referred to. Its format is obviously simple, and it is not lavishly illustrated with drawings of extinct plants and animals; we could not possibly rival those highly illustrated books, and the purpose here is not to compete with them but to prepare you to read them with greater understanding. If you finish the book and still have a sense of dissatisfaction, a sense that there is a lot more to know, this book will have served its purpose. I hope, then, that you'll be prepared to read further. This book is intended, also, as something of a companion book to the earlier guide *Genetics*, cowritten with my colleagues Tony Griffiths, David Suzuki, and Tara Cullis. Although this book is quite self-contained within the limits of its subject, the combination of the two books might just provide the interested reader with the extra bits of insight into genetic processes that will make evolution even easier to comprehend.

In particular, I've made an effort to make sense of evolution in its proper ecological setting, an emphasis that I think has been generally ignored (or assumed implicitly). Once functioning organisms appeared a few billion years ago, they were forced to start carving the world up into places to live and ways of living that did not compete too strongly with other organisms. They started, in other words, to form communities and ecosystems, as explained here, and all organisms since that time have evolved in the same ecological frame of reference: emerging as new species from nearly identical relatives and surviving only as long as they could maintain a satisfactory ecological niche for themselves.

In today's fast-moving society, with its adulation of the new and disdain for the old – where popular music of 30 years ago can be labeled "golden oldies" – there is a tendency to think that only the latest hot discoveries are worth our consideration. Many of the newest books about evolution present the subject from the viewpoint of contemporary investigators using molecular methods, which have provided important new insights. Evolution is fundamentally a genetic process occurring in genetic creatures, who carry records of their histories in their genes; today's automated methods for determining the sequences of DNA molecules allow us to start reading those encoded histories, to clarify the stories previously told only by studies of anatomy. I deal with these methods and insights in their proper places. Invaluable as this work is, however, the fundamental understanding of evolution and evolutionary ecology that I'm trying to develop here is based on classical ideas and research from the mid-twentieth century, much of it derived from investigations of organisms in their natural settings. Beginners have to understand these foundation ideas of the science, and that will be the emphasis throughout.

The story of evolution on Earth for the past few billion years is itself fascinating; the stories about how scientists have pieced all this together is perhaps equally fascinating. There has been room here for only a little of this story, especially in chapter two. It is a triumphant story of the power of modern science, of the inquiring and creative human intelligence that has uncovered the secrets of biology and geology from the complexities of cells and the layers of the Earth. But the story has a kind of sour companion, for as we celebrate our modern understanding of evolution and try to pass it on to the next generation with the hope that they will also celebrate it – and that some of them will even want to join in the exciting adventure of science – we meet an adversarial force that wants to deny the whole business. This counterforce, called creationism, is strongest in the United States (and, I understand, in Australia). In the name of a fundamentalist religion, and for rather inscrutable reasons, it puts its faith in the recorded mythology of some Bedouin tribes of around 3000 years ago and imagines that their story of creation is superior to all the discoveries of modern science. If the purveyors of creationism would simply tell their story to themselves and not bother the rest of us, we would have little reason to complain; people ought to be free to believe what they want, even including little men in flying saucers, appearances of Elvis, or the predictive power of the stars. But creationists of various stripes keep trying to impose their beliefs on society in general, and especially on public education. As explained in chapter ten, I believe creationists are not only wrong but can be positively dangerous to a democratic society. One of my minor hopes for this book is that citizens who want to prevent democracies from turning into theocracies may find it useful as a handbook for action before school boards and legislatures.

Chapter one includes some general words about the nature of science and how it operates. Readers who want just to get on with the science itself can ignore that section, but I've included it because evolution has such broad implications, of the kind raised by creationism and of the kind addressed by more philosophical writers. I think it is important to have a clear conception of science as part of exploring one particular story of science, and I hope readers will find it useful in that context.

In writing this book, I have received particular help from Larry Ross and Nancy Cordell, who set me straight on some matters of human evolution. Donald Morisato helped me understand some matters of developmental genetics, and Mark Ridley caught some errors and made some valuable suggestions for changes throughout. My editor, Victoria Roddam, has been the very model of a modern major editor in her encouragement and her sharp criticism of drafts, particularly steering me around the messy waters of creationism. I thank Deborah Martin for her intelligent copy-editing, which caught some of my lapses; Mark Hopwood for his work on the cover copy; and Deirdre Prinsen for putting the whole book together so beautifully.

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chapter one

diversity, science, and evolution

explaining diversity

One of the most obvious things about the world is the diversity of life. Look out the window. You will see trees, flowers, bushes, probably some insects, surely some birds – even an apparently sterile city has its pigeons, starlings, and sparrows. Although you can't name everything you see, you would need several identification guides to catalogue them all, and your final list would be long. Anywhere outside an urban environment, you will be surrounded by hundreds of identifiable types of plants, by many species of birds at any season, perhaps a dozen kinds of mammals. Carefully sifting a few shovelfuls of soil would reveal a variety of life that would tax your skills of observation and identification.

We start to learn this diversity as infants. Parents show their children books with pictures of many creatures, and they teach songs like "Old MacDonald" about what the horsie says, what the piggy says, what the sheep says. All but the most deprived children see flowers and trees and learn about their variety.

Primitive humans, too, observed this variety and depended on it for their survival. They learned to distinguish various animals that could be used for food or for skins – or, alternatively, animals that must be avoided as dangerous. They learned to distinguish nourishing or medicinal plants, or those that could provide clothing or shelter, from those that were poisonous or merely attractive. As they began to wonder about this variety, they made up stories to explain where all these plants and animals had come from, sometimes telling how propitious gods and spirits had created them.

Humans are classifiers. This is one way we make sense of the world. We name the variety of actions with verbs, the variety of objects with nouns. The words we use intrinsically set boundaries. We like to put things in boxes, both physically and verbally, for it unclutters the world, makes order out of what would otherwise be chaos. If we can name something and put it into a category, we can learn to deal with it appropriately. Things that resist classification and want to sit on the borderlines make us uncomfortable. They are messy. We try to push them into one box or the other. So as civilization developed, as some people were able to leave off plowing, sowing, reaping, and building long enough to contemplate the world, they put the living things of the world into neat categories and gave them names. Even in quite primitive societies, as the biologist Ernst Mayr noted, the native people often have become so well acquainted with the birds around them as to identify all the species distinguished later by modern ornithologists.

The dual activity of putting living things into neat, labeled boxes and telling stories to explain their origins satisfied human curiosity for a long time. For many cultures and people, it still does. But as modern science developed in Europe, especially in the seventeenth and eighteenth centuries, some observers began to have their doubts, to think in different directions. One source of this newer thinking undoubtedly was the rise of scientific classification, called taxonomy or systematics. Of course, it had been obvious for a long time that living things fit into categories. It is a commonplace that there are birds of many kinds, fishes of many kinds, trees of many kinds. Our modern way of thinking about such categorization began with the Swedish naturalist Karl von Linné, usually called by his latinized name Carolus Linnaeus. Linnaeus invented the system we now use of putting species into small groups called genera (singular, genus), of putting similar genera into families, and so on up the hierarchy to the great kingdoms, originally a plant kingdom and an animal kingdom. Still, for Linnaeus and other naturalists of his time and some time to come, there was no question about the origin of all these species; God had created them, as the Bible tells, and there were just as many species as God had seen fit to create.

Naturalism, the philosophy of the natural science that developed after the European Renaissance, differs from the older worldview in seeking to explain the phenomena of the world strictly by means of natural entities and events, rather than interpreting the world as a creation and plaything of gods and demons. And once a naturalist has observed many species that look very much alike, a nagging doubt may arise. For instance, both Europe and North America are inhabited by many types of small sparrows or buntings, little seed-eaters with very similar plumages of brown, gray, black, and white. They are a delight to the eye of both bird-watcher and artist, but why are there so many of them? Without pretending to fathom God's purpose, we may observe the seeming strangeness of creating so many, so much alike that identifying them can be a real challenge. Linnaeus, being a botanist, knew many species of oaks, of maples, of just about any other family of plants familiar to a European scholar; identifying each species also tests the naturalist's skill, since they are often so similar, and one might wonder why it was necessary to create them all, each as its own separate species.

As we shall see in chapter two, where we review this story at greater length, some early naturalists sought natural explanations for the origins of all this diversity. They also observed the fossilized remains of plants and animals of the past. Perhaps, some began to think, species are not as immutable as tradition had taught. Perhaps they can change, and perhaps this variety is the result of gradual changes in form as plants and animals spread out, both in time and space, and diverged from one another – perhaps, in other words, we are seeing the result of an *evolution* of living organisms. The idea, of course, did not sit well with a Christian European and American society, including many other scientists, who had been brought up with unquestioning belief in the biblical story of creation. The idea of evolution was heretical, even sinful. It raised a storm of controversy that is still with us today.

Now we moderns, at the beginning of the twenty-first century, contemplate the situation. On the one hand, we live in the most scientifically and technologically advanced society that has ever existed. Our lives are shaped by all the discoveries of modern science, such as medical advances that have eradicated some diseases and have given us the power to cure others, to live far longer and more healthfully than our ancestors did. Europeans and North Americans have been major contributors to these scientific and technological advances, and major beneficiaries of them. We are also citizens of nations whose actions and policies contribute most to the problems generated by modern science and technology. It is hard to generalize about citizens of other countries, but, paradoxically, Americans on the whole are abysmally ignorant of even the most basic scientific ideas, let alone the advanced knowledge that drives our society. The National Science Foundation's "Science & Engineering Indicators 2000" reported that less than half of those questioned knew that:

1. The earliest humans did not live at the same time as the dinosaurs;
2. It takes the Earth one year to travel around the sun; or
3. Electrons are smaller than atoms.

Only 29 per cent could define the term "DNA," only 13 per cent could define "molecule," and only 21 per cent were able to explain what it means to study something scientifically; just over half understood probability, and only a third knew how an experiment is conducted.

Furthermore, Gallup polls show that only about half or fewer Americans say they believe in evolution. This might just be viewed as another instance of Americans' general ignorance. In another arena, the National Geographic Society surveyed young adults, aged 18 to 24, in November, 2002, and found that almost one-third could not locate the Pacific Ocean, fewer than half correctly identified the United Kingdom, France, Japan, and the state of Pennsylvania, and three out of ten thought the U.S. population was "1 billion to 2 billion," instead of the correct number, about 280 million. So when one hears that many Americans don't believe in evolution, one is tempted to reply, "So what? Americans don't know nuthin' from nuthin' anyway, so that doesn't mean anything." However, no one is campaigning to keep Americans ignorant of the definition of a molecule or the location of the Pacific Ocean, while a vigorous campaign is being waged to convince people that the "theory of evolution" is not only wrong but evil, sinful, and destructive of the fabric of our society.

Thus, this introduction to evolution cannot simply address the scientific concepts alone. We will have to devote some space to questions of the nature of knowledge, the structure of science in general, the domains of science and religion, and the place of science in society.

the logic of science

People have always wanted to know about the world around them – how it works, what kinds of things are in it. They have been motivated by fear of the unknown, by the need to gain control over the world, and by simple curiosity. The anthropologist Bronislaw Malinowski pointed out that all human societies have science, magic, and religion, their roots reaching far back into prehistory. Even ancestors of *Homo sapiens* had some scientific knowledge, which we find expressed in their ability to make instruments and tools. They must have known the variety of plants and animals in their environment, which of them were good to eat and which were dangerous, and when and how to hunt their prey. This practical knowledge was essential for their survival. At the edge of their pool of knowledge, which we must count as science, they had magic and religion: ideas about the nature of the world embodied in myths and stories regarding what they did not know empirically and could not control with their own hands but could only seek to control through rites and rituals and prayers.

Science is distinguished from other human activities by its overall philosophy of naturalism, as mentioned earlier, and by its reliance on obtaining information through the evidence of our senses developed through carefully controlled observations. And this is simply the foundation that all rational people use for ordering their lives on the basis of experience and reason. Thomas Henry Huxley made the point in 1863 in a little essay entitled "We Are All Scientists." The scientific way of thinking and acting is just a somewhat more rigorous version of the way we all must act day by day to learn the mundane facts about our world and to live effectively, avoiding stupid and dangerous actions. Part of our task in this book is to examine knowledge about evolution obtained empirically and to contrast it with contrary assertions – based on revelation and authority – about how the various creatures that inhabit this world came to be.

Nonscientists tend to think of science as a body of Truths about the world. People are eager to have Truths with a capital T – eternal verities that are absolutely certain, guidelines for their lives, which they can rely on without doubts. Religions have always claimed to provide such Truths. But I avoid the word "truth" in talking about science, because science does not really deal with Truth with a capital T – perhaps one reason nonscientists may denigrate and mistrust it. Science actually deals at best with more humble "small-t" truths, stated in the form of *falsifiable hypotheses.* A scientist notices some unexplained phenomenon and tries to devise a rational explanation for it, reasoning in a way that the American physicist and logician Charles Sanders Peirce called *retroduction*: "Here is a strange state of affairs; but this state of affairs would be understandable if something else – call it X – were true; therefore, I have good reason to believe that X is true." Postulating X is inventing an explanation for the strange state of affairs. It requires a leap of the imagination, and for this reason science is as creative as the arts or any other human activity. It is amusing that Sherlock Holmes, Arthur Conan Doyle's remarkable consulting detective, is always extolling "the science of deduction" though his method is clearly retroduction, albeit with brilliant imaginative leaps.

Science imposes several limitations on what X might be like. As the philosopher Wesley Salmon has written, to explain a phenomenon means placing it within the causal structure of the universe – showing the causal chain of events resulting in this phenomenon. This means that X must be in the realm of ordinary physical reality; a scientist cannot postulate something supernatural or in principle unobservable, such as a god or demon or some kind of magic. But most important, the postulate about X is a hypothesis that must be subject to an *empirical* test – it must have consequences that are testable through observation and experiment. Then we can challenge the hypothesis by testing some of these predictions.

Nonscientists may imagine that in doing experiments or in making critical observations, scientists are trying to prove that their hypotheses are correct. In fact, they are trying to prove that their hypotheses are *wrong*. Of course, people always hope they are correct, but a quirk of logic dictates that they can't try to prove this. To be a meaningful scientific idea, a hypothesis, *H*, must make some prediction, *P*, about the outcome of an experiment or an observation. *H* and *P* are related by a hypothetical statement: "If *H*, then *P*." So we test to see whether we do observe *P*. Suppose we do. Can we reason, "If *H* then *P*; *P* is true, therefore *H* is true"? No, we can't. This pattern of reasoning is a logical fallacy called "affirming the consequent." (Try reasoning, "If my car is out of gas, it will not start. My car will not start, therefore my car is out of gas." How many other explanations are there for your car not starting?) But suppose *P* is not true – that we observe not-*P*. Then we *can* reason ("denying the consequent"), "If *H*, then *P*; not-*P*, therefore not-*H*." As the philosopher Karl Popper emphasized, the hypothesis must be *falsifiable* – it must be possible in principle to show that it isn't true. If the results of a test don't support the hypothesis, it is rejected or at least modified. (Of course, another argument is that the test wasn't conducted correctly and is not an adequate challenge to the hypothesis.) If the results support the hypothesis, it survives, and we gain greater confidence in it. This doesn't make the hypothesis true, at least, not in the capital-T sense – merely an acceptable explanation for the observations.

As we develop a better understanding of some subject and have more hypotheses that survive empirical tests, we can piece together larger explanatory structures called *theories.* A theory is a logically related set of statements that explains how some aspect of the world works, but it is not simply a more mature version of a hypothesis. The British philosopher of science Stephen Toulmin suggested that a theory is like a map, a picture that can summarize a set of facts and create an overall understanding of them. But like a hypothesis, a theory must be subject to empirical tests. If the theory truly represents reality, we should be able to draw inferences from it about the outcome of other observations that haven't been made yet, so we can challenge it empirically and, in principle, show that something is wrong with it.

All science is based on theoretical structures. A prominent theory of chemistry, for instance, explains how atoms bond together to form molecules; it is an excellent, satisfying theory because it predicts so accurately just how certain atoms will form molecules with specific properties. Geology is based in part on a theory of tectonic plates, which postulates that solid segments of the Earth's crust rest on a fluid foundation and are slowly moving past one another; this is also a strong, successful theory because it explains phenomena such as mountain building, sea-floor expansion, and earthquakes so well.

then what about the "theory of evolution"?

Given this background about theories in general, what is the status of the "theory of evolution"? First, we should agree not to use this phrase; it is used wrongly and often, particularly in the form "Charles Darwin's theory of evolution," as if biology were just as it was in the mid-nineteenth century while all the other sciences have been advancing. In daily life – as contrasted with science – people tend to contrast "theory" with "fact." The tough-minded man in the street, to conjure up a somewhat moth-eaten image, expresses his commitment to "facts" and his contempt for tender-minded visionaries who live in ivory towers and deal only with "theories." But as I have just shown, theories are never in conflict with facts. Theories summarize, organize, and explain facts; facts substantiate (or perhaps fail to substantiate) theories. To clarify the issue, consider two questions about the idea of evolution:

1. Have the various kinds of living organisms on earth achieved their present form through a process of evolution?
2. What are the mechanisms of evolution?

The answer to the first question is Yes; it is a *fact* of biology that this is true, just as much as it is a fact of biology that plant leaves use their chlorophyll to convert light energy into chemical energy, that food is digested in the intestine, or that normal humans have 46 chromosomes. As we proceed through the next few chapters, I will try to show that this fact is so solid that denying it would make nonsense of virtually all of biology. The evidence accumulated over the past 150 years or so has uniformly supported (and hence failed to falsify) the general thesis that species evolve and that evolution accounts for the diversity of organisms that have inhabited and now inhabit the Earth.

At this point, an astute reader might raise an objection. "You say that evolution explains the origin of all the organisms on Earth. But you also say that every theory, every hypothesis, must be falsifiable. It seems to me that if all biologists are looking at the world with their belief in evolution, they can't be objective observers of the world. They will interpret every observation in the light of evolution, so the idea of evolution is really not falsifiable – in other words, not scientific!" An astute objection indeed, and one worthy of an answer. When we say that evolution explains the great diversity of organisms on this planet, we mean that very strong evidence shows that every existing species and every structure of a species is connected in some obvious way to similar species and to similar structures elsewhere. But suppose something were to break this pattern. For instance, existing animals move in a variety of ways: with legs of various kinds, with wings, by squirming and wiggling, by swimming with fins and other propelling and stabilizing structures. But no animal moves on wheels. Now, such a motion isn't absurd biologically. We know of at least one kind of motility structure with a wheel-like basis: motile bacteria generally swim by means of flagella – long, thin protein fibers – that swing around and around, propelled by circular, wheel-like structures. Suppose, then, we were to discover an animal that really does move on wheels. The animal wouldn't have to be very large, perhaps no more than a millimeter or two. It might have round appendages with "axles" held in bases that could drive them around and around, much like bacterial flagella. I am imagining that the animal is unique in this regard and that analysis of the proteins involved shows them to be unique – not obviously related in any way to proteins of any other animal. I believe that if we were to find such a creature, we would have to conclude that it did not originate through evolution from any other species on Earth. We might conclude that it had been created by some intelligence and placed on Earth; or we might conclude that it was a species that had evolved on some other planet and had been left here by extraterrestrial visitors. But we could not explain its existence by reference to biological evolution on this planet. Even more broadly, it is conceivable that we would find an organism whose structures show no homologies to anything else on Earth. (The concept of homology is explained in chapter two.) So it is perfectly conceivable that we would find individual cases whose origin could not be ascribed to evolution, at least evolution on this planet. But, to repeat, that the idea of evolution in general could be overthrown seems inconceivable.

The second question raised above is about the *theoretical foundation* of evolution, about *how* evolution occurs, and this theory is analogous to theories in other sciences of the kind I mentioned above. Evolutionary theory has survived many challenges and has thus become very strong. As I will show in the following chapters, there is broad agreement about the principal mechanisms of evolution, although, like any scientific theory, it is subject to constant refinement, additions, and revision. But current evolutionary theory explains so much – it is so *robust*, in current jargon – and is so obviously compatible with everything else we know about biology (indeed, essential to explain much of biology) that it is virtually inconceivable that anyone could present contrary evidence that would make us abandon our current model. That will be the main subject of the rest of the book.

conceptions and misconceptions

The whole idea of evolution is so fraught with misconceptions that I want to start by considering some of them. The following brief answers to these misconceptions may provide a kind of overview of what is to come, with references to chapters in the book that go into more detail.

1. *Evolution is incompatible with religion: you have to choose whether you're going to stick to your religious beliefs or be an evolutionist.* This is one of the principal contentions I am at pains to combat. It is basically a fundamentalist Protestant viewpoint, and fundamentalist Protestants are a small minority among religious people. The dichotomy is certainly true if your religion maintains that the biblical story of creation, as told in Genesis, is absolutely, literally true. If you are so firmly committed to that position that nothing can change your mind, you might as well put the book down and stop reading right now, because nothing else in this book is going to make sense to you or have any influence on your thinking. However, if your religious beliefs entail a more liberal interpretation of the Bible or if those beliefs are based on quite different teachings, there is no reason to feel any incompatibility between the two. The vast majority of religious people, including members of most Christian denominations, recognize evolution as a natural phenomenon revealed by modern science; they usually say that they believe God created the living things on Earth and that evolution is the way he chose to do so. By the way, let us agree at the outset not to use the word "evolutionist." This is a label used by strict creationists to set their beliefs aside, and outside this context it doesn't really mean anything. (See more in chapter ten.)

2. *Evolution means improvement – progress from lower to higher forms of life.* No, evolution says nothing about "progress." Progress is a conception of modern civilization. We may apply the idea to human affairs and human history (though that point, too, is arguable), but it is wrong to apply it generally to the biological world. An old tradition in biology is to use terms such as "lower animals" for worms, clams, and the like while promoting birds and mammals to the lofty status of "higher animals," but modern biologists should, and do, try to avoid those labels. The very words "lower" and "higher," when applied to the world of organisms, stem from a human misconception of progress, a reading of something into the world that simply isn't there. It is based on the archaic idea of a Chain of Being, reaching from the lowliest, simplest creatures to the most complex – humans, obviously! – and then beyond humans to angels and God. Now, it is true that the overall history of life on Earth has seen the evolution of larger, more complex creatures, but even given this conception of "progress," evolution has entailed plenty of changes in direction that no one could identify as progress.

3. *There is good reason to have our doubts about evolution because even the scientists who subscribe to the idea and are supposed to be studying it can't agree among themselves.* Scientists always disagree about what they study. It's part of the game. Controversy leading to clarification is the road to scientific truth. We have long lists of generally established facts about the world, even though scientific specialists disagree about their details. All biologists agree very strongly about the major outlines of evolution; here too, the disagreements are about the fine points and details.

4. *The fossil record that biologists depend on as evidence for evolution is really full of big holes, with none of the "transition" forms that should be there if evolution is true, and the biologists gloss over this fact or try to hide it.* This is one of those canards perpetuated by anti-evolutionists, what Stephen Jay Gould has called a kind of urban legend. Although the fossil record is incomplete, like any historical record, it is rich and extensive enough to support fully the general fact of evolution, and it gets better every year. Furthermore, many evolutionary episodes are documented by as rich a fossil record as one could want, with plenty of transitional forms to show how later groups of organisms have descended from their ancestors.

5. *Living things are so wonderfully, perfectly designed for their varied ways of life that it is just impossible to believe that all these complicated creatures have evolved by chance, through the blind operation of random forces. There must have been a guiding intelligence behind the process.* This is an interesting, complicated issue. The first point to make, however, is that it just ain't so: you can only believe in the "wonderful, perfect design" of living organisms if you don't look closely enough. We will see that organisms are *historical* creations, which carry with them all the genetic baggage inherited from their ancestors, so any new features must be designed by slowly modifying what is already present. Take that supposed paragon of design, the mammalian eye. The cornea and lens focus light on the retina, a layer of light-sensitive cells, but the eye is really so poorly designed that the retina is upside-down, and the light has to first pass through a layer of nerves and blood vessels; this layer doesn't absorb much light, but the larger blood vessels can cause minor problems, and an excellent designer would never have made the eye like that. Furthermore, the optic nerve formed from extensions of the retinal cells has to leave the eye through a hole, creating a blind spot in each eye. We aren't aware of these difficulties because each eye covers the blind spot of the other and because the eyes are constantly jiggling

and the brain produces continuous images from their input. Another example of poor design is our breathing and swallowing apparatus; as lungs gradually evolved, the tube we breathe through (trachea) came out on the wrong side of the esophagus, making it necessary to evolve a complicated epiglottis to cover the mouth of the trachea when we swallow. Yet the apparatus commonly fails and something tries to "go down the wrong tube," making actions such as the Heimlich maneuver necessary for survival.

In spite of such facts, many people have taken the viewpoint that biological function implies a designer, and in recent years this has been cloaked in scientific garb by the proponents of "intelligent design theory." We will discuss this idea in chapter ten, because it raises the question of whether this "theory" is a legitimate scientific theory or a philosophical viewpoint outside science.

chapter two

stories in the rocks

Modern science tends to be all of one piece. The discoveries and concepts of all the special sciences are so interlinked and interdependent that innovations in one tend to affect the others. For a long time in the development of European science, much of science was simply "natural history," without the distinctions we now make between such topics as geology and biology. Indeed, the whole idea of evolution itself evolved in these two sciences together. I want to begin here with some of this history, to provide a context for establishing a few of the geological and biological concepts that are most essential to understanding evolution. The play of biological evolution has taken place in the theatre of the evolving earth, and the record of past performances is locked in the layers of rock.

geology becomes a science

Western civilization's conception of the Earth and its place in the universe has long been dominated by a blend of Greek science and Judeo-Christian theology. People saw the Earth as the center of a universe made of larger and larger spheres, bearing the sun, moon, planets, and stars. Lacking any real conception of the vastness of time and space, there was no reason to doubt the biblical story that the universe had been created by divine fiat about 4000 B.C.E., followed by a separate creation of each living thing. This picture, however, began to fall apart with the Renaissance, when the new view of the universe developed by Copernicus, Kepler, and Galileo showed the Earth to be only one of several planets orbiting the sun, stripping it of the central place that human vanity had assigned it. New generations of astronomers started to portray the universe as a vast space occupied by many suns, and far older than a few thousand years. However, European thought, even among scientists, was molded – and in a sense held captive – by the biblical conception of a week in which the Earth and all life had been created, with little change following the creation except for a universal flood in Noah's time. Naturalists had little reason to doubt that all living organisms had been created independently in a very short time. Some doubts about these traditional beliefs started to creep in as people began to take a more naturalistic view of the world, uncolored by their religious heritage. Yet one of the main impediments to these doubts was the belief that the Earth is so young that there has been little time for any significant change.

Challenges to the biblical story arose in large part because of *fossils.* The word comes from the Latin *fossilis*, meaning "something dug up." Scientists and amateurs have dug up many fossils, and great collections are stored in museum trays – largely the shells of ancient animals such as clams and snails, the bones of larger animals, petrified tree trunks, the impressions of plant leaves, the tracks and burrows of animals, and even some petrified animal feces (called coproliths). We now accept fossils routinely for what they are, the remains of ancient organisms preserved one way or another in the rocks. Fossils are remarkably easy to find. As a kid in Minneapolis, I chiseled them out of the hard limestone on the banks of the Mississippi. Years later in Kentucky, we found coral fossils, among others, in the softer limestones. While driving from Lexington to Louisville one day, we stopped on a country road, and as I stepped out of the car, I found myself standing on a gravel made of enormous numbers of brachiopod fossils. Here in Washington State, the soft rocks of Cenozoic age in several nearby locations hold quite recent fossils of many snails, scaphopods, and other molluscs. And in a small town on the eastern slope of the Cascade Mountains, we found a large pile of reddish rock that turned out to be a huge slagheap of limestone rich in leaf fossils, providing a beautiful record of the trees in some ancient forest in the region.

Early naturalists such as Xenophanes and Aristotle took note of fossils of clams and other marine animals in rocks far from the oceans; they concluded, quite rightly, that these rocks were once ocean beds and that powerful forces in the Earth must have converted them into hard rock and moved them far away to the hills and mountains. However, even such rudimentary knowledge was lost to Christian Europe during Medieval times, while the writings of the classical philosophers were preserved by Arabic civilization. Medieval Europeans who observed fossils ascribed them to fanciful causes such as germs from the stars or vague formative forces in the rocks. Bible theology could also explain fossils as the remains of creatures lost during the Noachian flood, though why aquatic creatures should have died during that time is a little hard to explain.

One of the first to look at fossils for what they are was the Italian artist and natural philosopher Leonardo da Vinci (1452–1519). He saw that fossil shells in rocks in northern Italy were the remains of marine animals many miles from the sea. Clams, he argued, could not have traveled such a distance during the short time allotted to the Flood – and, again, why would they have died in the Flood anyway? Leonardo even took a modern ecological view of the world by noting that the apparent communities of animals preserved in the rocks resembled modern communities in the ocean. Furthermore, he pointed out that fossil-rich layers of rock were separated by layers without fossils, suggesting that the rocks had been formed in a series of distinct events, not in a single catastrophe.

One of Leonardo's followers in the mid-seventeenth century, Nicholas Steno, made careful observations of fossils. Although Steno clung to the idea of a young Earth and badly misinterpreted some fossils (he thought fossilized mammal bones were the remains of the elephants Hannibal had marched over the mountains to attack Rome), he set forth some important basic principles of geology. He realized that each layer of rock, or *stratum*, must have been formed gradually as particles settled out of water. The larger particles would have settled first, followed by smaller and smaller particles. Any change in the material being deposited would show up in the formation of distinct horizontal layers, a process called *stratification* and clearly observable in sedimentary rock formations. So one of his first principles was that strata would originally form horizontally; layers standing vertically or tilted or rolled into curves are evidence of later geological forces – very powerful forces – that must have moved them and twisted them. Steno also recognized a principle of superposition: the oldest sediments must be those on the bottom, with younger and younger strata piled on top. Finally, Steno recognized a principle of lateral continuity, meaning that each stratum extends in all directions until it reaches the edges of the basin in which it was deposited. These are now fundamental to geological thought.

These ideas were taken up later by William Smith (1769–1839), an English civil engineer. Because he was engaged in practical activities such as visiting coalmines and excavating for canals, Smith had the opportunity to observe many rock strata. Known as "Strata Smith," he was valued throughout England for the depth of his knowledge of these rocks. Smith particularly observed the fossils embedded there. Recognizing that each stratum contained a distinctive group of fossils, he contended that those fossils could be used to identify these strata in any location. On this basis, he created the first geologic map of England. Smith also stated the principle of superposition that Steno had recognized, that the lowest strata must be the oldest, thus strengthening the foundation of the science of geology.

At about the time Smith was doing his work in England, Antoine Lavoisier – one of the first modern chemists – made similar observations in France. He, too, realized that each stratum had its distinctive fossils, which must reflect environmental conditions at the time it was deposited. Lavoisier's observations were extended by Georges Cuvier (1769–1832) and Alexandre Brongniart, who published a geologic map of the Paris basin comparable to Smith's map, showing the locations of various strata.

Some naturalists, seeing how much the fossils in each stratum differed from one another, postulated that the Earth had experienced a series of *catastrophes*, geological events that had wiped out all life on Earth, or at least all life in some large area. The germ of the idea seems to have arisen in the work of George Louis LeClerc, Comte de Buffon (1707–88), although he did not necessarily think of the changes he described in the Earth's history as major upheavals. His successor Cuvier, however, was a student of vertebrate paleontology, and the fossils of large animals clearly define quite distinct species with very significant differences in form; seeing these differences, Cuvier elaborated the idea that each epoch of the Earth's history had ended with a catastrophe, after which life was created anew, perhaps with each new flora (plant life) and fauna (animal life) a little more advanced than those before. Catastrophism became the norm in geologic thought during the eighteenth century. To explain some observations, though, catastrophists had to postulate over twenty separate extinctions and creations, and the idea began to look ridiculous.

Meanwhile, James Hutton (1726–97) was laying the foundations for a more modern view of geology. In his *Theory of the Earth* (1785–95), Hutton developed the *uniformitarian* view that geological forces are constantly and continually shaping the Earth's features over exceedingly long times. He saw that erosion by wind and water constantly breaks the rocks down, while the internal heat of the Earth is a force behind volcanic activity and the upheavals and bending of rock layers. The uniformitarian viewpoint achieved its modern form in 1830–33, when Charles Lyell's great work *Principles of Geology* laid the foundations for a modern science of the Earth by showing clearly how the kinds of forces outlined by Hutton create the geological forms we observe. Of course, devastating earthquakes, volcanic eruptions, and collisions with meteors occasionally rock the Earth, but none of these events destroys all life on the planet. It is clear now that even as movements of the Earth's crust are raising new mountain chains, the mountains are being worn down slowly by erosion and their substance deposited in beds where plant and animal remains become buried and eventually fossilized. Uniformitarian thinking in geology helped prepare the way for thinking that organisms, too, are gradually changing.

As early geologists extended the work of Smith and Cuvier to other sites in Europe, the strata began to acquire names that we still use today. Each stratum must have been laid down over a long time, and that time is now named as a segment of the standard geologic time-scale, which is divided into this hierarchy:

- eras
  - periods
    - epochs
      - ages

The names first applied to local rock formations were extended as people began to correlate the strata in different regions. Thus, some strata identified in the Jura mountains of France and Switzerland were called Juras, and the same strata were identified in France lying under strata that had been named Cretaceous (from *creta*, chalk, because of their characteristic chalky limestone layers). But in Germany the Juras laid above a series called Trias. Today we identify the times when these formations were laid down as three distinct periods called Triassic, Jurassic, and Cretaceous, which all constitute the Mesozoic era. The coal-bearing strata of England had been named Carboniferous, and these now identify a period before the Triassic, in the Paleozoic era.

The current geologic time-scale is shown in Figure 2.1. Although its main divisions were first defined by rock formations in Britain and Europe, the system has now been extended throughout the world. Many geologic ages, however, are defined uniquely on each continent.

Era	Period	Epoch	Myr ago	Major events
Cenozoic	Quaternary	Holocene	0.01	Agriculture, civilization
		Pleistocene	1.6	Neanderthals, modern humans
	Tertiary	Pliocene	5.3	Earliest hominids (prehumans)
		Miocene	23.7	Rapid evolution and spread of grazing mammals
		Oligocene	36.6	First elephants
		Eocene	57.8	First horses, rhinoceroses, camels
		Paleocene	66.4	First primates
Mesozoic	Cretaceous		144	Great evolution and spread of flowering plants Extinction of dinosaurs
	Jurassic		208	First birds and mammals Peak of dinosaurs
	Triassic		245	First dinosaurs
Paleozoic	Permian		286	Mammal-like reptiles
	Pennsylvanian		320	First reptiles. Large insects
	Mississippian		360	Sharks, insects
	Devonian		408	First amphibians. Forests abundant
	Silurian		438	First air-breathing animals (scorpions), land plants
	Ordovician		505	Peak of trilobites; first fishes
	Cambrian		543	Rapid diversification of animals
Precambrian	Proterozoic	Ediacaran	610	Diverse early animal fauna
			2500	Eucaryotic cells
	Archean		3800	First simple (procaryotic) cells
Hadean			4500	Formation of the earth

Figure 2.1 *A geologic time-scale showing major events since the Earth's formation. Times given indicate the beginning of each period.*

ages and time

As these advances in geology were being made, the issue of time obviously had to arise. As the early geologists saw how rocks must have been deposited gradually and then often uplifted into hills and mountains, it became clear to them that the traditional age of the Earth of less than 6000 years was way too short a time. Eventually some investigators began to ask scientific questions about the age of the Earth and to extend the time-scale a little. For example, Buffon took seriously the idea that the Earth and the planets had been formed from very hot material, and he conducted experiments on the rate at which metal balls cool off after being heated. From his data, making the false assumption that the sun's radiation has little effect on the Earth's temperature and that there was no other internal source of heat, he calculated that the Earth must be about 75,000 years old. Although he was wrong, at least he had started to ask the question empirically, through observation and experimentation. In 1846, the English physicist Lord Kelvin (William Thompson) estimated that the Earth is between 20 and 30 million years old, based on the assumption that the Earth was originally formed from molten materials and has been gradually cooling. From measurements of the rate at which the temperature increases as one descends into the Earth in a mineshaft, Kelvin calculated how old the Earth would have to be to generate that temperature gradient. Again, he was far off the mark, in part because his assumptions were wrong. Another estimate based on observations of rates of deposition in contemporary sediments and the thickness of the geologic column, was that at least 75 million years had elapsed since the Cambrian period.

An unrecognized factor in geology, and the key to eventually getting accurate measurements of geologic age, lies in radioactivity. Remember that atoms have nuclei made of positive protons and neutral neutrons, with negative electrons around the nucleus; generally the numbers of protons and electrons are equal, making the atom neutral. All atoms of a given element have the same number of protons, the *atomic number* of the element; the number of protons plus neutrons is its atomic mass, or *mass number*. However, most elements have variant forms called isotopes: atoms of different mass numbers, because they have different numbers of neutrons. For instance, hydrogen atoms all have a single proton, but hydrogen has three isotopes. Atoms of ordinary hydrogen – the most common form – have no neutrons; the isotope deuterium has one neutron, and the isotope tritium has two neutrons. Giving different names to the isotopes of an element is exceptional; generally, they would just be known by their mass numbers as hydrogen-1, hydrogen-2 and hydrogen-3, denoted ^{1}H, ^{2}H, and ^{3}H.

Hydrogens-1 and -2 are stable, but hydrogen-3 is radioactive. The combination of two neutrons with one proton is an unstable situation, and if we watch a bit of tritium for a while (using special instruments), we will see that every once in a while a tritium atom will go *pop* and change into an atom of helium. One of its neutrons will change into a proton, and it will shoot an electron off into space. This electron, which is what the special instruments can detect, is a form of radiation (β-radiation), and the phenomenon of giving off such radiation is called radioactivity.

Radioactivity was discovered in the element uranium by Henri Becquerel around 1896 and was then pursued by Marie and Pierre Curie, who discovered the elements radium and polonium. A radioactive isotope – that is, a radioisotope – may give off electrons, high-energy photons (γ-radiation) or a cluster of two protons and two neutrons (α-radiation). In any case, its nucleus changes, and we say that the element *decays*. Several decay sequences are known, for sometimes one radioisotope decays into another, which decays into still another. For instance, uranium-238 (^{238}U) decays into thorium-235 by giving off an alpha particle; thorium-235 decays into protoactinium-234, which then becomes uranium-234, and this sequence continues to the stable isotope lead-206 (^{206}Pb).

One source of heat in the Earth is internal radioactivity. Atomic decay releases energy, and it does not take much radioactivity to account for a considerable amount of the Earth's heat. More important, for present purposes, is that radioactive decay can be used as a clock to determine the ages of rocks. Atoms decay randomly, so one can never predict which atom will decay next. But each radioisotope decays at a certain rate, which is conveniently measured by its half-life – the time required for half the initial atoms to decay. For instance, phosphorus-32 decays into sulfur-32 with a half-life of about two weeks. Suppose we could actually watch individual atoms and could arrange exactly 1000 ^{32}P atoms under our powerful, imaginary microscope. Over the next two weeks, we would see them *pop*, *pop*, *pop*, one after the other (though we would never know which one would pop next), and after two weeks there would be just 500 left. They would continue to decay, and after another two weeks there would be 250; in two weeks more, there would be 125; and so on.

This regularity is the basis of geologic clocks. For instance, uranium-235 decays into lead-207 with a half-life of 710 million years. Suppose that at some time in the distant past some rocks had formed with a certain amount of ^{235}U in them and that nothing disturbed these rocks until we could examine them. We break up a sample of rock and put a small amount into a mass spectrometer, an instrument that separates out all the isotopes and measures the amount of each. Now, the older the rock, the less ^{235}U it will contain and the more ^{207}Pb. The equations that describe radioactive decay relate the ratio of these two masses to the time of decay, so by measuring the mass of each isotope we can calculate the age of the rock. Several such decay schemes have been used for materials of different ages (Table 1).

Table 1 Decay schemes used for geological dating

Parent and product	Half-life	Effective age range
Carbon 14 → Nitrogen 14	5730 years	<60,000 years
Potassium 40 → Argon 40	1.3 billion years	>100,000 years
Uranium 235 → Lead 207	710 million years	>100 million years
Uranium 238 → Lead 206	4.5 billion years	>100 million years
Rubidium 87 → Strontium 87	47 billion years	>100 million years
Thorium 232 → Lead 208	13.9 billion years	>200 million years

Critics will point out that there are difficulties with these methods. Indeed there are. Every scientific method has its limitations, and these are gradually overcome by improving the techniques. For instance, using the decay of potassium-40 to argon-40 faces the problem that argon is a gas that can leak out of a specimen if it isn't handled very carefully. If some argon does escape as a sample is being prepared, the sample will appear to be younger than it really is. But geologists continually improve their methods, and now different methods for measuring the ages of the same strata tend to give very good agreements.

These radiochemical methods are supplemented by others. One of the most interesting depends on the presence of some uranium atoms in crystals of the mineral zircon. When an atom of ^{238}U decays, it produces a minute track in the crystal, and these can be counted. Given zircon crystals in a geological deposit with a favorable concentration of uranium – neither too high nor too low – this method can be used to check dates obtained by other methods.

This geological and radiochemical work, which has now been going on for a couple of centuries, is the foundation for our saying how old the Earth is and at what age various kinds of organisms lived or became extinct. It is one foundation of geology and for the whole story of evolution.

comparative anatomy

Aristotle didn't know everything, but the old man knew a great deal. Tracing the history of an idea, we often find ourselves going back to Aristotle's writing, for he reflected and recorded much of the knowledge of his time. He knew something about plants and animals, and in his book *Parts of Animals* he recognizes that similar animals have a common body plan, a common shared anatomy, with only minor variations in this plan for specialization to different ways of life. We find him writing:

> The course of exposition must be first to state the attributes common to whole groups of animals and then to attempt to give their explanation. Many groups present common attributes, that is to say, in some cases absolutely identical affections, and absolutely identical organs – feet, feathers, scales, and the like, while in other groups the affections and organs are only so far identical as that they are analogous. For instance, some groups have lungs, others have no lung but an organ analogous to a lung in its place; some have blood, others have no blood but a fluid analogous to blood, and with the same office. To treat of the common attributes in connection with each individual group would involve, as already suggested, useless iteration. For many groups have common attributes.

After the long decline in science following Greek civilization, the European Renaissance brought renewed interest in anatomy, although at first it seems to have been an interest only in human anatomy. With the eighteenth century, a few anatomists turned their attention to comparative studies. Buffon, recognizing the value of the comparative method, studied the fossils of extinct animals, often very different from any now alive; but detailed comparisons of their bones with those of living species could often show their similarities and thus their relationships – ancient mammoths and modern elephants, for instance. From such comparisons we might reconstruct some of the history of life. Serious comparative anatomy, however, begins with Cuvier. He performed detailed studies of the bones of fossilized animals, and in the words of the historian Sir William Dampier, "His great claim to distinction lies in the fact that he was the first among naturalists to compare systematically the structure of existing animals with the remains of extinct fossils, and thus to demonstrate that the past, no less than the present, must be taken into account in any study of the development of living creatures."

Comparative anatomical studies have shown the similarities and relatedness of the soft parts of animals – for instance, the changes in the structure of the heart and the circulation as vertebrate evolution ran its course from fishes to amphibians to reptiles to birds or mammals. These parts do not fossilize, however, and the kind of studies that Cuvier originated, which paved the way for Darwin, focused on the parts that do fossilize, the bones and teeth. The vertebrate skull is especially fertile ground. We tend to think of the skull as one huge bone. It isn't. One insight into its true anatomy comes from the attention good parents give to their infants; they know that a baby has a "soft spot" on the top of its head, which has to be carefully protected. The spot is a region where the several bones that form the skull have not yet grown together and fused; this is easily seen in the skeletons of infants, although such relics are generally confined to anatomy departments, hidden from a public that might be upset by them. But close examination of an adult skull reveals many places where separate bony plates grow together, generally meeting along a somewhat scalloped line. The skulls of birds and mammals are made of about thirty distinct bony elements, several of which are visible in Figure 2.2. Some of the greatest successes of comparative anatomy entail showing how this pattern of bones has changed in the various groups of vertebrates, and also how remarkably it has been conserved. By "conserved" I mean simply that the basic elements remain very much the same in all vertebrates and are simply modified in rather small ways to make the enormous variety of vertebrate skulls.

Comparative anatomy – of the vertebrate skull or any comparable structure – shows why biology only makes sense in the

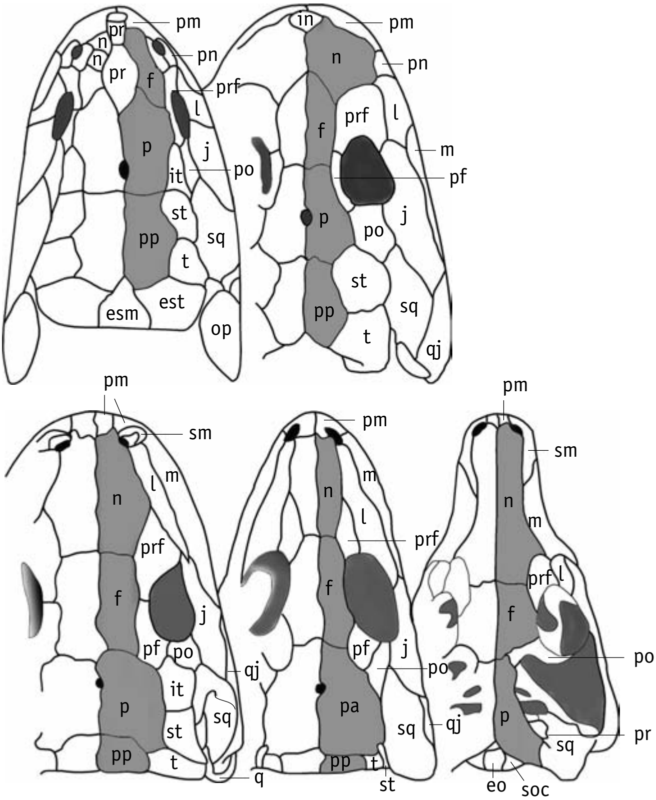


Figure 2.2 *A series of vertebrate skulls shows how each skull consists of the same bones with slightly different forms in comparable positions.*

light of evolution. It shows clearly how a versatile anatomy evolved in the most primitive vertebrates and has simply been modified by more subtle evolutionary changes in each later group. Another anatomical series (Figure 2.3), the familiar vertebrate limb, reveals another lesson. The bones of the human arm include the larger humerus of the upper arm, the paired radius and ulna of the lower arm, a series of small bones in the wrist and hand, and then five series of phalanges making each finger; in the human leg, the sequence is the femur of the upper leg, the tibia and fibula of the lower leg, another cluster of small bones in the foot, and another series of phalanges in the toes. This pattern is modified in each species of tetrapod vertebrate – tetrapod meaning "four-limbed," to include amphibians, reptiles, birds, and mammals. It is particularly interesting to see how the limb has been modified in quite distinct ways in the three types of flying tetrapods:

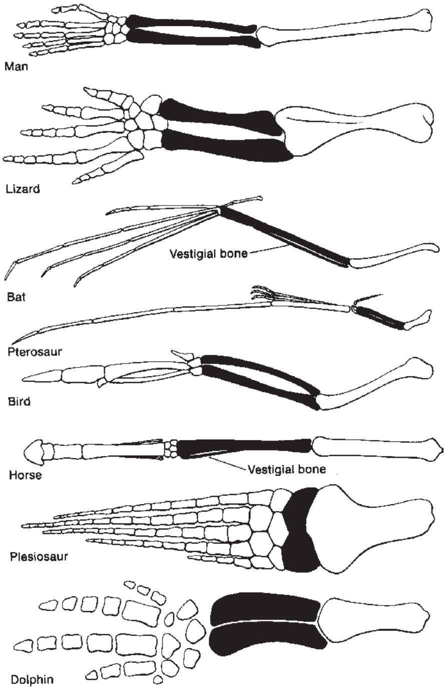


Figure 2.3 *The limbs of vertebrates are made of the same bones, modified for each animal's way of life.*

pterodactyls, birds, and bats. Each group achieved flight by stretching a membranous or feathered wing between greatly elongated bony elements, but each one used different particular elements. Oh, but hold on: what is this? The limbs of horses and bats (to pick out just two) contain some apparently excess elements – small, thin bones that have no functions and are termed *vestigial*. What are they doing there? Evolutionary biology provides a simple answer: the ancestors of these animals had two bones in the lower limb, and even though bats and horses require only one functional bone in these positions, the genes directing the formation of a second bone are still present and they direct the formation of the useless vestigial elements.

An important new concept, *homology*, emerges directly from comparative anatomy. If all tetrapod limbs have the same general series of humerus-radius-ulna-wrist-phalanges, then we can point to a single bone – say, the ulna – in any species and say, "This long bone is *homologous* to the equivalent long bone in all these animals." We can point to part of the skull and say, "This frontal bone (or nasal, or parietal, or postparietal, or whatever) is *homologous* to the equivalent bone in all these other animals, even though its shape may be considerably modified." The fact that we can point to homologies so regularly and simply is part of the evidence that all these diverse creatures have attained their structures through evolution from common ancestors, and homology is fundamental to evolutionary thinking. When we examine the structure of proteins in more detail, it will become apparent that homology applies at the molecular level, too, and that it can be an even more persuasive argument for evolutionary relationships than anatomical homology. By the way, structures with similar functions that lack anatomical homology are said to be *analogous* – the difference between an insect wing and a bird wing is a classic example.

impediments to the idea of evolution

Anatomists of the eighteenth and early nineteenth centuries did their careful studies of anatomy, both of living and fossilized creatures, still in the broad cultural context of biblical history. They became convinced that there had been life before our own era, often creatures with quite different forms, preserved in the various strata. But they did not make the intellectual leap, now so obvious to us, to an evolutionary viewpoint. The intellectual burden of thinking in the framework of biblical history and catastrophism was still too strong, and they continued to see the life of each stratum as the residue of a separate creation and destruction.

One reason the question of evolution arose slowly was that people had little conception of the age of the Earth. Even if they could have imagined a change from one species to another, such a change would have to take a long time. But the geologic work I described earlier started to remove the time-barrier to thinking about evolution by showing that in fact the Earth was far older than 6000 years, though no one yet knew just how old.

Thus, while scientists of the late eighteenth and early nineteenth centuries knew about fossils and the anatomical similarities that we now call homology, almost all stuck tenaciously to the idea of separate creation. That may seem peculiar, but old ideas die hard. Indeed, when Robert Chambers ventured to propose an evolutionary theory in 1834, he did so anonymously, and with good reason. His book, *The Vestiges of the Natural History of Creation*, was roundly attacked and castigated, even by some who later became fierce advocates for evolution. Even though Chambers could see that evolution must have occurred, he could not provide a mechanism to account for it, and other theorists had the same difficulty.

The evolutionary biologist Ernst Mayr has pointed out that another impediment to the idea of evolution was the philosophy of *essentialism*, which goes back at least to Plato; it proposes that everything in the world has a distinct, unvarying *essence* underlying its outward features. All horses, for instance, are supposed to partake of an ideal of "horseness;" though some may be short and some tall, some swaybacked and some straight, all horses are fundamentally the same below their surface appearances because they all share those ideal characteristics – the same essence.

In biology, this way of thinking became *typology.* Early biologists considered that every species conforms to an idealized, characteristic *type* and that all members of the species really are just like that type. This is the collector's mentality. A collector – of seashells, for instance – believes the world of life can be neatly and simply divided into distinct species. Even if some organisms are really quite variable and hard to classify, the typological mind tries to ignore the variation among individuals and sorts them into neat species anyway. I pointed out earlier that humans tend to do this as we try to bring order to a world that may not be quite as orderly as we would like.

People who see the world typologically, as biologists did in the seventeenth and eighteenth centuries, think the variations among individuals are trivial, and they have no reason to question the idea that each species was created separately. John Ray (1627–1705), one of the fathers of modern biological classification, reflected his contemporaries' thought when he said that two individuals belong to the same species if one is the ancestor of the other or if they are both descended from a common ancestor. With this definition in mind, typological thinkers could not even ask a question that implied evolution. A question such as, "Could the wolf and the fox have had a common ancestor?" would make no sense to them. Such an ancestor must have been either a wolf or a fox. If it were a wolf, it could not have been the ancestor of a fox, and vice versa. So the question would never even arise.

One of the few early naturalists to espouse the idea of evolution was Jean Baptiste de Lamarck, in 1809. His ideas are worth mentioning if only because similar ideas, labeled "Neo-Lamarckian," keep reappearing in biology. Lamarck's philosophy postulated a harmony between an organism and its environment, so the environment naturally imposes itself upon heredity. In his history of heredity, François Jacob describes Lamarck's views thus:

> … only the transmission to descendants of experience acquired by individuals appeared to account for the harmony between organisms and nature. Never had this idea been exploited so systematically and with so much detail, however – nor so confidently since Lamarck took for granted that an organ disappears because it is of no use. For him, whales and birds have no teeth because they do not need them. The mole lost the use of its eyes because it lives in the world of darkness. Acephalous molluscs have no head because they have no need for it.

In a world lacking an understanding of heredity or physiology, Lamarck's viewpoint made good sense. Organisms do acquire modifications in response to environmental conditions. A running animal develops strong running muscles, and an animal that continually rubs some part of its body grows protective calluses. Lamarck thought that such acquired features were somehow incorporated into an organism's heredity, endowing its offspring with a greater tendency to have the same useful features; in the same vague way, an organism that didn't use something would simply lose it. Although Lamarck's proposal had a certain appeal, it did not really *explain* evolution, as explanation is understood by modern science: it didn't provide even the outline of a real mechanism to account for a hereditary change in response to the environment. It happened, too, that the prevailing intellectual climate in both France and England was inhospitable to Lamarck's philosophy and to all ideas about evolution, and they were not accepted.

We have now seen how geology and biology grew together, as naturalists came to understand the forces laying down strata of rock and began to study the anatomy of the organisms buried in these strata in a comparative manner. These studies became a foundation on which Darwin and Wallace built their ideas about evolution. The principal problem Darwin faced in developing the idea of natural selection was that it depends on heredity, but in his time heredity was a mystery. To understand this whole issue – what a species is and how species evolve – we must first understand what organisms are, and we turn to this question next.

chapter three

biology – some basics

what are organisms?

taking a close look at the world

Imagine yourself in the place of an early naturalist, and think about what you can observe as you try to develop some insights into the nature of life. You see, for example, a world of plants, mostly green, which grow up out of the ground and continue to grow. Isn't that extraordinary? This little green shoot pokes out of the ground, and it keeps growing and changing form until it has reached a characteristic size. It may even develop beautiful flowers. With careful observation, you could easily make a long list of animals, of an extraordinary variety, living in and on and around the plants. As you watch them, you'll see that the animals spend much of their time running around, finding food and eating it, and that quite often the food is a plant or part of a plant. With a good microscope – they were first used in the seventeenth century and greatly refined in the nineteenth – you would find that samples from a pond or even a little water-filled depression in the ground contain a variety of tiny creatures; some look rather plantlike, some rather animal-like, and some of them will be eating one another. You'll see, also, that there are many places for organisms to live – fields, forests, ponds, swamps, oceans – and that each environment harbors only a certain characteristic group of organisms. Finally, you only have to watch these creatures for a year or two to see that one outcome of all this activity is that they reproduce, or try to reproduce, so each year there tend to be more of them – or, perhaps, there would be more if they didn't keep eating one another.

What's going on here? Growth, movement, living together, and reproduction. Early naturalists did not know all the essentials we know today, yet all of biology could be summed up in these four words or phrases.

growth

Organisms grow. They take in raw materials from their surroundings and transform them into their own substance, so they get larger. For plants, the raw materials are carbon dioxide from the air plus water and elements such as nitrogen, sulfur, and phosphorus from the soil or water. For animals, the raw materials are plants, or their parts, or other animals, or the wastes of other creatures. Some microorganisms live much like plants, some like animals, and a few carry out quite distinctive chemical activities, but they all grow. They grow by transforming their nutrients through complicated chemical processes, all summarized under the heading *metabolism*, into their structural molecules. Metabolism requires energy, which they obtain either from light or from energy stored in their nutrients.

movement

Movement is a kind of adjunct of metabolism. Movement is most obvious in animals and in some microorganisms, but even plants that don't show the large-scale movements of animals are moving streams of water through internal tubes, carrying nutrients and wastes; and parts of their cells are moving. Most movement happens because some of the complex materials that organisms are made of – some of their proteins – are able to pull on one another. Movement also requires energy, and part of metabolism is storing energy in a form that can be used for movement as well as for growth.

reproduction

Organisms reproduce. Some do it alone, often just by growing larger and then dividing in two, or by spreading shoots and runners out into their surroundings. Others do it cooperatively, as by combining sperm and egg cells (or their simpler equivalents) to form new individuals. The most extraordinary thing about reproduction, however, is *inheritance*. Organisms reproduce "after their own kind," to use the old biblical phrase. Violets produce violets, cocker spaniels produce cocker spaniel puppies, and tall, red-headed parents with a tendency toward hyperthyroidism produce tall, red-headed children with a similar tendency. We'll return to inheritance shortly.

living together

The various climates and physical features of the Earth provide distinct environments such as marshes, swamps, streams, lakes, hot springs, coral reefs, city parks, prairies, forests, backyard gardens, and deserts. Each of these places, with the organisms living there, is an *ecosystem*. It is a physical environment of water, soil, and air that supports a *community*, a collection of different organisms that live in the same area and can interact with one another: certain plants that can live in that environment, with characteristic animals and microorganisms living among them. The members of a community share living spaces and interact in complex ways. They eat each other and are eaten. They afford shelter and are in turn sheltered. They provide stages for one another on which each one acts out the drama of its life. No organism could live without the others in its community.

a modern way to understand biology

Now given these four big ideas about what organisms *do*, how can we find a general way to understand what organisms *are* – a way that will help to explain what we see them doing? Many people have tried to answer this question, generally by trying to enumerate the characteristics that make something *living*. But I will specifically avoid words such as "living," "life," and "alive" because they get us into too many verbal traps. Surprisingly perhaps, "life" just isn't a useful technical term in biology, although it has important nontechnical uses. Instead, we can understand evolution – as well as virtually everything else in biology – by recognizing that organisms are fundamentally *genetic systems*: they carry information that specifies their structures and they reproduce, which means that the organisms of one generation pass that information on to another generation of similar or identical organisms. Briefly, an *organism* is a *mutable, self-reproducing structure*. (I will explain the "mutable" part shortly.) This conception of an organism was stated clearly by Norman Horowitz, who later discovered that the idea was first formulated by the geneticist Hermann Muller in 1929. More explicitly:

> An organism is a structure that operates on the instructions encoded in a *genome* so as to mobilize energy and raw materials from its environment to maintain itself and, in general, to reproduce itself by producing other similar or identical organisms.

This definition emphasizes the central role of a substructure, the *genome*, which has two main functions:

- It encodes a *genetic program* that specifies the structure (and general mode of operation) of the whole organism, including its ability to reproduce.
- It *replicates*, or specifies the structure of a new replica of itself, so each of its offspring will have its own copy. However, occasional errors, called *mutations*, are sometimes made during replication, so some of the offspring may have mutated copies of the genome. Also, during sexual reproduction the genomes of two parents can recombine to produce offspring with distinctive genomes.

Because the genome is subject to mutations (and because of recombination of genomes during sexual reproduction), some of the offspring of any organism may be different from their parent(s) in a stable, heritable way. Some changes in heredity from generation to generation are inevitable, just because it is physically impossible for all the copies of a genome to be made without errors. And without such changes, organisms as we know them could not exist, because these changes underlie evolution. Thus we see that evolution and the entire Darwinian worldview emerge naturally from the very concept of an organism as a genetic structure.

Self-reproduction implies that an organism is carrying out metabolism, transforming materials from the environment into its own structure. This is true, and important. But we don't base our definition of an organism on it. In fact, it is the genetic conception that allows us to understand how the metabolic machinery could have come into existence through evolution.

heredity and structure

what is a genome?

A genome is the structure that carries *genetic information.* Information is the ineffable something we possess when we have specified one out of a number of possibilities. American telephone numbers could range from 000-000-0000 to 999-999-9999, 10^{10} possibilities. If I tell you that my phone number is 206-866-1234 (it isn't!), I have specified one of those sequences and have given you information. Genetic information takes the form of *genes*, which specify the structure (and operation) of the rest of the organism. We now know the nature of many genes, in many kinds of organisms, including humans. For a greater understanding of genes and genetics, it would be well to read *Genetics: A Beginner's Guide*, in this series but I'll briefly outline a few concepts here that are useful for understanding the role of genes in evolution.

The laws of heredity in the great majority of plants and animals were worked out around 1865 by Gregor Mendel, using pea plants. Mendel showed that genes (although this term was not invented until 1900) determine simple characteristics such as the color of the peas, whether the peas are smooth or wrinkled, the color of the flowers, and so on. Every plant (or seed) has two parents, and it receives equal sets of genes from them, so it has two copies of each gene. But many genes occur in two or more forms, called *alleles*; for instance, the gene that determines pea color has one allele that determines yellow pigment and another allele that determines green pigment. A pea that carries two identical alleles – we say it is *homozygous* – will have the color determined by those genes. However, if a pea carries two different alleles – we say it is *heterozygous* – then commonly the characteristic determined by one of them, the *dominant* allele, is visible, and the characteristic determined by the other, the *recessive* allele, is hidden. Thus, a pea that carries one allele for green color and one allele for yellow color will be yellow because the yellow allele is dominant and the green allele is recessive. (This is actually a very simple situation; there are other cases of incomplete dominance and situations in which several alleles of a single gene show complicated dominance and recessiveness relationships.)

Think about a homozygous pea plant with two alleles for yellow color compared with a heterozygous pea with one allele for each color. You can't tell the difference between them just by looking. They have different *genotypes* – different genetic constitutions – but they have the same *phenotype*: the same appearance. The difference between genotype and phenotype is critical in genetics.

When we think about human genes, we commonly think of genes associated with defects and diseases, such as sickle-cell anemia and cystic fibrosis. These conditions are generally determined by defective alleles that are recessive. Thus, many people may be heterozygous for such alleles and may never know it; we call them *carriers* for the disorders in question. However, if two people who are both carriers for, say, cystic fibrosis happen to marry and have children, they may produce a child that is homozygous for the defective allele and thus has the illness. Call the defective allele *c* and the normal allele *C*. The parents are both heterozygotes, *Cc*. Each of their eggs or sperm carries only one copy of this gene, either *C* or *c*. On the average, a quarter of their children will receive the *C* allele from both parents and will be normal, *CC*. Half of their children will receive a *C* from one parent and *c* from the other (notice that this can occur in two ways) and will be carriers, *Cc*, like their parents. And a quarter of their children will receive the *c* allele from both parents and will have cystic fibrosis. The alleles for any other gene will be inherited in the same pattern.

We now know that genes are arranged in *chromosomes*, which are long, threadlike structures in the nucleus of each cell. Each species has a characteristic set of chromosomes. For instance, humans normally have 46 chromosomes, forming 23 sets of *homologous* chromosomes; within each set, one chromosome has been inherited from the mother and one from the father. The total number of human genes is estimated to be in the range of 35,000–70,000, so each chromosome must carry many genes. Generally the two chromosomes in each set carry identical *sequences of genes*, but they commonly carry different *alleles* of many genes. In fact, every natural population harbors an enormous amount of genetic diversity – that is, many distinct alleles of many genes – and humans are no exception; so parents with diverse family histories will have many genetic differences, and their children will be similarly mixed.

To make better sense of this it is necessary to examine organisms at the chemical level, to explore the chemical structures of genes and some of the other materials that constitute the structures of organisms.

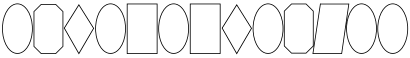
cells

All organisms are made of one or more distinct cells. A cell is a fundamental structural unit whose boundary is a surrounding *membrane*; this is a thin and very flexible sheet of molecules that keeps the cellular components inside and controls the movement of materials inward and outward. The simplest organisms are just single cells. Bacteria are very small, with dimensions of the order of one micrometer (μm, a millionth of a meter), mostly single cells with minimal internal structure; such cells, lacking the nucleus characteristic of most other organisms, are called *procaryotic*, and bacteria themselves are therefore *procaryotes.* The genome of each procaryotic cell is just one long chromosome, a ring-shaped molecule of DNA. The cells of plants, animals, fungi, and many tiny creatures observable in a drop of pond water are *eucaryotic*; their typical dimensions are of the order of 10–40 μm, and each one has a nucleus, a rather large spherical body that contains the chromosomes and thus most of the genes. The human body is made of about 100 trillion (10^{14}) cells. Each cell contains other characteristic structures, called *organelles*, such as mitochondria, small bodies that derive much of the energy from food molecules and store it in a usable form; mitochondria also contain a few genes. Other organelles are the factories where proteins are made, or they move materials from one place to another.

The biological world, incidentally, includes a multitude of complicated structures called *viruses*, which are quite distinct from organisms. Organisms are cellular; viruses are not (though some have a somewhat cellular appearance). A virus is basically a genome wrapped in some protective material, mostly protein, that parasitizes organisms. Viruses don’t have their own apparatus for obtaining energy and manufacturing proteins, as cells do; a typical virus has an apparatus for invading a host cell, disabling (sometimes destroying) the cell’s genome, and turning the cell into a little factory for replicating the viral genome and producing a lot of new viruses. The cell eventually ruptures, releasing all these viruses that can go on to find and invade other cells. Each type of virus is very specific in its choice of hosts; some of the best-known viruses, called bacteriophage or simply phage, grow in bacteria.

polymers

Cells are made mostly of large molecules (macromolecules). The molecular mass of a molecule is the sum of the masses of its constituent atoms; thus water, H_2O, has a molecular mass of 18: the sum of 16 for the oxygen atom plus 1 for each hydrogen atom. Chemists call the units of mass *amu*, for atomic mass units; biologists commonly call the units *daltons*, after the pioneering chemist John Dalton. A small molecule such as the sugar glucose ($C_6H_{12}O_6$) has a mass of 180 daltons; you can derive this number by adding up all the masses of these elements in the formula (carbon atoms have a mass of 12). On this scale, macromolecules are truly huge, with masses of many thousands of daltons. However, the structures of these huge molecules are actually quite simple, in spite of their size. Every macromolecule is a *polymer*, a molecule made by putting together many small molecules, or *monomers*. Generally, the monomers are assembled like beads on a string, making a very long molecule:



... and so on.

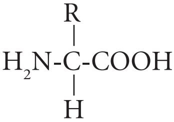
Simple examples come from the world of plastic and rubber, which are human-made polymers. For instance, ethylene is a small molecule: $H_2C{=}CH_2$, where the double line shows two bonds between the carbon atoms instead of the usual single bond. Many ethylene molecules can be combined into long molecules of polyethylene, the plastic from which food wraps are made:

$$CH_2{-}CH_2{-}CH_2{-}CH_2{-}CH_2{-}CH_2{-}CH_2{-}CH_2{-}CH_2{-}CH_2{-}CH_2{-}CH_2{-}\ldots$$

and on and on for thousands of units. Similarly, substituting fluorine atoms, F, for the hydrogen atoms in these molecules, we would start with the monomer tetrafluoroethylene and produce the polymer teflon.

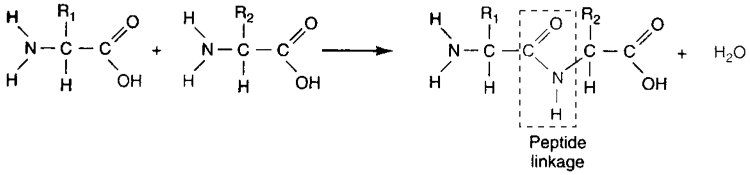
proteins

In plastics, all the monomers are identical. Some biological polymers have this structure. For instance, molecules of the sugar glucose can be linked in chains in one way to make the polymer *cellulose*, the principal structure of wood, or they can be linked to one another in a subtly different way to make *starch*. However, the principal biological polymers are made with several distinct types of monomers, so the resulting polymers can be much more complex. Proteins – the molecules that perform most of the functions in an organism – have this structure, and they are the most complex biological molecules. Their monomers are amino acids, which look like this:



$$H_2N\text{-}\underset{\displaystyle H}{\overset{\displaystyle R}{C}}\text{-}COOH$$

The $-NH_2$ group is an amino group, and the $-COOH$ group is an acid[1] group – hence, amino acids. The portion of the molecule denoted R varies and determines the particular amino acid; thus, the amino acid glycine has an H atom in this position, alanine has CH_3, and serine has CH_2OH. Then two amino acids can be linked through a peptide linkage like this:



Notice that the linkage is made by removing a molecule of water: H from the amino group and OH from the acid group. The resulting molecule is called a *dipeptide*, because it has two monomers (*di-* = two). But since it has amino and acid groups at its ends, a third monomer can be linked by removing another water molecule to make a *tripeptide*. There is no limit to the number of amino acids that can be linked in this way, to make *polypeptides*; and a protein is one distinctive kind of polypeptide.

All proteins are constructed of twenty types of amino acids, with names such as glycine, alanine, serine, valine, glutamic acid, and tryptophan. This means that in constructing a polypeptide there are twenty choices for the first position and twenty for the second, so there are 20 × 20 = 400 possible dipeptides. Given another twenty choices for the third position, there are 8,000 possible tripeptides. Then there are 20^{100} possible sequences for a polypeptide of 100 amino acids – a relatively small protein. That number is inconceivably large. More typical proteins may be made of 300 amino acids, or even more. Every possible polypeptide has distinctive properties and might be a functional protein. Every kind of protein has a unique sequence; for instance, part of the human hemoglobin A molecule, the red substance that carries oxygen in our blood, begins with the sequence Val-His-Leu-Thr-Pro-Glu-Glu-Lys-Ser-Ala-Val-Thr-Ala-, using the three-letter abbreviations for the amino acids. Every molecule of hemoglobin A in a normal person has precisely this structure. Once a polypeptide chain has been made, it folds up into a particular shape and has the ability to perform a particular biological function. What are these functions? Proteins perform virtually all of the jobs needed to make an organism do the complicated things it does, such as:

- They are the *enzymes* that operate metabolism – that make all the chemical reactions in an organism occur rapidly and in a controlled way.
- They form prominent structures: keratins make hair, skin, and feathers, and collagen forms much of the substance of cartilage and bone.
- They form filaments that push and pull on one another to create movement in muscles and other movable structures, such as cilia and flagella.
- They are an important class of *hormones*, which carry signals between different kinds of cells in the body.
- They form *receptors*, which receive signals by binding to other molecules. A cell receives a signal from a hormone because the hormone molecules bind to one of its receptors. Receptors like those we use for tasting and smelling allow organisms to detect the presence of small molecules in their environment and respond to them.
- They are transporters that carry ions and small molecules across cell membranes, thus maintaining the right contents in each cell and also forming the basis of our nervous systems and organs such as kidneys.
- They are regulatory elements that control all kinds of processes so they occur at proper, coordinated rates.

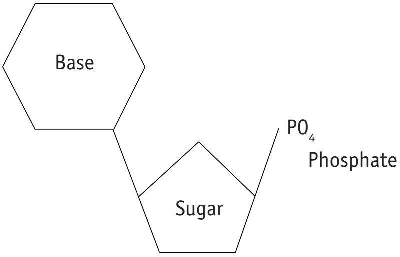
So every organism consists of thousands of distinct proteins that perform all its functions, and having its own particular proteins makes each species the unique thing that it is.

One of the major activities of every cell is making its own set of proteins. Take away the water of a cell, which makes up most of its normal weight, and half or more of the remainder will be protein. So *growth primarily means protein synthesis.* Simple organisms such as bacteria may grow in the water and soil or on other organisms by taking in amino acids from their surroundings, or by synthesizing their own from other food molecules. The cells in our bodies make their proteins from amino acids circulating in the blood (derived from our food), or they synthesize their own amino acids from other molecules.[2] However, to make a particular protein, the cell must "know" its amino-acid sequence. Thus, every cell that is becoming a red blood cell must "know" to make hemoglobin molecules by making many proteins with the string Val-His-Leu-Thr-Pro-Glu-Glu-Lys-Ser-Ala-Val-Thr-Ala-…, rather than all the other possible strings. This requires *information*, *genetic* information. And the information for making a particular type of protein lies in the genes. *The function of a gene is to specify the amino-acid sequence of a particular protein.*

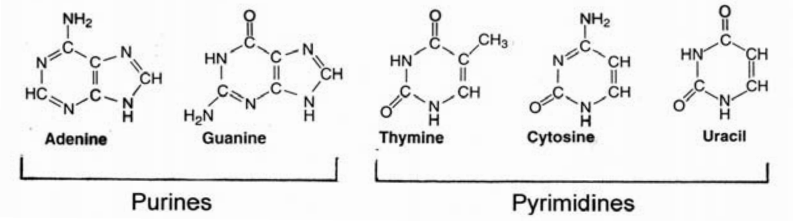
So we have replaced the vague idea of a Mendelian gene as a "thing" that is inherited regularly with the idea of a gene as a structure carrying the information for a protein. The next step, then, is to understand the structure of nucleic acids, the molecules that genes are made of.

nucleic acids

The second most abundant macromolecules in cells are polymers called polynucleotides or nucleic acids, whose monomers are *nucleotides.* A nucleotide is more complicated than an amino acid, as it consists of three smaller molecules: a *base* linked to a *sugar*[3] which is linked to a *phosphate* (PO_4).

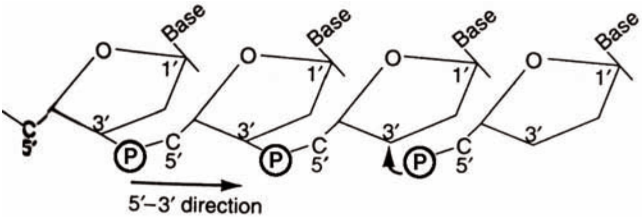


A nucleic acid is named for its sugar; ribonucleic acid (RNA) contains ribose, and deoxyribonucleic acid (DNA) contains deoxyribose (ribose with one oxygen atom removed). The bases are large ring-shaped, nitrogenous molecules; DNA nucleotides have one of four bases: *adenine, guanine, cytosine* and *thymine* (A, G, C, and T); in RNA, *uracil* (U) replaces thymine.



Cytosine, thymine, and uracil are based on a single ring of atoms and are called *pyrimidines*; adenine and guanine have a double ring of atoms and are called *purines*. Notice that the carbon and nitrogen atoms in the rings are all numbered for reference; those of the sugar are numbered with prime marks, from 1' to 5'.

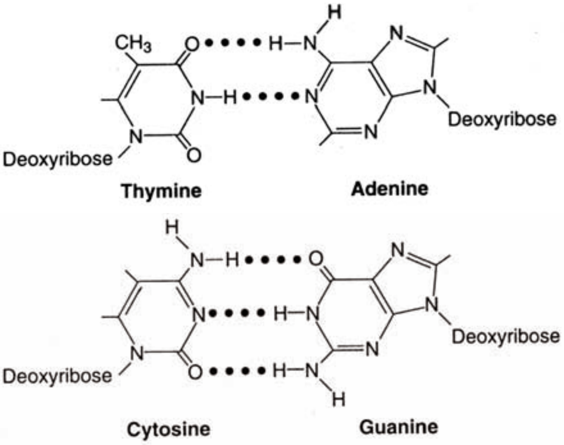
A nucleic acid is constructed by stringing nucleotides together by linking the phosphate of one to the sugar of the next:



This makes a "backbone" of sugar-phosphate-sugar-phosphate ..., on and on for thousands or even millions of units. The bases, you'll notice, extend to the side of the backbone. Notice, also, that the phosphate connects the 3' C atom of one sugar to the 5' C atom of the next, so the chain has a polarity: it runs 3'–5' in one direction, and we can talk about its ends as the 3' end and the 5' end.

It is now a commonplace of biology that the genomes of all organisms consist of DNA. (The genomes of many viruses consist of the very similar molecule RNA.) A DNA molecule, as determined by James D. Watson and Francis H. C. Crick in 1953, consists of two polynucleotide strands wound together to make a double helix

(Figure 3.1). The strands are held together in the middle by bonding between the bases from the two strands, but adenine can only bond to thymine and guanine only to cytosine:



These base-pairs are held together by weak attractions called *hydrogen bonds*, in which two somewhat negative atoms such as O and N hold a somewhat positive H atom between them. We say that two bases that

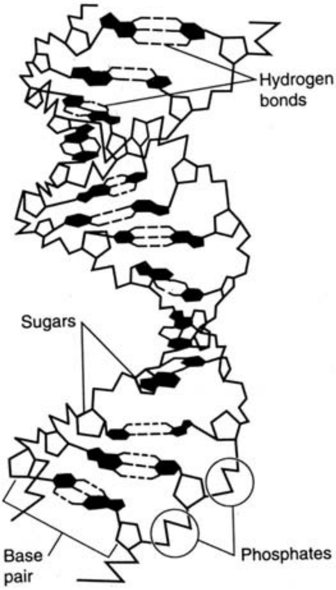


Figure 3.1 *A DNA molecule consists of two polynucleotide strands held together by hydrogen bonding between their complementary bases.*

can bond this way are *complementary* to each other, in the way that a hand is complementary to a glove or that the curve of one jigsaw-puzzle piece is complementary to the curve of the piece it fits with.

Complementary base-pairing accounts for virtually everything in heredity, and for much of biology in general. It means, first, that a DNA molecule can easily replicate – that is, it can produce two molecules that are replicas of each other. This must happen every time a cell divides in two, because each daughter cell must have its own genome – its own complement of chromosomes. DNA is replicated by a complex of enzymes (called DNA polymerase) that move along the molecule, separating it into its single strands. The cell contains many nucleotides, which it synthesizes as part of its metabolic activities, and these nucleotides bind to the components of the DNA strands. Thus, where a strand has an A base, it will bond to a T; where it has a C, it will bond to a G; and so on. The enzyme complex links these fresh nucleotides, one by one, into a new strand that is complementary to the existing strand, so when it has moved the length of the DNA molecule it will have produced a new complementary strand and thus a new double-stranded molecule.

Now, just how does a gene specify the structure of a protein?[4] The essential point is that the sequence of bases in each gene creates a *genetic code* that specifies a sequence of amino acids. Each sequence of three bases in the gene constitutes a *codon*, which specifies one of the twenty amino acids. There are sixty-four of these triplets; three of them are stop signals, which mark the end of a gene. The meanings of the other sixty-one are now well known. Thus, the codons TTT and TTC both mean "phenylalanine," all four triplets that start with GG mean "glycine," and so on.

The details of protein synthesis needn't concern us here, but it occurs in two stages. First, a complicated enzyme (called RNA polymerase) moves along one gene in the DNA; this enzyme recognizes genes because each one is marked by distinctive base sequences at both ends. As it moves, the RNA polymerase synthesizes a strand of *messenger RNA* that is complementary to one strand of the DNA, essentially the way a DNA polymerase makes a new strand of DNA during DNA replication. Second, this messenger RNA attaches to a large particle (made of protein and RNA molecules) called a *ribosome*, a factory that makes new proteins. The cell is also rich in amino acids, and they are attached to molecules called *transfer RNAs*. Each transfer RNA recognizes one codon on the messenger RNA and brings the proper amino to this position where the messenger RNA is attached to the ribosome. Then one by one these amino acids are linked into a polypeptide, by enzymes in the ribosome, until an entire new protein molecule has been made. Its amino acid sequence will be the sequence of codons in the gene.

This explanation, stripped of many subtleties and details, should provide a picture of how the genetic apparatus of cells, and organisms, operates. A large organism such as a human or an oak tree operates through the coordinated actions of its individual cells – and its organs, such as the heart, brain, and liver in a human. In turn, these cells and organs operate by virtue of their component proteins, and each cell makes its complex of proteins by reading the instructions in its genes. For now, we will ignore the much more complicated question of how a blood cell "knows" to make one group of proteins, a brain cell "knows" to make another, and a liver cell "knows" to make still another. This is a topic for chapter seven, where we'll explore this problem as a prelude to exploring how complicated creatures, like animals, can evolve into so many different forms.

evolution

historicity: carrying your story with you

Every organism has become what it is through a long evolutionary process in which its ancestors were shaped, generation after generation, by the forces we explore in this book. It has a unique combination of genes and is thus a unique historical object.

History is shaped by a unique series of happenstances. If any of them had been a little different, the world we live in would be different. What if a little twelfth-century Mongol boy, Temujin, had been a shy lad instead of the aggressive, ambitious leader who became Genghis Khan? What if King George III of England and his Parliament had recognized the true value of the American colonies and had not provoked them into revolution? What if John F. Kennedy had not gone to Dallas in November 1963? What if ...?

It is important always to consider evolution in such a historical light. There are no natural forces driving organisms to have any particular characteristics; they just have whatever features they were able to acquire that allowed them to survive. Why, for instance, do we have five digits on our hands and feet instead of four or six? Because the ancestral amphibians that first adapted to the land just happened to have the genes to produce five, that's all. In particular, we will see that most species have become extinct after, at most, a few million years of existence, presumably because they were unable to adapt to changing conditions. We are tempted then to ask, "Why didn't this species acquire the particular genes needed to adapt and survive?" The only answer will be, "Because the right combination of genetic events simply didn't happen." Writing about human evolution, Elaine Morgan has pointed out how we are inclined to imagine that all the modifications and adaptations that might be nice to have for survival could simply be ordered from some celestial mail-order catalogue. But, of course, this is mere fantasy and sloppy thinking, and it is important not to fall into this trap.

Some of the large, elaborately illustrated books listed under Further Reading narrate the full story of evolution on Earth over the past few billion years, sometimes with color paintings to show what the world must have looked like at various times. The following brief summary will provide some guidelines about the general course of evolution and the time at which major events occurred.

origins

It would be logical to begin with the origin of life. However, this is really a different topic from evolution in general, and I don't want to dwell on it, although many people will consider it the most critical, and controversial, event in evolution. The trouble is that in dealing with the beginnings of organisms on Earth we are reduced to a great deal of speculation – well-founded, scientific speculation, but speculation nevertheless. There is no fossil record of the earliest events; there cannot be, because the earliest things that were on their way to becoming real organisms were simply collections of organic molecules that disappeared completely.

Scientists thinking about the origin of life once assumed that the Earth's atmosphere has always been much as it is now. But in the 1930s the Russian biologist A. I. Oparin pointed out that molecular oxygen in the atmosphere would have attacked and oxidized any simple organic compounds that might have formed, so the primitive Earth must have had a reducing atmosphere, made mostly of hydrogen, methane, ammonia, nitrogen, and water. Molecular oxygen must have been scarce. Building on the previous work of J. B. S. Haldane, Oparin proposed that the energy of ultraviolet light and lightning discharges could have turned the gases in the hypothetical reducing atmosphere into a "primordial soup" of organic molecules.

In 1953 Stanley Miller tested the Haldane–Oparin hypothesis while he was a graduate student in Harold Urey's laboratory. He constructed an apparatus that simulated the hypothetical primitive conditions, complete with electrical sparks to simulate lightning. To his great delight, Miller found that the mixture in his apparatus formed a variety of organic compounds, including some of the common amino acids, the building blocks of proteins, as well as fatty acids, the purine and pyrimidine bases of nucleic acids, and other substances important in metabolism. Other investigators have shown that the monomers of proteins and nucleic acids can polymerize rather easily into the gigantic molecules so critical for a functioning organism. In fact, polymerization might be enhanced by environmental features, such as certain clay minerals that can hold monomers on their surface at the right spacing for polymerization.

Since lipids such as fatty acids are produced in primitive reaction mixtures, and since lipids and proteins assemble easily into membrane structures, there is little difficulty in seeing how primitive cells could form, since a cell is fundamentally a unit enclosed by a membrane. Here we have the beginnings of a fossil record for guidance, because the record in the Onverwacht sediments of South Africa, and some other localities, shows that simple cells already existed at least 3.4 billion years ago. These cells were procaryotes, some similar to our modern types. Excellent procaryotic fossils are found in rocks from that age up to 2 billion years ago in the Gunflint iron formation of Ontario.

However, the most critical feature of an organism is its genome. Without it, there can be no biological evolution, since evolution depends on the selection of individuals with variant genomes. So primitive biological systems could not have been shaped by natural selection unless they were specified by a genome. Although nucleic acid molecules do not form in primitive mixtures as easily as proteins do, they have been produced under simulated primitive conditions, and at least small polynucleotides must have formed on the primitive Earth along with other organic compounds.

A genome directs the synthesis of proteins. The greatest difficulty in understanding the origin of functioning organisms is to understand how nucleic acids could get *control* over protein structure and come to specify that structure. The best answer lies in the hypothesis that the first functional nucleic acids were RNA molecules, so for a considerable time there was an "RNA world," a critical stage in evolution. RNA molecules have an inherent ability to interact with one another through base-pairing, so they can replicate as DNA does. They can also fold up into complicated forms and act as *ribozymes* – that is, RNA molecules that catalyze chemical reactions just as protein enzymes do. Without going into all the molecular details, we can draw plausible scenarios of the interactions between various kinds of primitive RNA molecules. Some, having structures most conducive to self-replication, must have acted as primitive genomes; others acted as ribozymes to perform the steps of protein synthesis, lining up along the genomes (as transfer RNA molecules still do) to align amino acids and polymerize them into proteins. The evolution of these primitive systems into efficient systems of the modern type must have been a long, slow process, and several hundred million years were required for the first functioning cells to appear, a time at least as long as the entire time multicellular organisms such as plants and animals have been evolving.

early cellular evolution

The earliest procaryotic cells evolved into a great variety, many of which are still with us. Some, known as Archaea, have unusual structures and metabolic features that set them aside from all other known organisms; they mostly persist today in very unusual environments, such as very hot springs or places with high concentrations of salt or sulfur. Others evolved into a variety of bacteria. Metabolically, the first cells probably lived by consuming organic molecules in their environment, but after a time the first *autotrophs* appeared – organisms that can make all their components from CO_2 and other simple substances (*auto-* = self, *-trophy* = a mode of nourishment). Among the most important modern autotrophs are the *phototrophs* (*photo-* = light), those that, like plants, get their energy from light through photosynthesis – as the name says, a light-driven synthesis. Surely some phototrophic bacteria evolved early on, and the first of these did not produce oxygen as a by-product, as plants and most other phototrophs do today; many contemporary phototrophic bacteria carry out a different kind of metabolism. But eventually oxygen-producing phototrophs did evolve; geological evidence shows that they first appeared around 2.7 billion years ago, and they changed the atmosphere over to the present oxygen-rich atmosphere by around 2 billion years ago (perhaps with a later spurt of oxygen production after 1 billion years ago). That change in the atmosphere is recorded in part in geologic formations called Banded Iron Formations, rocks in which atmospheric oxygen combined with iron to form layers of red oxides. The significance of this atmospheric changeover lies primarily in the opportunity it afforded for future evolution; organisms could then arise that carried out a complete respiration, using oxygen – a process that yields energy quite efficiently and allows complex, active creatures such as animals to function.

Plants and animals are eucaryotes, with cells containing nuclei as well as mitochondria, the places where oxygen-based respiration is carried out. Eucaryotic phototrophs have chloroplasts, the rather similar structures that perform photosynthesis. Both mitochondria and chloroplasts have their own small DNA molecules that encode some of their proteins. From this fact and other clues, it has become clear that both mitochondria and chloroplasts arose from primitive bacteria, which were incorporated into other primitive cells through a process of endosymbiosis; symbiosis is a common ecological arrangement in which two types of organisms live together intimately, each performing functions that benefit them both. Lichens, for instance, are symbiotic associations between fungi and algae. In *endo*symbiosis, one organism lives inside the other, and there are good examples of this among living organisms. At some times in the remote past (and in quite separate events), an oxygen-respiring bacterium became incorporated into some other cell and became the first mitochondrion; and an oxygen-producing phototroph became incorporated into some other cell and became the first chloroplast. In fact, since there are now phototrophs with different types of chloroplasts, this endosymbiosis apparently happened a few different times with different types of cells. Fossils in beds such as the Bitter Springs formation in Australia show that eucaryotic algae existed by 1 billion years ago, and there is evidence for eucaryotes even 2 billion years ago, perhaps even earlier. Certainly a variety of simple eucaryotes – protozoa and algae – were living by 700 million years ago; the first complex, multicellular organisms appeared at about the same time.

animal evolution

Near Ediacara, in southern Australia, lie beds of sandstone containing a remarkable series of fossils that have been the subject of considerable speculation and controversy. The creatures preserved there – and in sediments of the same age elsewhere, defining the Ediacaran period – are surely animals, but they resemble no animals found at any later times. They apparently represent a first evolutionary experiment with complex creatures, one that failed as all its members became extinct.[5] It took another 100 million years, until the middle of the Cambrian period, for the first successful early animals to appear, all in quite a short time in the so-called Cambrian Explosion. Here we find members of the principal invertebrate animal groups, especially sponges, molluscs, brachiopods, echinoderms, and arthropods such as trilobites and eurypterids. During the following Ordovician period, the diversity of invertebrates increased enormously. The first animals to occupy land habitats, scorpions and insects, appeared during the Silurian and became dominant during the Carboniferous. The first fishes, initially those without jaws, appeared in the Silurian and became widespread and diverse in the Devonian. Among these fishes were Crossopterygians, the first to develop lungs; most fishes breathe through their gills, which absorb dissolved oxygen from the surrounding water. One requirement of living on land is an organ that can remove oxygen from the air, and the Crossopterygian lung allowed one line of their descendants, the Labyrinthodonts, to become the first amphibians, during late Devonian and especially Carboniferous times. In spite of their ability to breathe air, amphibians have never become dominant, as they evolved only some of the adaptations required for living on land; modern amphibians are confined to wet habitats and still use water for reproduction. A life more independent of the water only came about with the reptiles and the evolution of the *amniotic egg*, an egg enclosed by a shell in which a developing embryo remains surrounded by water. The stem reptiles, called Cotylosaurs, appeared during the Permian period, toward the end of the Paleozoic era. The Permian ended in a still-unexplained event, a massive extinction that wiped out over 90 per cent of all existing species.

With the Triassic period, following the Permian, the reptiles underwent a massive diversification into the few types that still survive (turtles, snakes, lizards, crocodilians), and during the following Jurassic and Cretaceous periods, land habitats were dominated by the dinosaurs that have so captured the popular imagination. The dinosaurs belonged to two large groups, ornithischians and saurischians, differing primarily on the anatomy of their hips. The first mammals also appeared during the Jurassic, and around the same time, one small line of saurischian dinosaurs, the theropods, had produced the first birds; but both mammals and birds remained relatively obscure as long as the ecological niches they could use remained occupied by reptiles. Finally, at the end of the Cretaceous, another massive extinction occurred, ending the era of dominance by dinosaurs and ushering in the Cenozoic era. During early Cenozoic times, the mammals underwent another massive diversification into virtually all the orders that survive today, plus a few that have become extinct. Similarly, birds of the modern type also became much more diverse, leading eventually to today's vertebrate fauna. One branch of the mammalian tree eventually produced humans, as detailed in chapter eight.

plant evolution

Animals are ecologically dependent on algae and plants, which were undergoing a similar evolution and diversification during this entire time. During late Cambrian times, some green algae evolved into much larger multicellular forms (dasyclads and codiums) with complex reproductive structures. This evolution of both red and green algae continued into Silurian and Devonian times, where we find plants now known as stoneworts or brittleworts with a whorled arrangement of branches that begin to resemble land plants. The first fossils of fungi also appear in Devonian rocks. (It is worth noting that although fungi resemble plants and were once classified with them, recent genetic evidence shows that fungi and animals are really closely related.) All these plants were aquatic. Plants that could occupy niches on land required the evolution of certain essential adaptations, especially *vascular tissues* consisting of tubes that transport water and nutrients; most critical is the *xylem* that moves water upward from roots into the rest of the plant. It happens, also, that xylem tissue consists of heavily walled cells that can support a plant growing up out of the ground, culminating in the development of very strong woody tissues characteristic of trees. The first vascular plants, rhynias, appeared in the late Silurian and became much more diverse during the Devonian. The Devonian was a time of great plant diversification; here the first lycopods (club mosses) and the first horsetails appeared, along with plants named *Psilophyton*, with a main axis that produced side branches; these were probably the ancestors of all the later, more dominant groups, including ferns and progymnosperms, from which the later seed plants all evolved. First, however, the lycopods and horsetails had their heyday during the Carboniferous (Mississippian and Pennsylvanian); the extensive fossils of this time show lush forests dominated by huge trees of both kinds, and these buried forests later turned into some of the large beds of coal and oil that we now extract for most of our energy needs.

A second plant adaptation needed for complete dominance of the land was a method of reproduction independent of water; the earlier-evolved plants generally depend on an aquatic stage in which reproductive cells can swim from one plant to another to effect fertilization. Independence of the water was achieved through the evolution of *pollen*, to carry sperm, and *seeds*, to enclose the developing embryo plant in a nutritious, protected environment. The first seed plants belonged to three groups that also appeared during the Carboniferous. The seed ferns (pteridosperms) reached 12–15 feet in height and lasted into the Jurassic; the cordaites were trees 50–100 feet tall with strap-shaped leaves; and the conifers became the familiar pines, firs, spruces, and their relatives that we still have today. Finally, the angiosperms, the flowering plants, appeared in the late Cretaceous and evolved during the Cenozoic era into the plants that dominate today's landscape.

summary and foreword

We have now developed the following general biological picture. All organisms live and grow in communities with other kinds of organisms, and through their various activities they get nutrients from their environment, which they use to grow and reproduce. They can carry out these activities because each organism contains a distinctive genome, a collection of nucleic acid molecules that contain genes. Most genes carry the information for synthesizing specific proteins, and an organism needs many distinct kinds of proteins to perform its various functions. One function of the genome is to replicate, to make more copies of itself so the next generation of organisms can have their own genomes; during the processes of replication and reproduction, organisms sometimes inherit genomes containing errors (mutations) and new combinations of genes.

To anticipate what is coming, evolution emerges naturally from this picture. In general, reproduction is so successful that each generation produces far more offspring than can possibly survive. Remember that all this activity is going on within ecosystems in which every organism has to fit into some way of making a living, what we call its ecological niche, and because of the little variations in their genomes, some individuals will be better at doing this than others. Then these better-adapted individuals will naturally be selected as the parents of the next generation, which will inherit the features that made their parents better adapted. Through this and other processes, and because of natural environmental changes, organisms will tend to diverge from one another and to acquire new characteristics. In other words, they will tend to evolve. Now we will see in more detail how this happens.

notes

1. An acid is a compound that can liberate a hydrogen ion H^+, and the H of -COOH comes off as an ion, leaving a negatively charged $-COO^-$ behind.
2. Of the twenty amino acids used to make proteins, eight (called "essential" amino acids) cannot be synthesized by most animals, so they must be obtained in the diet. Plants and simpler organisms can make all twenty. But this fact has no particular significance for genetics or evolution.
3. I won't try to define a sugar formally, but it is a molecule with several -OH groups, and you can always tell a sugar by its name, which always ends in -*ose*.
4. Some genes specify the structures of certain RNA molecules that form the apparatus for synthesizing proteins.
5. This issue is discussed at length in Gould's *Wonderful Life*, especially in sections of Chapter 7.

chapter four

a broad view of the process

One of the themes we will develop in this book is a kind of truism that every biologist recognizes: that biology only makes sense if you see that organisms have acquired their forms and functions through evolution. Beyond that lies an additional truism: that evolution only makes sense if you see it ecologically. That is, we have to see every type of organism as being suited for a particular role in an ecosystem. In the metaphor of the noted ecologist G. Evelyn Hutchinson, the drama of evolution is played out in the theatre of the ecosystem; so at the risk of straining the metaphor, each species has a particular role in the drama. The result of natural selection is *adaptation*: each kind of organism becomes shaped for one particular way of life in one environment, and that way of life is called its *ecological niche*. The terms *niche*, *adaptation*, and *selection* are interrelated; a niche is the particular place and way of life that each species occupies, adaptation is the evolutionary process by which it is shaped to live in that way, and the shaping occurs through selection of genetic differences. Our first task, in this chapter, will be to take a broad look at how evolution has proceeded. Then we will amplify the idea of natural selection and flesh out the idea of the ecological theatre in which all this happens.

the major features of evolution

the modern synthesis

Although Charles Darwin had laid out the essential ideas of evolution, with the emphasis on natural selection, he was unable to flesh out the idea satisfactorily because of the primitive state of biology in his time, especially the general ignorance of heredity. Ironically, Darwin's contemporary Gregor Mendel – unknown and unrecognized – was doing experiments in his modest Czech monastery that would lay the foundation for genetics, but his work did not become widely known until 1900. Meanwhile, Darwin struggled to make sense of natural selection with the burden of misconceptions about heredity. When genetics finally became a science in the early twentieth century, some geneticists with a mathematical bent were able to start understanding how genes behave in populations, the realm in which evolution actually occurs; the names of R. A. Fisher, J. B. S. Haldane, and Sewall Wright stand out. Then in the 1930s, the Russian geneticist Theodosius Dobzhansky began to investigate the behavior of genes in populations experimentally, and by 1937 he was able to start summarizing the bearing of population genetics on evolution in his pioneering book *Genetics and the Origin of Species.* Meanwhile, Ernst Mayr, a young ornithologist who had been studying birds in the South Pacific, began to formulate his ideas about the ways new species arise, which he summarized in his book *Systematics and the Origin of Species* (1942). Paleontology, too, had been growing in sophistication, providing more detailed pictures of the actual evolution of particular groups of organisms, and biogeography, the science of the geographic distribution of organisms, was developing insights important for understanding evolution. Thus, a modern conception of the evolutionary process was developing, and it was summarized by Julian Huxley (grandson of Darwin's colleague Thomas Henry Huxley) in his edited volume *The New Systematics* (1940) and in *Evolution, The Modern Synthesis* (1942). Though our understanding of evolution has grown enormously since that time, most of the conceptions of the modern synthesis remain intact and form the foundation for current evolutionary thought.

what is a species?

Darwin's seminal work was entitled *On the Origin of Species*, and several later books have used the same phrase. This naturally raises the critical question, "What is a species?" Because the question is more complicated than it might seem to be, I want to take the answer in steps, especially in chapter six, but it deserves a preliminary answer here. Naively, a species is simply a "kind" of organism, with the obvious proviso that males and females and young (and various odd larval and intermediate stages) are all members of the same species, even though they may look quite different. (So a species may take on a cycle of forms during each generation, as the cycle of a butterfly species from egg to caterpillar to pupa to winged adult.) Some good concrete examples of species come from birds. Everyone knows at least a little about birds, and many people enjoy watching and identifying them. But bird-watchers are often confronted with some knotty problems.

Figure 4.1 shows birds called chickadees in North America and tits in Europe. An American birder could see Black-capped, Carolina, Boreal, Chestnut-backed, Mountain, Mexican, or Gray-headed Chickadees by traveling around the continent. The American Ornithologists' Union (AOU), which keeps the official list, has determined that they are all distinct species. But why? And how can you tell what species an individual belongs to?

The answer to the first question is twofold. Initially, a species is defined *morphologically* – by its visible structural features (*morph* = form). Each of these species consists of adult birds with a distinctive size, shape, and coloration, so an observer can generally assign a bird to one group. However, morphology alone is often not adequate, and a better answer is, "Because each species consists of individuals that only breed with one another, not with members of the other species." The best general definition, according to the so-called *biological species concept* (*BSC*), is that a species is a group of all the individuals that are actually or potentially able to breed with one another but are reproductively isolated from other such groups. However, we will have to consider this definition at length later.

Placing an individual in one species or another on the basis of morphology is generally easy. A birder in Western North America can usually recognize the rich, rusty-brown plumage of a Chestnut-backed Chickadee or see the distinctive line through the eye of a

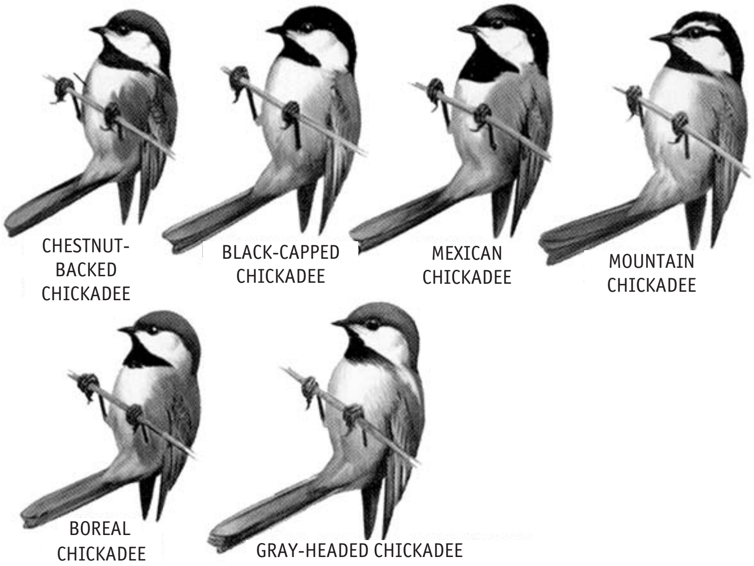


Figure 4.1 *Several species of chickadees, which are distinguished from one another primarily by their morphology. (Plates from* A Field Guide to Western Birds, *2nd ed. © 1990 by Roger Tory Peterson. Reproduced by permission of Houghton Mifflin Company. All rights reserved.)*

Mountain Chickadee. But someone in the mountains of Arizona will sometimes encounter Mexican Chickadees, and it takes some care and sharp observation to see their distinguishing features. Similarly, a birder in the Eastern United States can be reasonably confident that the birds in the northern region are Black-capped Chickadees and those in the south are the slightly smaller Carolina. But anyone observing birds in a middle region, roughly from Missouri through Pennsylvania, has to look sharp at any chickadee, because the two species differ primarily in the amount of white in the wings, but this feature is quite variable; expert birders with good ears tend to rely more on distinctions between the birds' call notes and songs. To make the situation even more confusing, experts agree that the two species hybridize to some extent where their ranges overlap, so one may see intermediate birds.

What can this talk of hybrids and intermediates mean? The very definition of a species depends on the birds breeding only with their own kind and *not* hybridizing! Is there something wrong with the definition, or with these particular "species," or both? Well, some biologists will argue that the definition, based on patterns of breeding and reproduction, is at fault, and they have sought alternatives. We will revisit the issue in chapter six.

a big picture: the major features of evolution

Biologists customarily divide the processes of evolution into three broad categories. *Microevolution* refers to changes that occur within a single species. *Speciation* means division of one species into two or more. And *macroevolution* refers to the larger changes in the variety of organisms that we see in the fossil record. We will begin with an overview of evolution as a whole.

Fossils provide a record of the organisms that were living at each time in the past. A century ago, before many fossils had been discovered and the fossil record was relatively sparse, biologists were sometimes misled into thinking that evolution takes the form of simple, straight-line changes in each group of organisms (a pattern they called orthogenesis). They thought, for instance, that horses have changed steadily from *Hyracotherium* of Eocene times, around 60 million years (Myr) ago, a little, three-toed creature about the size of a small dog, into the big, one-toed modern horse, *Equus*. In fact, the many fossil horses that have been discovered show that horse evolution followed a much more complicated, more haphazard course (Figure 4.2). "Phylogeny" means an account of the history of a species and how one has changed into others, so this representation is a *phylogenetic tree*. It shows four kinds of events. First, one species – one line in the tree – often divides into two or more species, representing the process of speciation. Second, most species lines eventually end in *extinction*, the death of the species. Third, a lack of change in a species, or *stasis*, is no evolution at all, and is represented by lines that continue straight on until they branch or end. Fourth, a line may change gradually in one direction, indicating what has been called *phyletic evolution*, a consistent change in morphology such as a gradual increase in size or a gradual change in the shape of a body part. But does phyletic evolution actually happen?

Only a few years ago, we would have drawn typical phylogenetic trees with the lines moving gradually to the left or right, to denote phyletic evolution. The view that such gradualism is the typical pattern of evolution was one feature of the modern synthesis. However, Steven M. Stanley, summarizing a vast amount of evidence, has

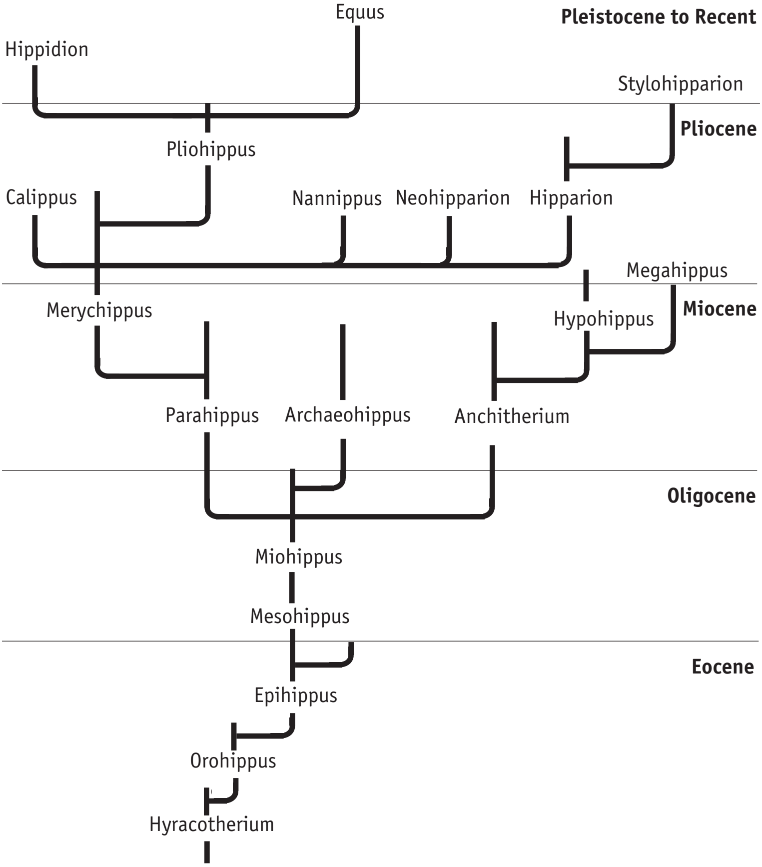


Figure 4.2 *The evolution of horses is shown by a phylogenetic tree. The origins of new species (designated by their generic names) are shown as abrupt transitions on the geological time-scale, although each event may have taken several thousand years. Where two or more events are shown as occurring simultaneously, the events actually may have been separated by millions of years.*

shown that evolution is realistically portrayed by a different pattern; species appear to change little, or not at all, during their lifetimes, with change arising primarily through a series of speciations. Each speciation event occurs quite rapidly in geological terms, so rapidly that it has sometimes been called "quantum speciation," on analogy with the "quantum jumps" that occur in atoms and molecules when electrons move instantaneously from one energy level to another. Rapid speciation was inherent in the speciation models developed by Mayr, and the emphasis on this mode of evolution was stimulated in large part by the work around 1972 of two paleontologists, Niles Eldredge and Stephen Jay Gould, who called this pattern "punctuated equilibrium."

Perhaps because we see little change in the natural world during our lifetimes, we tend to think that natural selection continually shapes each species so it successfully weathers the stresses of life, remains well adapted to its particular niche, and is always becoming better adapted. This is an optimistic view. A realistic view of evolution is more pessimistic, because the dominant feature of evolution is not success but extinction. There is no guarantee that a population will be able to adapt to environmental demands, and few species seem to be successful for long, on the geological time-scale. Where the geological record is very good, it shows that a typical species lasts for a few hundred thousand to a few million years and then disappears, often after a new species has arisen from it. The paleontologist George Gaylord Simpson estimated that 99.9 per cent of all species that ever lived have become extinct. The few million species of contemporary organisms are the remnants of a few billion species that have lived in the past. Among multicellular organisms, the few species and genera that have endured for very long times, perhaps 300–400 million years, live in the depths of the oceans where conditions change much more slowly than they do elsewhere.

Human interference has caused the extinction of many species, sometimes quickly. One of the burdens of guilt our species must bear is the history of destroying abundant, well-adapted species, such as the Passenger Pigeon of North America, out of sheer greed or perhaps ignorant carelessness. Many species of animals have been exterminated on islands, sometimes by rats, dogs, or pigs introduced accidentally or intentionally. Other species have been eliminated because they had very specialized niche requirements and lacked the genetic potential to adapt to changes humans imposed on the environment. The ornithologist James Fisher estimated that in the West Indies the average bird species had a lifetime of 180,000 years before human intervention. This was reduced to 30,000 years by the aboriginal natives and to only 12,000 years since European colonization in the seventeenth century. In spite of efforts to keep humans from destroying the natural world, the sad fact is that we must expect many more species to become extinct.

converging and diverging

Phylogenetic trees generally show diversity and divergence. We call them "trees," after all. Trees grow from a single base and diverge into smaller branches that spread widely. Similarly, a phylogenetic tree shows how the descendants of one type of organism have branched out and evolved into diverse forms. This is the pattern we would expect, because evolution depends upon accidental, unpredictable events: mutation and other random changes in genomes, coupled with selection for adaptation to diverse habitats. Though it is not impossible for organisms to reverse their evolutionary history and take on the form of an ancestor, it is highly unlikely because they are

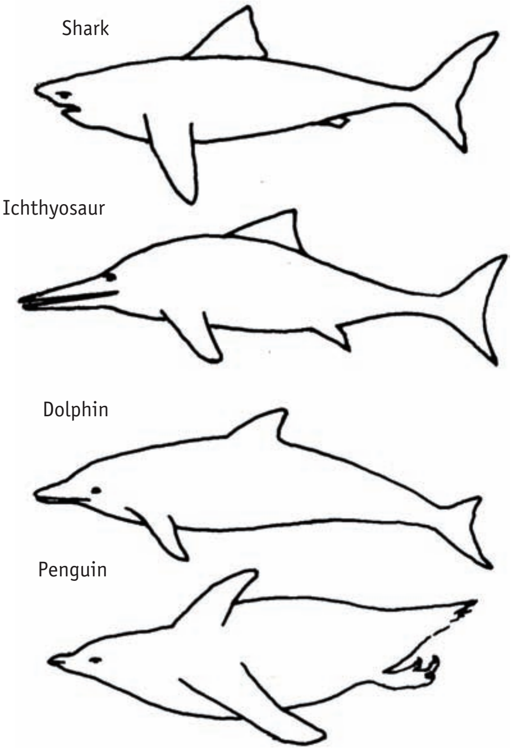


Figure 4.3 *Sharks, ichthyosaurs, dolphins, and penguins have all acquired similar forms through convergent evolution, even though their ancestors were quite diverse.*

responding to current environmental pressures and their genomes are experiencing new, unique mutations. So the general course of evolution will be divergence from ancestral forms, rather than reversion to them. (The apparent lack of reversals in evolution was once called Dollo's Law, but it really isn't a law of nature in the physical sense.) Sometimes that divergence leads to "degenerate" forms, to organisms that are simpler in structure than their ancestors – parasites, perhaps. But this isn't a reversal of evolution.

In one kind of contrast to divergent evolution, species that evolve into similar ways of life commonly develop similar forms, even though they come from quite different ancestors. This pattern of *convergent evolution* is exemplified by the similar forms of some streamlined swimming vertebrates (Figure 4.3). The ancestors of these animals were quite diverse: a primitive fish, a four-legged land reptile, a terrestrial bird, and a four-legged land mammal – yet the aquatic animals look very much alike. Their internal structures, however, have not become very similar. Figure 4.4 shows the wing structures of three flying vertebrates; they are independent responses to the same opportunity – to occupy niches involving flight – and in spite of similar outward appearance, each one emphasizes quite different bones of the vertebrate limb. For this reason, these wings are only partly homologous, and the differences among them are one character that distinguishes the three groups of animals.

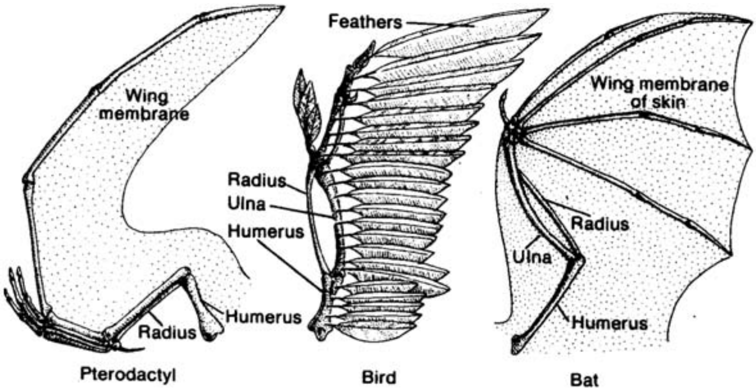


Figure 4.4 *Pterosaurs, birds, and bats have evolved wings with similar forms through the transformation of different bony elements.*

taxonomy, cladistics, and drawing family trees

We draw phylogenetic trees on the basis of the fossil record and comparative anatomy. Species with the most similar anatomical features are deemed most closely related. We now ascribe similarities to evolutionary relatedness; although early naturalists didn't think in evolutionary terms, they used their observations of similarities to create classifications, culminating in the work of Linnaeus, who originated the system of classification we still use. In classical taxonomy, or systematics, species that are very similar are combined in a single genus. Similar genera form a single family, similar families an order, and so on up the hierarchy to classes, phyla (singular, phylum), and kingdoms. Each of these categories – species, genus, family, phylum, and so on – is called a *taxon* (plural, *taxa*). To create complicated classifications, we can make other taxa with prefixes such as sub- and super-, and by adding other intermediate levels. An order, for instance, may be divided into a number of suborders and these into superfamilies. A family may be divided into subfamilies, and sometimes subfamilies are divided into tribes.

In modern taxonomy, classifications are intended to show not mere structural similarities, which might be due to some convergent evolution, but to reflect phylogenies. For this reason, taxonomists turn more and more to modern tools, especially to analysis of DNA, for more sensitive indications of relatedness among species. It has now become so easy to sequence DNA, using computerized instruments that can read long sequences automatically, that we are accumulating huge databases that can be used to establish phylogenies. Computer programs can turn a set of sequence data into trees reflecting the most likely chain of speciation events. And sometimes quite unique sequences appear that leave no ambiguity about events of the past; for instance, Sandra Baldauf and Jeffrey Palmer discovered that fungi and animals share a unique sequence of twelve amino acids in a certain protein, and in combination with other sequence data, this shows clearly that the two kingdoms are closely related. Other chemical markers of phylogenetic value include complex metabolic mechanisms that could only have evolved one time, thus uniting all the organisms that possess them; for example, two quite different pathways for synthesizing the amino acid lysine are known, and the diverse organisms that share the rarer of the two pathways surely derived from some common ancient ancestor.

We now tend to draw phylogenetic trees by using a method called *cladistics*, which was introduced by the German taxonomist Willi Hennig in 1950 and has become increasingly influential. It is based on the simple idea that as different species arise during the course of evolution, they acquire novel features at distinct times. Then we can use these features to infer the sequence of changes that has led to the various species, and on this basis we can classify them more rationally. A single branch of a tree drawn in this manner is a *clade*; it consists of all the organisms that arise from a single ancestral species. Then a simple family tree, or cladogram, can show the clades that arise from each evolutionary innovation. A cladogram of the chordates makes a good example (Figure 4.5). Chordates are animals that all have a rod of cartilage, the notochord, along the center of the back. The animals that have only this structure are rather obscure marine creatures. In all other chordates, the vertebrates, a notochord only appears early in embryonic development and is replaced by a backbone (vertebral column) made of separate vertebrae. All of the fishes have this feature. Then sometime later, the first species arose with four functioning leglike appendages, and these are the tetrapods (*tetra* = four, *pod* = foot). Later some species of amphibian became the first reptile by evolving an amniotic egg, an egg like that of a chicken with membranes enclosing an embryo in a watery environment. Later, in separate events, birds and mammals arose from certain reptiles.

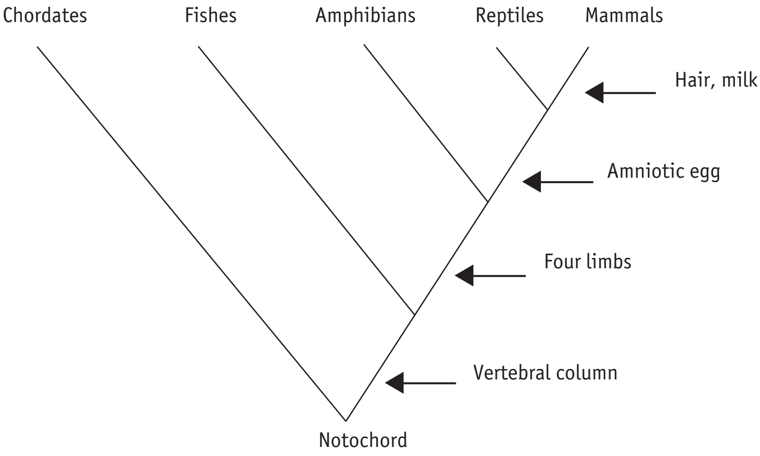
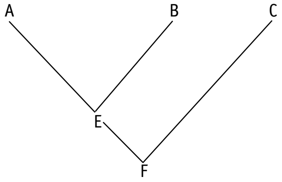


Figure 4.5 *A simple cladogram of the chordates, showing the appearance of some distinctive features of each group.*

Cladistics depends on distinguishing primitive from derived characteristics. Every evolutionary lineage must have started with some ancient species that had certain primitive characteristics that all its descendants retain. Having a backbone, for instance, is a *shared primitive characteristic* that defines the vertebrates as a group. As vertebrates evolved, they diverged into several distinctive groups that are defined by *shared derived characteristics.* Mammals share the characteristics of hairy skins, three small bones in the middle ear, and milk production by females. Birds share the characteristics of feathered skins, light hollow bones, and forelimbs modified into wings. It isn't always easy, though, to distinguish primitive from derived characteristics. Embryological development can often be useful; here, again, we see a structure like a notochord in an early-stage vertebrate embryo being replaced by a backbone. Fossils may also be very important clues, since they show the characteristics of ancestral organisms.

Let's take a simple case. Suppose species A, B, C, and D are closely related; but A and B share derived characteristic 1, which C and D don't share, and A, B, and C share another characteristic 2, which they don't share with species D. Then we may infer that a branch of the phylogenetic tree leading to A and B diverged from the branch leading to C; so A and B must have had a common ancestor, E, in which characteristic 1 first appeared. Similarly, there must have been another ancestor, F, from which A, B, and C were derived. We can now draw a partial cladogram.



The branch including A, B, and E is a clade, and the branch leading to C is a *sister* clade to it (just as the term "sister" is used for entities such as chromosomes or cells that have divided from each other). A larger cladogram could add species D and postulate a common ancestor, G, of all four contemporary species. The cladogram can be transformed directly into a classification, although the result may not look like a traditional Linnaean classification.

With these general ideas about the course of evolution in mind, we can turn to some of the forces that drive evolution and to questions about how organisms fit into their environments.

populations and selection

what is natural selection?

Darwin's fundamental idea – his great insight – is natural selection. His fellow naturalist Alfred Russel Wallace reached this insight at about the same time, and had published a paper in 1855 with ideas very similar to Darwin's. As Darwin and Wallace maintained a correspondence, when one of Wallace's letters finally laid out the essential ideas that Darwin had been developing for two decades, they settled the issue of scientific ethics and priority of discovery by means of a joint paper communicated to the Royal Society. Darwin and Wallace developed their ideas on the basis of their extensive experience as field naturalists. Rather than examining dead specimens in museums, they went out to distant lands and spent long times in the field observing, experimenting, and thinking about the lives of the organisms they saw. (Darwin spent many years writing other books derived from his natural-history studies.) Their field experience taught them to think about *populations* of organisms – all the individuals of one kind that live in one area – and they took several lessons from these observations.

They saw that populations are highly *variable*. An important part of *On the Origin of Species* is Darwin's precise cataloguing of just how variable populations really are, in contrast to the naive, popular viewpoint that the members of a species are all pretty much alike.

Darwin was strongly influenced by the writings of Thomas Malthus. Malthus's pessimistic view of human society developed from his observation that populations tend to grow rapidly in the pattern described mathematically as *exponential* (or "geometric," in the older terminology that Malthus used), whereas resources only grow in an *arithmetical* manner. By this he meant that populations tend to double in size periodically, from 1 to 2 to 4 to 8, and so on, whereas resources only grow by addition, as from 1 to 2 to 3 to 4. Therefore, he concluded, people must continually struggle with one another for the means of existence, and the losers in society are condemned to a poverty from which they cannot escape. When applied to the biological world in general, this means that every species tends to reproduce more individuals than can possibly survive; occasionally someone astonished by the potential of exponential growth makes an example of animals that produce so many thousands of eggs that if all their offspring were to survive their total mass would soon equal that of the whole Earth, and a calculation for a slowly reproducing species such as an elephant – which starts to breed at about age thirty and produces only one offspring every few years – shows that the offspring of one pair would number in the millions after a few hundred years. But Darwin and Wallace saw that populations tend to remain quite stable in size, in spite of their immense capacity for reproduction, so most individuals must die before they can mature and reproduce.

They also observed that breeders of domestic plants and animals shape their subjects generation after generation by consciously selecting individuals with desirable characteristics to be the parents of the next generation. This is quite obvious to us now, but let's note that it depends upon the inheritance of genomes, which determine the characteristics of each individual. And let's note that artificial selection can only work if there is a pool of individual variation from which differences can be selected. If all the cows in a herd or all the plants in a field were genetically identical, a breeder would have nothing to select.

From these considerations, it was only a short step to the conclusion that a process similar to artificial selection must be operating in nature. In each generation the individuals show different degrees of fitness or adaptation to their particular habitats, and those that are most fit – those with the best adaptations – are more likely to be successful in producing the next generation. In outline, the principle of natural selection may be summarized by four points:

1. Every organism has the potential to produce more offspring than can survive.
2. There is always variation among individuals in a population; much of this variation is inherited, so the next generation inherit some of these variable features from their parents.
3. Specific variations may make an individual either more or less likely to survive and reproduce than other individuals with different features.
4. Those variant traits that enhance survival and reproduction will be passed on to offspring and will be found in an increasing fraction of the population in each succeeding generation.

A most enlightening conception of natural selection – originally from George Wald – is to think of it as an *editing* process. Just as in editing rough writing into polished writing, an early "draft" of some organism might be a rather crude approximation to a well-adapted form. That "draft" is encoded in a genome, which reproduces with variations; the poorer versions of the genome are discarded, because most organisms die, and the better are retained to reproduce another generation. The metaphor of selection as editing is valuable to keep in mind. It will become especially important in addressing the contention that the probability of a functioning organism arising through mere chance is so small as to be unbelievable. This is a willful misunderstanding of the principle of natural selection. Yes, of course it is impossible to conceive of a complex, functioning organism arising merely by chance in a single step. Evolutionary theory would be absurd to claim it could happen. But it is easy to understand organisms undergoing a gradual, subtle editing generation after generation, through random mutation generating diversity plus selection operating on that diversity.

populations are variable

It may be hard to appreciate just how variable natural populations are. But it is easy to see that variability in human populations. Just pay attention to the differences you see in the people on the street, to the different faces, shapes of bodies, heights, hair colors, skin colors, eye colors. You might argue that the people you pass in a typical city or town in America or Europe aren't natural populations, that they may be mixtures of people of many ancestries; but we see considerable individual variation even in an isolated village, even in a tribe living in Stone-Age conditions in a remote jungle. People are easily recognizable as individuals. A population showing such heterogeneity in form is said to be *polymorphic* (*poly-* = many, *-morph* = form).

Darwin gave an example of variation in plants by citing the work of his contemporary naturalist De Candolle:

> He first gives in detail all the many points of structure which vary in the several species, and estimates numerically the relative frequency of the variations. He specifies about a dozen characters which may be found varying even on the same branch, sometimes according to age or development, sometimes without any assignable reason. … De Candolle then goes on to say that he gives the rank of species to the forms that differ by characters never varying on the same tree,

> and never found connected by intermediate states. After this discussion, the result of so much labour, he emphatically remarks: "They are mistaken, who repeat that the greater part of our species are clearly limited, and that the doubtful species are in a feeble minority. This seemed to be true, so long as a genus was imperfectly known, and its species were founded upon a few specimens, that is to say, were provisional. Just as we come to know them better, intermediate forms flow in, and doubts as to specific limits augment." He also adds that it is the best-known species which present the greatest number of spontaneous varieties and sub-varieties.

Polymorphism is the general rule in natural populations of other organisms. Even if polymorphism isn't apparent to the eye, every population that has been studied reveals its genetic variability in polymorphisms of protein structure. It has been clear since the 1960s that many "laboratory" mutants of the fruit fly *Drosophila* occur in wild populations, and analysis of proteins from individual flies shows that wild populations harbor allelic forms of many enzymes. Both *Drosophila* and human populations typically have two or more alleles at about a third of their genes. But the demonstration that so many loci show polymorphism and considerable heterozygosity has put a new perspective on evolution. Previously, theorists assumed that every new mutation either would be deleterious and therefore eliminated from a population quickly, or would be advantageous and would quickly become fixed – that is, it would become the sole allele in the population. But Motoo Kimura and others proposed a *neutral theory of evolution*: that many mutations have little or no effect on protein function, and that mutant alleles accumulate in a population by random processes (see the concept of genetic drift, on page 73). The existence of neutral mutations is now well established, although they vary from gene to gene. Some proteins are very sensitive to mutation and can bear relatively few allelic forms; others are more tolerant of variations in their structure, so their genes exhibit more variation and heterozygosity. There is some controversy regarding the relative importance of neutral evolution and natural selection, but it seems clear that both processes operate – we would abandon all reason in biology if we did not believe that evolution is driven largely by selection and adaptation.

We will take up this theme of variability and polymorphism again when we consider the question of defining a species. It is especially important that populations (species) commonly show considerable geographic variation, so individuals in different areas have quite different features.

populations may have different forms

A species is made of closely related individuals spread over a certain area, and because of variations in geography, its members can be unified or isolated to various degrees. At one extreme, the entire species may be one population in which any individual can contact and mate with any other individual of the opposite sex. More likely, though, the species will be divided into many local populations, or *demes*, but with a certain amount of genetic mixing, or *gene flow*, among them. At the other extreme, some or all of the demes may be isolated from one another, so little or no gene flow occurs. Most speciation depends on having such partially or completely isolated populations, but analyzing the genetic structure of populations begins with a large, undivided population of the first type.

the idea of a Mendelian population

So populations are extremely variable genetically, and selection acts upon this variation. Evolution is a phenomenon of populations, and our understanding of the process has been aided enormously by understanding how genes behave in populations. Population genetics begins by setting up an idealized model – in fact, a model in which there is no evolution at first. In 1908, the English mathematician G. H. Hardy and the German biologist Wilhelm Weinberg independently discovered that an idealized population will come to an *equilibrium* for each gene, a condition in which its genetic composition doesn't change. This fact, now known as the *Hardy-Weinberg Principle*, is the foundation of population genetics. The theory begins with an ideal population with these features:

- It reproduces sexually and is *diploid*, which simply means that each individual has two copies of its genes, one inherited from each parent.
- It is large enough for the laws of probability to operate.
- Mating occurs at random.
- No mutation takes place.

- No genotype has a selective advantage over any other, and all members of the population survive and reach reproductive age.
- No genes enter from other populations.

Notice that since no mutation and selection occur, such an idealized Mendelian population *is not evolving*. This is a common scientific way of analyzing a situation – to start with a very simple model that doesn't show the effects we want to study, and then later to add in those effects: mutation and selection in this case. Finally we will add in geographic variation in natural populations and see the effects of this important factor.

The condition of *random mating* means that any male and female can mate with each other. One alternative to randomness, called *assortative mating*, is that individuals prefer mates with features similar to their own. People, for instance, commonly mate assortatively, because they tend to marry those with the same skin or hair color, with comparable intelligence, or with some other shared feature. But we can illustrate random mating, and the Hardy-Weinberg Principle, with a convenient human trait, the MN blood types. Everyone has blood type M, N, or MN. These types are encoded by two alleles, *M* and *N*, of a single gene. A person with the genotype *MM* has M-type blood, one with the genotype *NN* has N-type blood, and a heterozygote with the genotype *MN* has MN-type blood, because the alleles are *codominant* – they are both expressed equally. Also there seems to be no selection for either M or N blood type, and human populations conform perfectly to the Hardy-Weinberg principle for this trait.

The abundance of each allele in a population is given by its *allelic frequency*: the frequency of the *M* allele, denoted by p, is the fraction of all these genes in a population that are *M*; and the frequency of the *N* allele, denoted by q, is the fraction that are *N*. Allelic frequencies can vary from 0 to 1; if there were equal numbers of the two alleles in a population, p and q would both be 0.5. Since the gene has only two alleles, every copy must be one or the other, and $p + q = 1$.

Even though neither M nor N types have any selective advantage, populations don't necessarily have equal numbers of the two alleles, and the frequencies of *M* and *N* in different human populations vary quite a lot (Table 2). Suppose we have a population of 1000 people, with 500 M people, 400 MN people, and 100 N people. Since everyone has two genes for this character, there are 2000 genes in the population. The type-M people all have two *M* genes, making 1000, and the type MN people have 400 more *M* genes, making a total of 1400. Then $p = 1400/2000 = 0.7$. Similarly, the type-MN people have 400 *N* genes, and the type-N people have 200 more, for a total of 600. Then $q = 600/2000 = 0.3$. Of course, after finding the value of p, we could have subtracted it from 1 to get the value of q, but I did the explicit calculation of q to show that the formula gives the correct value. In general, we determine the value of p or q by taking twice the number of homozygotes for one allele plus the number of heterozygotes, and dividing by twice the number of individuals in the population.

Table 2 Percentages of MN blood types in various human populations

People	Place	M	MN	N
Eskimo	Greenland	83.5	15.6	0.9
Pueblo Indians	New Mexico	59.3	32.8	7.9
Australian Aborigines	Queensland	2.4	30.4	67.2
Ainu	Japan	17.9	50.2	31.9
Basques	Spain	23.1	51.6	25.3
Germans	Berlin	29.7	50.7	19.6
Chinese	Hong Kong	33.2	48.6	18.2

The members of a population are said to share a *gene pool*, a metaphorical common space where all their genes are combined, mixed, and then reassorted to make the next generation. So the species reproduces as if all the males and females put their *gametes* – their sperm and egg cells – into a big pool where each new individual is made by randomly combining one sperm and one egg. The probability of choosing a gamete carrying *M* is p and the probability of choosing one carrying *N* is q. Then:

1. The probability of forming an *MM* zygote is just $p \times p = p^2$.
2. The probability of forming an *MN* zygote is $(p \times q) + (q \times p) = 2pq$. (This is the probability of getting an *M* sperm with an *N* egg or an *N* sperm with an *M* egg, so it is just twice the same elementary probability.)
3. The probability of forming an *NN* zygote is $q \times q = q^2$.

The principle of the Hardy-Weinberg equilibrium is that a randomly mating population reaches a ratio of $p^2 : 2pq : q^2$ for the three genotypes of a single gene and then *does not change.* By the way, notice that the sum $p^2 + 2pq + q^2$ is equal to $(p + q)^2$, by simple algebra. Since $p + q = 1$, $p^2 + 2pq + q^2$ also is equal to 1.

What happens if we apply this calculation to the imaginary population with $p = 0.7$ and $q = 0.3$? We find that $p^2 = 0.49$, $2pq = 0.42$, and $q^2 = 0.9$. If the next generation also has 1000 individuals, there will be 490 Ms, 420 MNs, and 90 Ns. If you would like to do the calculation all over again to see what happens when a third generation is formed, you would find that it is exactly like this one. So after one generation, the population has come to a Hardy-Weinberg equilibrium.

To test your understanding of these ideas, try calculating the allelic frequencies for a population that has 360 *MM*, 480 *MN*, and 160 *NN*. After you have determined p and q, use the Hardy-Weinberg formula to calculate the frequencies of the three genotypes; you should find that in a population of 1000 individuals, the numbers will be exactly those of the population you started with, thus confirming that this is truly a population at equilibrium and that the allele frequencies will not change.

For illustration, I used a gene locus with no dominance, where we could distinguish *MM* and *MN* individuals. But how can we determine the frequencies of alleles when dominance gives both homozygous dominants and heterozygotes the same phenotype? Although these individuals are identical, we can recognize and count all the homozygous recessives. Their frequency is q^2. Therefore, the square root of that frequency is q, and $p = 1 - q$. Suppose, for instance, 1 per cent of a population (0.01) have a certain recessive genetic condition. Since $q^2 = 0.01$, $q = \sqrt{0.01} = 0.1$. That is, 10 per cent of the alleles at this locus in the population are recessives and 90 per cent are dominants.

the effects of selection

Hardy-Weinberg analysis assumes there is no selection for any genotype, but for most traits the three genotypes *AA*, *Aa*, and *aa* have different reproductive potential or *fitness* (sometimes called Darwinian fitness). The fitness of a genotype is a measure of its contribution to the gene pool of the next generation, in comparison with other genotypes. Fitness is always a *relative* measure; we cannot have an *absolute* measure of fitness because a more fit genotype could always appear, so the best-adapted genotype is arbitrarily assigned a fitness of 1. Quite commonly, with complete dominance at some locus, both *AA* and *Aa* individuals have a fitness of 1, but homozygous recessives are at a disadvantage and have some lower fitness. In a flowering plant, different genotypes for flower color may have different fitnesses because one color is more attractive to pollinators; genotypes that affect the length of an insect's leg may have subtle effects on the insect's ability to run or to hold onto its food. Then in each generation, instead of the three genotypes being at their classical ratio, p^2 *AA* : $2pq$ *Aa* : q^2 *aa*, the *aa* individuals will actually occur at a lower frequency $q^2 (1 - s)$. This expression defines *s*, the *coefficient of selection* against *aa*. The fitness of this genotype is then defined as $W = (1 - s)$. We know how many individuals of each genotype to expect in a population, and if we consistently find less than that number for some genotype, we know it has lower fitness, which we can easily calculate.

With this mathematical definition of selection, population geneticists have developed an extensive, complex theory, which shows how evolution will proceed in populations of various sizes, with different degrees of selective pressure, and other variables. One example will show the kind of insight this theory can yield. People carry various recessive mutations that produce disorders that are always fatal in childhood, so affected individuals never have a chance to have children. Intuition tells us that since these individuals are being eliminated, the gene should disappear from the population rapidly, but it doesn't. The reason is that most copies of the recessive allele are carried by heterozygotes, who aren't affected by it. If $q = 0.01$, for instance, $q^2 = 0.0001$, and only one person in 10,000 shows the disease and is eliminated; but the frequency of carriers is $2pq = 2 \times 0.99 \times 0.01 = 0.02$, so 2 per cent of the population carry the deleterious allele.

Population genetic theory allows us to calculate just how rapidly the allele frequency will change in this situation. It says that the number of generations required to reduce the frequency of the recessive allele from q_0 to q_1 is $1/q_1 - 1/q_0$. Suppose q is initially 0.01 (so one person in 10,000 is affected); how long will it take to reduce q to 0.001 (so only one person in a million will be affected)? The answer is $1000 - 100 = 900$ generations. At 20–25 years per human generation, that would take a long time. Furthermore, when the allele frequency falls so low, mutation becomes a significant factor; the human population will never be free of the allele because it will be created by mutation as fast as it is eliminated by selection.

gene frequencies may change rapidly in small populations

The Hardy-Weinberg Principle applies to a population that is large enough for random mating to occur, so the genotypes of the next generation are made in proportion to the allelic frequencies of the current generation. Natural populations may be very small, however, especially those that are somewhat isolated, and small populations can behave very differently from large ones.

You know that a long series of coin flips will turn up as many heads as tails, but in the short run you will probably have streaks in which one side or the other occurs more often than expected. In a large population the genetic "coins" are being flipped so much that the Hardy-Weinberg Principle applies: the frequencies of all alleles remain constant, in the absence of mutation and selection. In a small population, as the geneticist Sewall Wright first pointed out, the gene pool may not behave this way, because each generation is made by only a few flips of a genetic coin. Suppose a population has equal numbers of two alleles for some gene locus: $p = q = 0.5$. If only a few sperm and eggs are drawn to make the next generation, they may not be a representative sample, so they deviate from the expected 50 per cent of each allele. Perhaps in the next generation the frequencies will change to 0.48 and 0.52. Then in the following generation, since the frequencies are already somewhat lopsided, they may change a little more – say, to 0.46 and 0.54.

People have done this genetic experiment with a computer that simulates the evolution of a small population, starting with equal frequencies of two alleles. In different computer runs, the frequencies of the alleles tend to drift rapidly in one direction or the other. In natural populations such a rapid change in gene frequency is known as *genetic drift*. A common result is that after several generations one allele is eliminated (its frequency becomes zero) while the other is said to be fixed (its frequency becomes 1). Genetic drift may be an important factor in speciation, as we discuss in chapter six.

If genetic drift really occurs in human populations, we might expect to see a lot of genetic variation among small populations. For instance, if we could find small, isolated villages where people marry within the village and few marriages occur every year, we might find gene frequencies changing radically just by chance. Luigi Cavalli-Sforza and his colleagues found the perfect test situation in the

Parma Valley of Italy. In the upper reaches, the Parma river has carved out a steep-sided, inhospitable valley where villages typically number 200–300 people. Migration is inhibited in this region, and the vast majority of marriages are between people from the same village. Further downstream, the terrain becomes hilly and the villages are larger, and finally the valley becomes a plain containing the sizeable town of Parma. Thus, mobility and migration also become greater as one moves downstream. The geneticists examined variation in blood types from village to village. They showed very high variation in the mountain villages, falling steadily to low variation in the plains, just as expected.

sources of variation

mutation is the source of all genetic change

The frequency of an allele can also change by mutation. *Mutation rate* is the probability per individual per generation that a gene locus will mutate; in simple creatures such as bacteria, this means that a cell must replicate its genome every time it divides in two, and each time there is a small probability that one copy will be mutant. Measurements in organisms ranging from bacteria to mice show that these rates are very small, usually 10^{-5}–10^{-8}. The highest rate in this range, 10^{-5}, would mean that if 100,000 copies of a gene are replicated, one of them on average will be mutant. All genes aren't equally likely to mutate because they are of different sizes, but suppose we assume an average mutation rate of 10^{-5}; then if the human genome contains 50,000 genes, one mutation would occur in half the replications to produce a new sperm or egg, and thus each of us would carry, on the average, one new mutation. (Mutations also occur when our somatic, or body, cells reproduce; they are important causes of disorders such as cancer, but they don't contribute to the gene pool and to evolution of the species.)

Because mutations occur so infrequently, persistent mutation to a certain allele can only change its frequency quite slowly. In microorganisms that reproduce rapidly, such as bacteria, mutation can make a significant contribution to a population, though this contribution may only become apparent after some selective agent has taken effect. For example, every time a bacterial cell reproduces, there is a small chance that one daughter cell will become resistant to an antibiotic, and such resistant mutants may accumulate; but we only know that these mutants exist, and they only become significant, if the population is subjected to the antibiotic, which selects them by wiping out all the sensitive cells. On the other hand, mutation is a two-way phenomenon. If a mutation is only a minor change in a DNA molecule, such as replacement of a G-C pair by an A-T pair, then *back-mutation* or *reversion* to the original state will occur at about the same rate as a forward mutation, so mutation will have little overall effect on a population. Selection and mutation may work against each other, as mutation tends to increase the frequency of an allele, while it is eliminated by selection. The situation is analogous to a leaky tub of water that is filled from a faucet, so its level is determined by the rates of inflow and outflow; the frequency of an allele reaches an equilibrium level determined jointly by the rates of selection and mutation.

In spite of these considerations, *mutation is ultimately the source of all genetic variation and therefore the foundation for evolution.* A single mutation increases genetic diversity and thus increases the potential for future evolution, but by itself it is most likely useless or detrimental. An organism, after all, is a complex and finely tuned system, and a random change in its genome is not likely to improve it. However, on pages 93–97 we will consider some effects of mutations on protein structure and show how slight changes in proteins have the potential for evolutionary innovation.

sex and variation

The variation underlying evolution arises not only from mutations producing new alleles but also from sexual reproduction. Germ cells – sperm and eggs, or their equivalents in other organisms – are formed through a special process of nuclear division called *meiosis*, whose details we can ignore. In ordinary nuclear division (*mitosis*), the complete set of chromosomes in a cell is reproduced, so both daughter cells (the products of the division) have identical sets. But in meiosis the diploid set is reduced to haploid sets. Remember that the human diploid set consists of 46 chromosomes – 23 pairs of homologous chromosomes – so meiosis produces sperm or egg cells that have 23 chromosomes, one from each pair. Thus, each sperm or egg carries one of the two homologues numbered 1, one of the two numbered 2, and so on down to number 23.[1] Since each person's maternal and paternal chromosomes almost certainly differ in at least one gene, one person can produce $2^{23} = 8,388,608$ different sperm or egg cells. Thus, one couple, producing this variety of sperm and eggs, could produce over 7×10^{13} genetically different children! In any natural population, harboring even more genetic diversity, the potential for creating diversity merely through sexual recombination is enormous. Population geneticists generally consider that the principal source of variation in a population is recombination of alleles already in the population rather than the creation of new alleles through mutation.

In addition, chromosomes can undergo changes that are much larger than ordinary mutations, which typically just change one base-pair (or a few of them) in one gene. During the early stages of meiosis, a pair of homologues come into intimate contact with each other and commonly exchange parts, a process called *crossing over*. For instance, if one homologue has genes that we can represent by ABCDEFGHIJKLMNOP and the other can be represented by abcdefghijklmnop, they may break and rejoin with an exchange to produce chromosomes such as ABCDEFGHIjklmnop and abcdefghiJKLMNOP. It is fairly common for chromosomes to undergo *deletions*, in which a section is simply lost, or *duplications*, in which a section is duplicated. These changes may occur together because crossing over may happen irregularly, so one chromosome becomes ABCDEIJKLMNOP while the other becomes abcdeFGHfghijklmnop. The first one thus has a deletion and the second has a duplication. Another common change is an *inversion*, in which a segment gets turned around; thus, a chromosome might acquire the sequence ABCDEFKJIHGLMNOP. A segment of one chromosome might also detach and join a nonhomologous chromosome. Suppose another chromosome pair has the sequence RSTUVWXYZ. Then a part of the first chromosome might break off, leaving only FGHIJKLMNOP and producing the chromosome RSTUVWXYZEDCBA. This is called a *translocation*. These additional changes that chromosomes can undergo produce still greater variety in populations. We will show in chapter five that carrying different chromosome sets may confer significant differences in adaptation to particular environments.

One advantage of diploidy is that a population can carry some recessive mutations without harm, and that occasionally two such mutations could come together and produce a superior individual, even though either mutation is deleterious when homozygous.

duplication and diversification

Since we now know the sequences of so many proteins, and of the genes that encode them, we can see that new proteins often arise from gene duplication. The extra copy of a gene can become a kind of molecular toy for the processes of evolution to play with. Natural selection will maintain one copy of the gene in its original functional form, but the second copy can start to acquire mutations and can gradually become different, so different that its protein product takes on a new function. Genes related by this process of duplication and diversification are called *paralogues* of one another, or are said to be *paralogous.* Some classic examples of proteins that have arisen in this way are the mammalian hemoglobins. We have two types, A and A_2, in our blood to carry oxygen, as well as another (F) during the fetal stage, and we have myoglobin in our muscles to hold oxygen there. The hemoglobins are all made of two types of chains, such as α (alpha) and β (beta). All these proteins are very similar, and they all have their special roles in our physiology. Comparisons of their amino-acid sequences show that they arose by repeated duplications as shown in Figure 4.6.

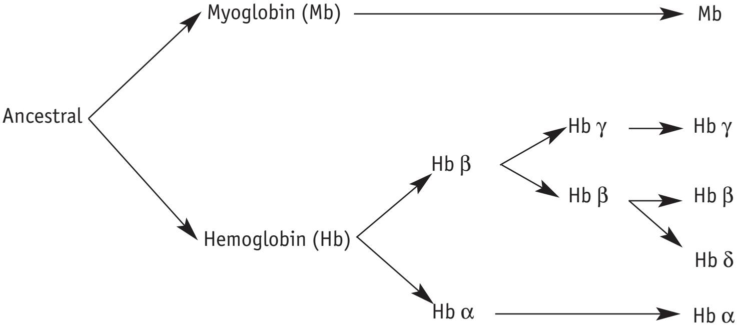


Figure 4.6 *The genes for myoglobin and different hemoglobin proteins have arisen through a series of duplications and diversifications.*

horizontal transmission

Since we draw phylogenetic trees with the time-dimension running down the page, the ordinary inheritance of genes in the course of reproduction is called *vertical* transmission. In the last few years, as investigators have determined the DNA sequences of genomes in more and more organisms, it has become apparent that an alternative, *horizontal*, transmission may be quite important in evolution. We have known for a long time that when bacterial viruses (bacteriophages, or simply phages) grow in some bacteria, they can sometimes pick up bacterial genes and carry them over to other cells that they infect. The process is called transduction. It is now becoming apparent that many bacterial genes have been acquired from other bacteria, sometimes those that are only distantly related. This must have happened by means of viruses in the past. We don't know yet how important horizontal transmission may be in the evolution of other kinds of organisms; but the cells of all organisms can harbor some viruses in a kind of hidden, quiescent state, and these viruses may have been carrying genes from species to species, giving their recipients novel characteristics. This is an aspect of evolution to keep our eyes on.

looking ahead: chance and necessity

In this chapter, I have tried to provide an overview of evolution as a process that can be seen in broad perspective over millions of years and in a closer view as the flux of genes in natural populations. Populations and entire species appear to persist for relatively short times on the geological time-scale, but on this scale new species frequently arise that have different characteristics, so that over long spans of time we see greater diversity among the surviving species.

In a grand overview of biology, the late French molecular biologist Jacques Monod summed up the essential processes of evolution as chance and necessity. Organisms (or their genomes, specifically) are subjected to random events that create novelty and variation. The organisms carrying these variations then face the necessity of surviving in a world of adversity. Only the best-adapted survive, to produce a new generation that must face the same kind of adversity. And though each species may manage to survive in this way for a time, perhaps as much as a few million years, its life, too, is finite. (Small wonder that Monod opens his book with a quotation from the essay *The Myth of Sisyphus*, by his friend Albert Camus, a book that explores the question of living one's life meaningfully in a world with no intrinsic meaning or purpose.) Having introduced the element of chance, it is now time to consider necessity and the question of just how organisms can fit into their surroundings and manage to survive.

notes

1. You may know that in the human genome, the 23rd pair actually consists of two X chromosomes in females and of one X and one Y in males. These chromosomes determine maleness or femaleness. However, this detail is unimportant for the present purposes.

chapter five

ecosystems: getting along with the neighbors

The purpose of this chapter is to add the important ecological viewpoint to our growing conception of how evolution happens.

adaptation and fitness

In talking about evolution, people are likely to say something such as, “Natural selection means survival of the fittest.” (The phrase “survival of the fittest” came from the writing of Darwin’s contemporary Herbert Spencer.) But “the fittest” are, by definition, those that are more likely to survive. So this sentence seems to be saying, “Selection means that those who survive are those who survive” – a tautology, rather than a brilliant insight. Perhaps we can make it more meaningful by unpacking the meaning of “the fittest.”

Being “fit” might mean being healthy or it might mean fitting into an appropriate place. Certainly organisms that survive must be healthy in some sense, but this doesn’t help much; it is more helpful to consider what they must fit into, and the general answer is that they must fit into a community and an ecosystem. No organism can live by itself. It is dependent in various ways on a variety of others, and the collection of organisms that live together, with their lives intertwined and interrelated, is a *biological community*. The community exists in some physical environment of rock, soil, water, and air; the combination of the community with this physical environment is an *ecosystem.*

Why can't one species live by itself? The fundamental reason is energy. All organisms require energy, and this energy has to come from the organism's environment, in one of two ways. The ultimate source of energy for life on Earth is the sun. For this reason alone, we only expect to find life on planets that are close enough to a star to receive a lot of light. The energetic base of a community consists of phototrophs, the plants, algae, and some bacteria. Phototrophs use the energy of light to synthesize the organic molecules of their own structure from carbon dioxide and other simple inorganic materials. As they grow, phototrophs are storing up energy in their structures. These energy-rich materials then serve as food for organisms such as animals – *chemotrophic* organisms or *chemotrophs* – which use a chemical energy source.

A very primitive planet, one whose organisms are in a very early stage of evolution, can probably have organisms living by themselves – for instance, simple phototrophs living off light. But it probably doesn't take long for even the most primitive organisms to begin living together, interacting in complicated ways, and starting to form communities. From that time on, they will become ecologically dependent on one another.

Organisms are related energetically as members of a *food web*, a tangled network of organisms that eat one another. Defined by their role in the community, the phototrophs act as *producers*, which bring energy into the system through photosynthesis. (Plants grow in the light.) Producers store energy in their structure and are eaten by *primary consumers*, or *herbivores*, which use some of that stored energy for their own growth and reproduction. (A deer eats leaves.) These, in turn, are eaten by *secondary consumers*, or *carnivores*, which use some of the energy in the herbivores' structure. (A wolf eats a deer.) Some carnivores may be eaten by still higher carnivores. (A killer whale may eat a seal or a porpoise.) These distinctions are somewhat idealized, and many members of an ecosystem are *omnivores* that eat a mixture of plant and animal materials. Finally, every organism – producer or consumer – dies and ultimately becomes food for *decomposers*, the molds and bacteria that decay biological molecules as they grow and take their share of energy.

the concept of an ecological niche

An organism fits into its community (and its ecosystem) by occupying an ecological niche. Biologists have entertained at least two distinct conceptions of a niche. The term arose between 1917 and 1928 in the work of ecologists such as Joseph Grinnell and Charles Elton, who emphasized the position of an organism in its community. Elton wrote that an animal's niche is "its place in the biotic environment, its relations to food and enemies, and the status of an organism in its community." He expressed the idea most pointedly when he wrote, "When an ecologist says, 'There goes a badger,' he should include in his thoughts some definite idea of the animal's place in the community to which it belongs, just as if he had said, 'There goes the vicar.' " The American ecologist Eugene Odum, in 1959, agreed with this conception, writing that a niche is "the position or status of an organism within the community and ecosystem resulting from the organism's structural adaptations, physiological responses, and specific behavior." Odum particularly distinguished niche from habitat, using the often-quoted distinction that a niche is an organism's "profession" whereas habitat is its "address." In 1952, Lee R. Dice defined a niche as a species's ecologic position in a particular *ecosystem*, rather than in its community, and wrote that the term includes "a consideration of the habitat that the species concerned occupies for shelter, for breeding sites, and for other activities, the food that it eats, and all the other features of the ecosystem that it utilizes." However, these conceptions contrast sharply with that of G. E. Hutchinson, who conceived of a niche as an *n*-dimensional space that specifies the total range of conditions in which the organism is able to live and reproduce; for instance, Figure 5.1 shows how an aquatic animal might occupy a niche defined by the factors of temperature, salinity, and the concentration of calcium. (Some biologists might feel that this "space" is more like a definition of habitat than of niche.) Finally, G. L. Clarke, in 1954, distinguished "functional niche" from "place niche." He noted that different species of plants and animals fulfill different functions in the ecological complex and that the same functional niche may be filled by quite different species in different geographical regions.

Although a full description of the niche of any species may be impossible, some brief examples can make the idea clearer.

american robin

One of the best-known birds in North America, its niche is that of a generalist in many habitats: forests, woodlands, gardens, parks, expanding into the grasslands. It feeds on fruit and on small

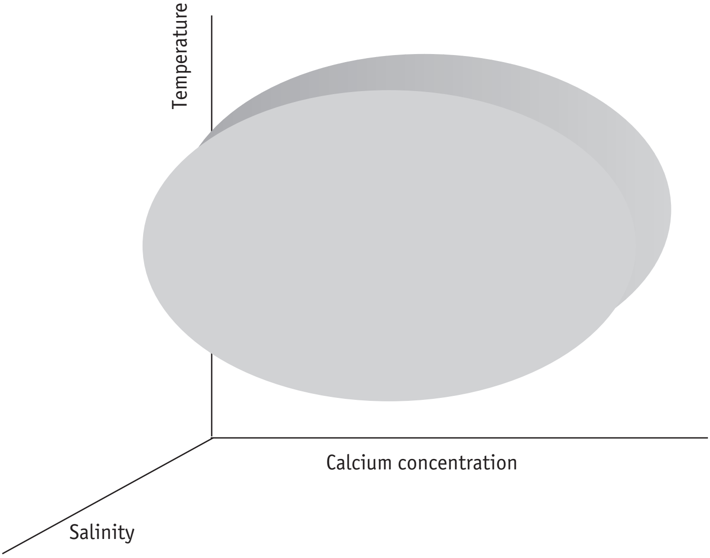


Figure 5.1 *According to Hutchinson's conception, a niche might be a region in an abstract space defined by several factors – three, in this example. The animal in this case is adapted to living within this space.*

invertebrates, including insects, largely by moving slowly over the ground and gleaning whatever it can find that is edible. It nests primarily in deciduous trees, at moderate heights, and some individuals, especially young birds still in the nest, serve as food for predators such as crows and hawks.

african lion

The lion, also, has quite a broad, generalized niche, since it lives (or lived – it is now severely confined by civilization) in most habitats in Africa except for the highest altitudes and the driest deserts. It is a predator that lives on other animals weighing primarily between 50 and 300 kg, although it will attack animals between 15 and 1,000 kg if necessary. During famine conditions, or if an individual is injured, it will take rats, reptiles, fish, or even groundnuts. Its method of hunting is a fast chase after skilled stalking. Individual lions will eat small animals by themselves; larger kills are shared with a social group, leaving remains for scavengers such as hyenas.

red-flowering currant

This deciduous shrub grows abundantly on dry to somewhat moist sites in the mixed coniferous-deciduous forests of the Pacific Northwest U.S. Its pink to deep-red flowers appear early in the spring, coinciding with the arrival on their breeding grounds of Rufous Hummingbirds, which depend upon the plant's nectar for their sustenance at this time. Deer and elk eat its branches and leaves. Its berries are persistent and do not ripen all at once, so they provide food for several kinds of birds, including grouse, jays, robins, towhees, waxwings, and Lewis's Woodpeckers, and for mammals including coyotes, foxes, skunk, squirrels, chipmunks, ground squirrels, mice, and wood rats.

These brief, inadequate descriptions of niches show how each species fits into its particular community or ecosystem by occupying certain segments of these spaces, perhaps by removing some species as food and by providing food for other species. The behavioral descriptions may be very important; noting that robins glean on the ground, for instance, shows that this particular place to gather food is occupied and that another species attempting to use the same methods and to hunt in the same place will face some competition. It would also be important to describe particular parasites or diseases that each species is subject to or resistant to.

The niche of each species is defined and limited in part by the way it interacts with other species in its community. Using Hutchinson's conception of a niche as a theoretical volume in a space, the volume a species could occupy in the absence of any competitors is its *fundamental niche*, but competition may force it to occupy a more limited volume, its *realized niche*. The difference may be illustrated by the work of A. G. Tansley, who experimented with two similar British plants called bedstraws. These species are somewhat specialized for growth in soils that differ along the dimension of acidity and alkalinity (measured by a number called pH): *Galium hercynium* lives in acidic soils (pH less than 7) and *G. pumilum* in basic soils (pH greater than 7). Tansley found that each species by itself would grow on both kinds of soils, but when planted together *G. hercynium* invariably outcompeted *pumilum* in acidic soil, and the reverse was true in basic soil. This experiment shows that the fundamental niches of both species are quite broad in the pH dimension, but when grown together each one shows its superior adaptation to a specific pH range, and they restrict each other to limited realized niches.

Gause's principle and its complications

Ask a biologist to name some foundation principles of biology and she or he is almost certain to include the principle that each species in a community must occupy a niche that is clearly different from the niches of other species. It is one of the most persistent beliefs in biology. We use the term *resources* for the items an organism needs to survive and reproduce that may be used up, such as food, shelter, living space, and even potential mates. Biologists have taken the common-sense viewpoint that if two species had identical or strongly overlapping niches, they would be competing for the same resources in the same habitat, and such competition is untenable. It cannot last for long. Avoiding such a situation has been considered a major driving force in evolution, because either one species would out-compete and eliminate the other or natural selection would change one or both species to eliminate the competition. In the 1930s, the Russian ecologist G. F. Gause formulated this concept, now generally called the *Competitive Exclusion Principle*: stable populations of two species cannot continue to occupy the same niche indefinitely, or more specifically, they cannot coexist on a single *limiting* resource. A limiting resource is one that limits the size of a population. This obviously makes good sense, and it is supported by experimental evidence, but the principle is actually more problematic than it might seem to be.

Gause's own experiments convinced him of the principle. He grew cultures of some single-celled organisms called ciliates, some of the most common little creatures to be found in pond waters, feeding them on bacteria and yeast, which in turn fed on oatmeal. When raised by themselves, the larger, slower-growing *Paramecium caudatum* and the smaller, faster-growing *Paramecium aurelia* each grew quite normally. In mixed culture, however, *P. aurelia* always won out while the *P. caudatum* population diminished to almost nothing. In contrast, when Gause grew *P. aurelia* with *P. bursaria*, the populations of both species reached about half the levels they would have achieved in isolation, with *bursaria* living on bacteria suspended in the top half of the culture tube and *aurelia* living on yeast in the bottom half. Thus, both survived by finding separate niches – different limiting resources – even in this simple situation.

Another way to express Gause's principle is to say that two competing species can only coexist through *niche differentiation* – evolution of one or both species so their realized niches don't overlap strongly and they are using different resources. Potential competitors can differentiate their niches by *partitioning* resources, either using different resources in the same space or dividing the space. This happened in the mixed culture of *P. aurelia* with *P. bursaria*, and it happens in natural situations. For example, Robert H. MacArthur studied the feeding patterns of five species of brightly colored little birds called warblers living in the same area in New England. Although the species are very similar and eat the same food (mostly insects, sometimes berries), they divide the space by hunting in different parts of the tree canopy, toward the center or outside, higher or lower. On a much smaller scale, my colleague Robert Sluss found how potentially competitive carnivorous beetles divide the space on black walnut leaves, where they feed on herbivorous insects; the red beetle *Hippodamia* hunts by walking down the middle of the leaf and back along one edge, while the greenish *Olla* searches back and forth across the leaf. Having evolved different behavior patterns, they divide a limited resource so both species get enough to maintain themselves. Species can also share resources by dividing the niche in time; flying insects are hunted by swifts and swallows during the day, by nighthawks and their relatives around dusk, and by bats at night.

In other situations, however, investigators have reported that they can't find any difference between the niches of species that appear to be in competition. D. R. Strong, Jr., studied thirteen species of tropical leaf-mining leaf beetles that use the same food and live in rolled-up leaves of *Heliconia* plants, but he could find evidence only that the niche of one species was weakly segregated from the niches of the others. These beetles apparently require exactly the same resources, but they live together without any aggression, either within or between species. Perhaps in this case these herbivorous insects, living in such a rich tropical forest, never reach large enough populations actually to be in competition, because they are exploiting such a large resource that their food supply isn't limited and predation keeps their numbers in check. Without competition, Gause's principle simply doesn't apply.

adaptations may be morphological, behavioral, or biochemical

If someone asks, "How does a species become adapted to a niche?" we are likely to give what sounds like a wiseguy answer: it is adapted by means of specific *adaptations*. Though this sounds unhelpful, it directs our attention to specifics, instead of the broad, vague notion of "being adapted." A successful species becomes and remains successful by evolving specific adaptive features over long periods of time that allow its individual members to meet short-term challenges. Some of these adaptations are *morphological*, or structural, such as having a certain shape of body, sharp claws for fighting, tough bark for protection, powerful leg muscles for running fast. To take the bird-watcher's perspective again, one of the first features one learns to observe in a bird is the shape of its bill, and some songbirds clearly have small, thin bills for eating insects, while others have larger, conical bills for eating seeds.

Other adaptations are *behavioral*. All animals engage in stereotyped behavior patterns and have repertoires of rapid, automatic responses to certain stimuli. The ability to learn, too, is an adaptation for dealing with short-term changes. Even a plant's ability to curl up its leaves in dry conditions to reduce evaporation could count as a behavioral adaptation. Behavior is such a fascinating topic in itself that pursuing the evolution of behavior could easily double the size of this book. And perhaps the most fascinating aspect of this inquiry would be the evolution of human behavior, including all that we think and feel. Darwin himself anticipated that an evolutionary perspective might dramatically change our way of looking at our own behavior and feelings, but this perspective had little influence in psychology until the 1960s, when a few students of evolution such as William Hamilton and John Maynard Smith took a fresh look at some aspects of human behavior. Hamilton, in particular, developed the concept of *kin selection*. On the average, each of your brothers or sisters carries half the genes you carry, and even your cousins carry an eighth of these genes. So from the genes' perspective – think of genes as being "selfish," in Richard Dawkins's terminology – it is reasonable for you to engage in loving, unselfish, altruistic behavior toward your kin that preserves those other copies of your genes, even if you sacrifice yourself. It will also be reasonable for men and women to engage in behaviors that maximize their chances of passing on their genes and have corresponding attitudes. Thinking along these lines has been important in the development of contemporary evolutionary psychology, but this is a topic to be left for further reading.

Biochemical adaptations include enzymes and metabolic processes, regulatory mechanisms that respond to changing conditions, and hormones that allow some cells to detect the need for a physiological response and signal other cells to respond. Furthermore, Robert H. Whittaker and Paul P. Feeny were the first to call our attention to the interesting and ecologically important *allelochemic* interactions, in which chemicals made and released by one species – substances called *allomones* and *kairomones* – have ecological effects on some other species. Allomones may repel or even kill competitors or enemies, while kairomones may give an animal a distinctive odor so its enemies can find it more easily.

We see that members of each species occur only in certain patches in an ecosystem. We don't expect every species to live everywhere, but what determines where each species will occur? The important factors are often subtle and chemical. James Fogleman and William Heed found chemical subtleties determining how four species of fruit flies (*Drosophila*) distribute themselves among five species of cactus in the Sonoran desert of southwestern United States and northern Mexico. Where the cacti are injured, bacteria and yeasts move in and create pockets of rot that attract the fruit flies, and one species of fly also lives on soil that has been soaked with juice from rotting cacti. The flies feed on fifteen species of yeasts on these plants. They are remarkably specific in their choice of cactus, as shown in Figure 5.2. Specific factors separate the niches of these fruit flies. The flies effectively divide the available resources, so all four species survive without competition. Notice that someone observing the flies and cacti casually would never have discovered any of this; only careful chemical analysis could show what is going on here.

The cacti produce distinctive sets of volatile compounds, mostly pungent alcohols, acetates, and acids, which attract different types of flies. However, other factors determine the needs of each fly species. *D. pachea* is restricted to Senita because the other four species of cactus lack sterols that the flies require but cannot make for themselves, and without these sterols females are infertile and larvae do not develop. *D. mojavensis* and *D. nigrospiracula* cannot live on Senita because they are intolerant of alkaloids that this cactus produces;

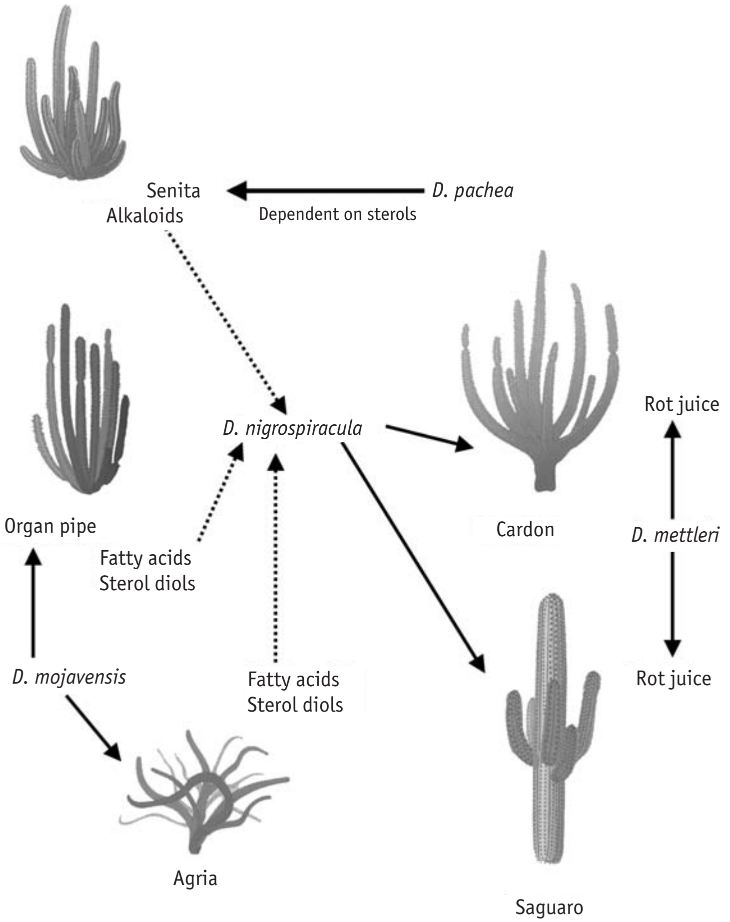


Figure 5.2 *In the Sonoran desert, four species of Drosophila divide a cactus resource through chemical interactions. The dotted lines show chemical inhibitions and the solid lines show which species of cactus each species of fly lives on.*

nigrospiracula is also intolerant of fatty acids and sterol diols produced by Agria and Organ Pipe, so it is restricted to Saguaro and Cardon. Since *mojavensis* tolerates the materials produced by Agria and Organ Pipe, it lives on these two species, free from competition by *nigrospiracula. D. mettleri* avoids competition with the other species primarily through its behavior; although the adults live on Saguaro and Cardon, the larvae live in soil soaked with Saguaro and Cardon rot juice.

adaptation and exaptation

Stephen Jay Gould and Elizabeth Vrba introduced a distinction that is useful in thinking about how evolution happens. We think of adaptations as features that have been shaped by natural selection into a functional form because they enhance the survivability of the organisms that carry them. But organisms often have characteristics that they have acquired in previous evolution – presumably for some function – that turn out later to have value in a different situation for a different function. Gould and Vrba give several examples. For instance, there is good reason to think that the most primitive birds (or dinosaurs on the line of evolution that eventually became birds) acquired feathers either for insulation or because of their value as insect nets on their wings. These animals were flightless. But when some of their descendants acquired flight, feathers then turned out to be wonderfully valuable as light flying devices. As another example, it is quite possible that bony structures evolved first as repositories for calcium phosphate, as supplies of phosphates for metabolism; if this is true, then they only became important as supporting structures for muscular activity during later evolution. Gould and Vrba suggest that characters acquired in this way should be called *exaptations*, rather than adaptations.

The concept is closely related to the idea of pre-adaptation, which has been a source of some distress and even embarrassment among evolutionary biologists. Biology textbooks have sometimes told stories of organisms that were able to adapt to some new situation because they already had the necessary features, which are called pre-adaptations. These scenarios call up spectres of teleology – a universal bugbear among biologists – or of predestination, which is philosophically troubling. Exaptation is a more neutral concept, a way of pointing out that characteristics may often have more than one function and that they can acquire such functions at different times.

different ways for selection to act

If evolution is fundamentally due to natural selection, acting on variation, different patterns of evolution must result from different modes of selection. Suppose we examine the variability of a population for any morphological factor – say size, for the sake of illustration, because it is so easy to envision; we graph size on the horizontal axis, so those at the left side of the scale are small and individuals gradually increase toward the right, and the number of individuals of each size on the vertical scale. We will find a roughly normal distribution curve, with the most individuals at an intermediate, average size and smaller numbers tapering off to smaller and larger sizes. Then natural selection can operate on a population in three general ways. *Stabilizing selection* tends to eliminate individuals on the extremes of the distribution, so average individuals have the greatest fitness; this mode of selection accounts for stasis in evolution – in other words, for no evolution. *Directional selection* favors individuals on one extreme, so the population tends to move in that direction over time, causing phyletic evolution. *Disruptive selection* favors two different parts of the distribution, dividing the population into two groups that are changing in different directions. This mode of selection may be involved in speciation.

Stabilizing selection is a conservative process that keeps a species well adapted to its particular niche by eliminating genotypes that are farthest from the norm. There is evidence that much of selection is stabilizing. For instance, in 1898 Hermon C. Bumpus collected English sparrows that had been exhausted by a snowstorm. In the warmth of his laboratory, seventy-two of the sparrows revived and sixty-four died. By carefully measuring many of their features, Bumpus showed that the females that perished were largely at the extremes of size, and the survivors were much closer to the average of the population. (Oddly, the male survivors tended to be shorter and lighter than average, with longer wings and legs.) Studies of this kind suggest that the average genotype of a population makes it well adapted to its niche and that selection tends to maintain this genotype. As another example, small songbirds tend to lay clutches of about three or four eggs, even though they could lay several more. One can imagine selection for birds that lay more eggs and therefore out-reproduce their competitors, but studies of these birds show that those who do attempt to raise larger broods typically are less successful than those who raise more modest broods, and thus selection favors the status quo.

the realm of the Red Queen

Stabilizing selection probably keeps a species adapted to its ecological niche in some environment, as long as that environment is stable. If each species were continually becoming better adapted through natural selection, one might expect species that have lived for only short times to have the highest extinction rates; extinction should be less common among older species, which presumably have had the benefits of greater selection. However, Leigh van Valen demonstrated that this is apparently not the case among some groups of invertebrates, which became extinct at a constant rate, regardless of how long they had existed.

If natural selection isn't making organisms better adapted all the time, what is it doing? Van Valen's answer is his *Red Queen hypothesis*, referring to the queen in Lewis Carroll's *Through the Looking-Glass*, who tells Alice that in her country it takes all the running you can do just to stay in the same place. By this hypothesis, an ever-changing environment constantly challenges each species just to keep pace and remain well adapted. Think of a predator and one of its prey species, for instance – perhaps a hawk and one of the songbirds it hunts. Perhaps an early version of the hawk has searching and hunting strategies that are quite effective against the songbird, and the hawks manage to catch and consume quite a few. But some of the songbirds have slightly improved vision that manages to pick out an image of the hunting hawk when it is still at a distance, so these songbirds get an early warning and head for shelter sooner. Little by little, the songbird population comes to carry genes for this kind of vision, and the hawks become less and less effective in hunting them. But the hawks will be able to change, too. Perhaps some of them get genes that give them a slightly different flight pattern, so the songbirds' eyes no longer recognize them. Perhaps some of them get to fly faster or their eyes become better at picking out the images of the songbirds hiding in their shelters. We can imagine unlimited versions of this kind of scenario.

The point is that for all its complexities and possibilities, adaptation is rather like an interminable game that no one ever wins. Each species may improve its lot by evolving some new structure or behavior or chemistry, and its position in the community may be enhanced for a while. But eventually some other species will evolve another mechanism which improves its position, and so it goes. In the long run, the total of all the winnings and losses is always zero, and – in gamblers' jargon – no species ever "quits the game winners."

My colleague David Milne has suggested that we think of a niche and a species as a spot of light focussed on a wall encompassing a bunch of bugs. The bugs are scattered across the spot in accordance with their genotypes, with the best-adapted types in the center. Those whose genotypes give them lesser fitness are trying to live in the twilight at the edge of the niche, and they tend to be selected out and eliminated. But the pool of light is moving slowly (with changing environmental conditions), and the bugs living in it continually struggle genetically to keep up through directional selection. They survive only as long as they stay in the spot of light; if they fall behind it, their fitness declines, and eventually they become extinct.

proteins and the subtlety of editing

Each species is adapted to particular conditions of temperature, pressure, and so on – Hutchinson's conception of how a niche should be defined. I want to focus on one particular example of temperature adaptation. Since proteins are the molecules that perform most of the essential biological tasks, it is instructive to develop a better understanding of protein structure while showing how that structure can be altered very subtly through mutation and selection.

The microbiologist Ogden Edwards once examined four similar species of bacteria and showed how closely their maximum growth temperatures correlate with the temperatures at which their enzymes lose their function. For instance, *Bacillus mycoides* can grow at up to 40°C, and its enzymes are stable to about that temperature, whereas *Bacillus vulgatus* will grow at 55°C, and its enzymes are stable to temperatures in the mid-50s. Now this is not remarkable. You may be inclined to respond, "Okay, so what?" Since an organism can function only if its individual enzymes and other components are functional, we expect the stability of its proteins to match the temperatures at which it can grow. These particular features are examples of adaptations. But I want to build on this case to show how remarkably easy it is to acquire such adaptations through mutation and selection.

An important strategy for molecular biology research is to use mutants, and those with temperature deficiencies or sensitivities are very useful. Bacteria such as the common *E. coli* generally grow in the temperature range from about 28 to 40°C and grow best at 37°C, human body temperature. But we can find temperature-sensitive (*ts*) mutants that can only grow at the lower temperature, up to about 30°C, and others that are cold sensitive (*cs*), which will only grow at the higher temperatures. What makes the difference?

Proteins are long chains of amino acids, folded into particular functional shapes, such as the myoglobin molecule of Figure 5.3. Although you can't see all the molecular details, the molecule is held in this shape by interactions among the side chains (the R groups) of all the amino acids. Like hands reaching out to grasp one another, these side chains hold on to one another through many specific chemical bonds. These internal bonds depend on the polypeptide chain having amino acids in each position that are able to interact. Merely replacing one amino acid with another can remove an important bond and make a molecule that cannot sustain its shape at an elevated temperature – thus, a *ts* mutant. On the other hand, a different change could add a new bond, thus making a protein that can endure higher temperatures. So the common finding of mutants makes it easy to understand how the proteins of one of the bacteria that Edwards studied could be shaped by mutation to become more stable at the characteristic temperature of its niche. (Other bacteria can live at far higher or lower temperatures, by the way.) In fact,

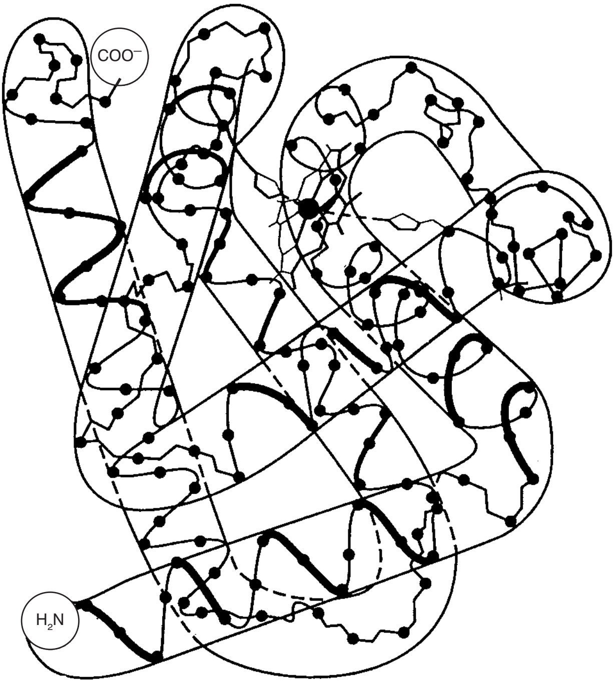


Figure 5.3 *A typical protein, such as this myoglobin molecule, consists of a chain of amino acids folded into an irregular structure.*

these lab results mean that a species could be shaped to a new temperature environment quite rapidly.

A further instructive example comes from the story of the protein hemoglobin, which carries oxygen (O_2) in the blood of all vertebrates (mammals, birds, reptiles, and so on). About 98 per cent of the hemoglobin in normal adult humans is hemoglobin A (Hb A); it consists of four globular polypeptide chains, two called alpha (α) and two called beta (β). The α and β chains are both very similar to one myoglobin chain. Each chain carries an iron atom inside a large molecule called a heme; the "globin" part of the protein's name refers to the polypeptide. Hemoglobin is a marvelous example of an adaptation, a protein wonderfully suited to picking up O_2 molecules where they are abundant, in an animal's lungs or gills, and releasing the O_2 where it is needed, in the other tissues of the body.

As excellent as hemoglobin is, even a small change in its structure can weaken or disrupt its function. People who come into clinics for diagnosis of various health problems, such as anemia, sometimes turn out to have mutant hemoglobins, due to a mutation in one of the genes that encodes the hemoglobin structure. (Since the protein has alpha and beta chains, we have alpha and beta genes [*Hbα* and *Hbβ*] that specify them.) Most of these mutant hemoglobin have a single amino acid replaced by another. Among the most interesting and most socially significant are people with *sickle-cell anemia.* Instead of normal Hb A, they have Hb S, in which the glutamic acid at position 6 in the β chain has been replaced by valine:

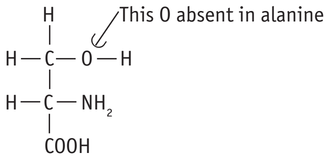
HbA: Val-His-Leu-Thr-Pro-**Glu**-Glu-Lys-Ser-Ala-Val-Thr-Ala- …
HbS: Val-His-Leu-Thr-Pro-**Val**-Glu-Lys-Ser-Ala-Val-Thr-Ala- …

That slight change has profound effects.

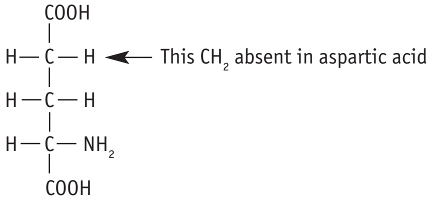
Remember that we have two copies of each gene, one inherited from each parent. Most people have two copies of the normal *Hbβ* chain and produce only normal Hb A. A small percentage of people are heterozygotes who have one *Hbβ* gene and one for hemoglobin S, *Hbβ*^{s}; they have both kinds of hemoglobin in their red blood cells (RBCs) and are generally healthy, but they are gene carriers who can transmit the mutant allele to their offspring. An even smaller percentage of people have two copies of *Hbβ*^{s}, so they produce only Hb S and become very sick. When subjected to reduced oxygen pressures, their RBCs change from their normal smooth, round, disc shape into bizarre elongated "sickle" forms because the protein crystallizes into long needles when it loses O_2. These sickled cells clog small blood vessels and cut off the oxygen supply to nearby tissues. Sickled cells are also destroyed more rapidly than normal RBCs, leading to anemia. Modern medical treatments can help relieve the symptoms of sickle-cell anemia, but without treatment the condition can cause fever, dizziness, pain, pneumonia, rheumatism, and heart and kidney disease, generally ending in death at an early age.

This one small amino-acid replacement has such an enormous effect because it changes some of the internal bonds that hold the molecule in its proper shape. Remarkably the tiny change from a glutamic acid to a valine in a β chain is enough to disrupt the structure of the whole protein, even though only two amino acids out of about 600 are changed in the whole hemoglobin.

Now recall the idea that natural selection is editing. When we edit something we have written, we make specific, intentional changes to improve the writing. Organisms can only acquire differences in their proteins as a result of random mutations that occur by chance. At first glance, we might expect every such mutation to be deleterious, or at least not helpful. In fact many mutations – probably most of them – are deleterious. But mutations can make small, subtle changes in the structure of a protein, and some of these may really be improvements. This is because proteins are polymers and *a mutation can change a single amino acid at a time.* For instance, the difference between alanine and serine is just a single oxygen atom and the difference between aspartic and glutamic acids is just a single -CH_2- group:



Serine



Glutamic acid

If a mutation directs a cell to insert a serine instead of an alanine in one place, its effect will be to *add only one oxygen atom.* That is a tiny, subtle change! Substituting a glutamic acid for an aspartic acid will only add a $–CH_2–$ group to one particular protein, leaving the thousands of other atoms in the protein as they are. Other changes are more severe, of course, but it is the potential for making such minute changes in the structure of a protein that allows proteins to be gently, gradually edited generation after generation so they have functional shapes.

Determining the amino-acid sequences of hemoglobin A from different species shows many slight variations. The functional explanation is that each species is adapted to different conditions, but it is unlikely that *every* difference in amino acid sequence really makes a difference in the life of the animal. Some of the changes that have occurred in the amino-acid sequences of proteins over the eons are too subtle to have any significant effect on protein structure and function. Much of the variation in populations is *selectively neutral*, so two or more alleles of a gene may be maintained in a population simply because there is no selection against any of them. However, any of these changes *could* have a distinct effect on fitness if circumstances change. Human blood groups such as M and N appear to be selectively neutral, though the more familiar ABO blood types may not be – type O people are slightly more susceptible to stomach and duodenal ulcers than type A, and the reverse is true for stomach cancer.

sickle-cell hemoglobin as an adaptation

The rest of the story of sickle-cell hemoglobin is fascinating for a different reason, as another fine example of adaptation to a particular environment. Sickle-cell anemia is relatively common in Africa, southern Europe, and other malaria-ridden areas, because heterozygotes who have one *Hbβ* gene and one $Hb\beta^S$ gene are unusually resistant to malaria. When their cells are infected by the malaria parasite, which is carried by mosquitoes, the parasite starts to reproduce in their RBCs. The malarial infection progresses as those cells release parasites, which infect vast numbers of other RBCs. While growing inside RBCs, the parasites lower the concentration of O_2 and cause the cells to become sickled. These misshapen cells are destroyed, along with their enclosed parasites, by scavenger cells that are part of the body's defense system. Consequently, where malaria is rampant, natural selection favors individuals with one copy of the $Hb\beta^S$ gene because such individuals are resistant to the malarial parasite. Of course, people unfortunate enough to have two copies of $Hb\beta^S$ have sickle-cell anemia and are poorly adapted to any environment. So the heterozygotes are fitter than either homozygote. A. C. Allison found that in some East African populations the frequency of the $Hb\beta^S$ allele is about 0.2 and that the relative fitnesses of the normal homozygotes, the heterozygotes, and the sickle-cell homozygotes are 0.8, 1.0, and 0.24, respectively. About three-quarters of the sickle-cell individuals die before they can reproduce, but heterozygotes have an advantage of 25 per cent over normal homozygotes.

how little changes can make big differences

People tend to think of fitness with dramatic and romantic ideals. Mottos such as the "struggle for existence" or "nature red in tooth and claw" call up images of bloody battles between predators and their prey, where greater fitness means an ability to run faster or to win a battle to the death. In reality, fitness depends mostly on subtle factors, such as the kind of small changes in protein we have just examined, which confer different metabolic abilities; or the ability to live at particular temperatures or oxygen pressures; or small changes in form.

Thinking about evolution is also plagued by the popular myth that adaptations are of no value unless they are fully developed; an eye, for instance, is said to be of no value unless it is fully formed, so there could be no selective value in acquiring any of the minute changes necessary to make an eye little by little over a long time. Modern studies of evolution, however, show how important very small changes can be. Peter and Rosemary Grant have conducted extensive studies of the wonderfully varied finches of the Galápagos Islands off the coast of Ecuador, often called Darwin's finches because they had such a great influence on Darwin's thinking when he visited the islands as a young man aboard the *Beagle* in 1835–36. These islands are subject to severe changes from very wet to very dry years. The Grants have shown that in very dry years the best-adapted Ground-finches, which eat seeds, are those with the largest, strongest bills, which are able to open the large seeds that become most common in these conditions. However, the average difference in bill dimensions between birds that survive the drought and those that die is only about half a millimeter, out of a length of about 10 mm. So the Grants' data show that a subtle difference in form can make an enormous difference in fitness.

Similarly, Craig Benkman and Anna Lindholm studied Red Crossbills, finches whose bill tips cross and make an excellent tool for removing the seeds from Western Hemlock cones, on which the species thrives. They cut off the bill tips of seven captive crossbills, an operation that doesn't hurt the birds since the bills have no nerves; in this way, they asked whether this highly specialized adaptation has adaptive value only in its fully developed form. The birds with uncrossed bills were able to remove seeds from dry, open hemlock cones but were helpless with closed cones. However, as their tips started to grow back and become slightly crossed, they were able to start extracting seeds from closed cones as before, and the birds became more proficient as their bills grew longer and more crossed. This experiment showed that a mutation in an ancestral population that produced even the slightest bit of crossing must have been advantageous and gave those birds superiority in occupying a distinct ecological niche.

living here may be different from living over there

So far, I've been trying to develop a picture of a natural population as a variable group of individuals that may differ significantly from one another, yet whose similarities and pattern of interbreeding with one another make them recognizable as members of a species. Every genotype represented in a population has a certain fitness, but it is important to see that fitness is not an absolute value that will never change. Fitness is measured relative to particular environmental conditions, and if there is any certainty about a natural environment it is that it will eventually change.

Polymorphism gives a population greater potential to maintain itself in spite of conditions that change geographically and in time. Even in a small area, differences in very local habitats may require different characteristics; organisms also have to adapt to changing weather conditions and other events. A population shows *balanced polymorphism* when it maintains the genes for two or more forms because selection favors each form in a different situation.

The value of polymorphism in different habitats emerged from a classic study of the British land snail *Cepaea nemoralis* by A. J. Cain and P. M. Sheppard. Snail populations are highly variable, with base colors of yellow, pink, and brown overlaid with various banding patterns and different colors of the shell lip. The base colors are due to three alleles at a single gene, with brown dominant to pink and pink to yellow. Another gene determines banding, the unbanded condition being dominant, and at least one more gene determines the banding pattern. Why all these different forms? Cain and Sheppard showed that they are associated with patches of different habitats. In woods with a carpet of brown leaves, the unbanded brown and unbanded or one-banded pink snails are particularly common. In hedgerows and rough green areas, the banded yellow snails are abundant. The critical factor in the regional distribution of morphs is their visibility, especially their visibility to the Song Thrush, *Turdus philomelos*, which preys on them. Thrushes bring snails to "thrush anvils," large rocks where they break open the shells to get at the soft body inside. This habit makes it easy to study predation, because the broken shells left around a rock show what kinds of snails have been eaten; the thrushes obviously eat the more visible snails in each patch, and visibility changes with time – for instance, as the background changes from winter brown to the green of spring.

Thrushes are clearly a major selective agent in determining the genetic composition of the snail population. The population of snails survives very well in spite of the thrushes because of their balanced polymorphism. Snails of a single color and pattern might survive precariously in a restricted habitat, but that way of life would be dangerous because the habitat patches are small and ephemeral. The species actually adapts to a much broader habitat by producing individuals that are camouflaged against different backgrounds. The snails pay a genetic price for this (it has been called a *genetic load* that the population must bear) by producing individuals with the wrong patterns in each habitat, but they buy survival in a varied environment by maintaining a variable gene pool.

fitness generally changes geographically

The organisms occupying a certain niche are, by definition, well adapted to that way of life, but the features required for occupying the niche may shift over a species's geographic range. (Some biologists might say that the niche is changing geographically, but if the species continues to play essentially the same role in its ecosystem throughout, I prefer to describe this as a single niche with different genetic requirements.)

In the 1940s, Theodosius Dobzhansky and his colleagues studied genetic polymorphism in wild populations of the fruit flies *Drosophila persimilis* and *D. pseudoobscura* in the southwestern United States and Mexico. After finding that these populations carry many different chromosome inversions, they performed a detailed study of 27 inversion rearrangements in the third chromosome. Figure 5.4 shows the gradients of genotypes that Dobzhansky and Carl Epling found. For unknown reasons, the Standard chromosome has a high fitness in California, but Arrowhead makes for

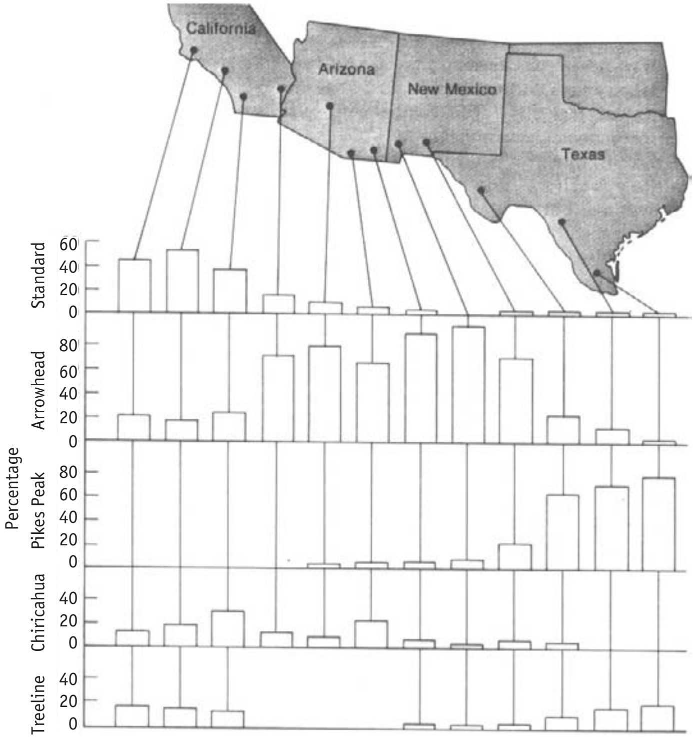


Figure 5.4 *Populations of* Drosophila pseudoobscura *from several places in the southwest U.S. have different frequencies of certain inversions of the third chromosome.*

much better adaptation farther to the east, Pikes Peak has some advantage still farther east, and Chiricahua provides better adaptation in Central Mexico. The frequencies of these chromosomes change gradually rather than abruptly, presumably because the critical environmental variables also change gradually.

The mere fact that the species harbors so many inversions is remarkable, and the geographic distribution of inversions shows that each chromosomal difference can make a difference. You might think that any sequence of genes would be as good as any other, but this isn't so. The expression of a gene may be influenced by its position, and the gene arrangements in *Drosophila* are obviously critical.

As the seasons change, so do the fitnesses of certain gene complexes, as shown by the frequencies of four inversion types of *D. pseudoobscura* at Piñon Flats, California. The Standard type is most common overall, but the Arrowhead and Chiricahua gene complexes provide better adaptations during the spring, for their frequencies increase in spring while that of the Standard gene complex decreases. In summer, the frequency of the Standard type rises again as the Arrowhead and Chiricahua types decline. (Some laboratory observations show that Standard is more advantageous in crowded populations, which may develop during the summer.) The relative fitness of each genotype clearly varies with time, and – as in the story of the snails – the population as a whole survives by maintaining several forms that are adapted to different conditions.

These studies often showed the superiority of heterozygotes, with some clear indications that flies heterozygous for a pair of inversions were more fit than either homozygote. This increased fitness is another reason populations maintain several different inversions.

Leopard Frogs in North America also show geographical change in phenotype. Though designated *Rana pipiens*, the frogs may actually be distinct species spread across eastern North America. These frogs are clearly adapted to the average temperature where they breed. Frog eggs taken from the northern part of the range can tolerate a temperature of 5°C and can develop in temperatures up to about 28°C, whereas those from Texas, Florida, and Mexico can tolerate nothing lower than 10–12°C and can develop up to 32–35°C. These differences in temperature tolerance must reflect distinct gene complexes that adapt each population to local temperature conditions.

Distinct features, such as color, size, and other aspects of form, may vary along different geographic gradients. Thus, a species might show a cline in size along a north–south line and a cline in color along an east–west line. Each of these differences shows an independent response to a different environmental pressure.

pushing the edge

Let's reconsider the bacilli that Ogden Edwards studied. I emphasized that it would be rather easy for bacteria to evolve resistance to higher and higher temperatures because we can so easily find mutants with restricted, or extended, temperature ranges, both cold and hot. Now imagine a species adapted to mid-range temperatures, say around 40°C or a little less, but living near a much hotter spot. As usual, some mutants arise in this population that can weather slightly higher temperatures, say up to about 43°. Some of them happen to be on the edge of the population, closer to that hot spot, and since most of the bacteria can't grow there, the mutants find themselves in unoccupied territory, and they begin to grow very well. Then in this population of somewhat heat-resistant mutants, another mutation occurs that provides even slightly better heat resistance, perhaps up to about 47 or 48°C. Any mutants of this kind who are living still closer to the hot spot will find themselves in a place where their relatives can't grow, but they will be able to grow there very well. You can see where this is leading, of course. We can expect that, little by little, a mutant population will develop that can occupy quite high temperatures, and along the way it may also develop other distinctive features, so we will want to call it a different species from the parents we began with.

I use this example because it is so simple. But we can generalize it to say that this is probably one common way for evolution to happen. Let me go back to Dave Milne's image of the bug population living in a niche represented by a (slowly moving) pool of light. I extended the metaphor a bit by imagining that the bugs in the center of the spot are best adapted to this niche and that those living toward the edge are less well adapted and most likely to fall into the surrounding darkness of extinction. Now those edge-dwellers are less well adapted because their genomes don't carry the combinations of genes that are optimal for this particular niche, but those genomes may give them some increased ability to occupy a related niche. As with the bacteria, it is easy to picture individuals living on the edges of their niche – whether geographically or in some other sense – whose genomes give them the ability to push the edges of that niche, to move into conditions that other members of their species cannot tolerate. And this may be a common factor in the origin of new species.

We have now seen how communities are made of distinct species living together and interacting, and how each species occupies a distinct niche, defined as a certain role or a certain place. We have seen that each species becomes adapted to its niche by means of distinct adaptations – chemical, morphological, behavioral – and that adaptation may be as subtle as the tweaking of a critical protein into a distinctive form. Now it is time to look into the meaning of this word "species" more carefully and to think about the general process of speciation, the origin of new species.

chapter six

making new species

The idea of evolution developed as an answer to various questions that were puzzling naturalists of the nineteenth century, such as how to understand homology in the light of a separate creation for each species, but a general question requiring a naturalistic answer was, "How did there get to be so many different kinds of living things in the world?" In contrast to the traditional answer, the naturalistic alternative was that each species had arisen through gradual evolution from distinctly different ancestral species. In chapter four, we considered a preliminary answer to the question of just what a species is. It is now time to revisit the issue in the light of the background we have developed about evolution and ecology, since the complications about defining and delimiting species are the result of evolution and are best explained on the basis of evolutionary history.

some difficulties in defining species

The biological species concept, as explained on page 54, is that a species consists of a group of organisms capable of interbreeding with one another. To get one possible point of confusion out of the way, it will be clear that this conception of a species applies only to those that reproduce sexually. Although that includes the majority of species, huge numbers of asexual organisms occupy every habitat. They generally reproduce by one individual dividing in two, by the two dividing again to make four, and so on, to form a *clone*. Many plants also reproduce this way, by sending out shoots or buds. A group of asexual individuals can only be called a distinct species by virtue of their common features. In this endlessly branching pattern, individuals will gradually diverge from one another. There is no firm criterion for including or not including an asexual individual in a species, and an asexual "species" is merely a convenient category, a collection of independent but very similar individuals.

A second side issue arises regarding species of the past. In drawing phylogenetic trees, we sometimes put different species names on a single line to indicate different "species" succeeding one another. This implies that speciation has been occurring, but it really reflects both a matter of taxonomy and incomplete knowledge. The taxonomic problem is that humans like to assign different names to fossil forms that may be members of a continually changing series. As we see in chapter eight, in the last two million years of human evolution, different fossil forms that have been given the names *Homo habilis, H. erectus, H. sapiens*, and others may all be stages in a single, unbranching course of evolution, or they may have been distinctive forms that arose one after another in a series of rapid speciations. If we had the fossils of all the individuals who lived during this time, we would probably find it difficult or impossible to draw lines separating them into different species. Since the existing fossils preserve only a tiny fraction of the individuals who ever lived, the populations of the past are conveniently broken up into segments, which have been called *paleospecies* to distinguish them from contemporaneous species.

Returning to the question of species living at the same time, remember that a species is initially defined morphologically, as a group of organisms that have essentially the same form. But every population is variable because its gene pool contains allelic variants of many, if not all, genes. According to the most commonly used conception of a species, the most critical feature is that all the members of a species are actually or potentially capable of interbreeding with one another, so in effect they share a common gene pool. That's why all humans are members of the same species even though we don't all look alike. Some examples will show how relying on morphology alone leads to great difficulties.

a. distinct species that are virtually identical

Any serious birder in North America could point to the problem of the *Empidonax* flycatchers. The "empids" are a challenge and a frustration to birders because they are so much alike. These small grayish-yellow birds are distinguished from other flycatchers by their distinctive eye-rings (a circle of light plumage around the eye) and by two prominent light bars on the wing. At least five species are recognized in eastern North America; experts can learn some features of plumage that are likely to distinguish one from another, but in general observers have to rely on a bird's voice and its habitat. Thus, the Least Flycatcher inhabits farms and open woods, and its call is *che-BEK*. The Yellow-bellied, though yellower than most, is best identified by its habitat in coniferous woods and bogs, and by its rising *chu-wee* call. The Alder, of swamps and wet thickets, says *fee-bee-o*; the Willow lives in wet or dry thickets and brushy pastures, and it says *fitz-bew*. There is no evidence that these birds hybridize with one another. They remain distinct, though confusing to human observers, and are a good example of *sibling species.*

b. geographic variation in a species

Many species of birds are fairly widespread, with ranges that cover large portions of North America or Eurasia, yet each one remains quite uniform within its range. A bird of this kind observed in one region will not be noticeably different from one of the same species observed far away. But other species of birds are divisible into quite distinctive *subspecies* that can be recognized morphologically. The Song Sparrow, a common bird throughout North America, has been divided into about twenty-five distinct subspecies. Throughout the east, the sparrows have backs of a moderate brown color streaked with black and lightly streaked breasts with brown lines that converge to a spot in the middle. But birds in the deserts of the west are distinctly lighter, as if bleached out by the sun, and birds of the Pacific Coast are much darker and have much rustier plumages, changing into still darker and larger forms as one goes up the Pacific Coast into British Columbia and Alaska. Because birds of neighboring populations interbreed with one another, they are all considered one species, but it is called a *polytypic species* because it includes populations with distinct morphologies.

c. different forms within a single population

On almost any flat beach along the southern Atlantic coast of North America you will find pockets of little clams called Coquinas at the water's edge. As each wave washes over them, they open to receive the fresh water and then squirm and burrow a bit into the sand. In only a few minutes you could collect clams with quite a variety of colors and patterns on their shells: light blue, streaks of tan, purple and tan, rings of red-orange, and so on. Many populations include two or more obviously different forms, or *morphs*; if species were defined only by morphology, the Coquinas might be classified into three or four different species, but all these forms are just different morphs of one species, *Donax variabilis*. We noted that every species harbors a lot of genetic variability and is genetically polymorphic; this is just a more striking example of polymorphism. Similarly, the Eastern Screech-owls (*Otus asio*) of North America contain two color morphs: reddish-brown and gray individuals, in the same population and even the same brood, just as humans have different eye or hair colors, even in a single family.

problems with the criterion of interbreeding

If we can't rely strictly on morphology to delimit a species, we might at least pin our hopes on the criterion of interbreeding. Other examples, however, show that interbreeding alone is not necessarily a good criterion for populations being members of a single species. The orioles of North America are spectacular orange and black birds. For a long time, the official AOU list recognized two widespread species, the Baltimore Oriole of the east and the Bullock's Oriole of the west. However, the two populations hybridize in a region of the midwest, and on this basis they were combined several years ago into a single species, called the Northern Oriole, much to the dismay of easterners, especially Marylanders, who were very fond of their own species and the Baltimore baseball team named after the bird. Now, one tool available to the modern taxonomist is DNA analysis. When Stephen Freeman analyzed the DNA of several oriole species, he discovered that they are related as shown in Figure 6.1. The DNA evidence shows that the Baltimore and Bullock's are not even one another's closest relatives. They don't hybridize with other orioles that are more closely related, and yet they do hybridize with each other. (They have now been elevated to their old species status, much to everyone's relief.) This kind of example is used by advocates of other species criteria to argue that hybridization should not be used as a criterion of close relatedness or for species definition.

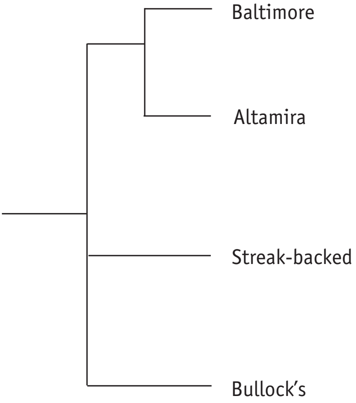


Figure 6.1 *Evolutionary relationships of four North American oriole species.*

In spite of the difficulties we sometimes encounter in applying the biological species concept, it is still fundamental to our thinking. A hallmark of modern biological thought is recognizing that a species is not just an arbitrary collection of organisms but has objective boundaries defined by reproduction. This is one of our legacies from Darwin. The question of defining a species is not primarily interesting because biologists want a catalogue of the world's organisms, but rather because the idea of a reproductively independent unit is so important. Unless a unit – a species defined biologically – becomes genetically independent of other groups, it can't go on to produce other, more diverse groups in another evolutionary step, and it is questionable whether it can become a stable part of a community.

the mechanism of speciation

All these difficulties in defining a species neatly make life tough for cataloguers, but they are a delight to the student of evolution because they show evolution in action in all its randomness and complexity. This will become clearer as we examine the general process of speciation, the process in which new species are formed. This general model of speciation through geographic isolation is due largely to the work of Ernst Mayr in the 1940s. The model is based primarily on studies of birds and insects. It undoubtedly applies to many sexually reproducing animals, and it applies to plants to a degree, although we will have to discuss special mechanisms in plants later.

The Song Sparrow example shows how a single species may vary geographically, and such variation is common; as a species spreads out across a wide range, its populations often acquire many differences. They may become so different that one is tempted to call some populations distinct species, but as long as neighboring populations can interbreed, genes are still flowing from one to the other and they are still all one species. It is only meaningful, of course, to consider reproductive isolation if the populations in question are positioned so they *could* interbreed. Two populations are *sympatric* (*sym-* = together; *patra* = fatherland, thus homeland) if their ranges overlap, *parapatric* (*para-* = next to) if their ranges are adjacent, or *allopatric* (*allo-* = different) if their ranges are separate. Clearly, we can only talk about reproductive isolation with populations that are sympatric or at least parapatric; with allopatric populations, there is no way to ask the question.

The present conception of speciation begins with a widespread species, often a polytypic species in which individuals living in one region are already genetically distinct from those in other regions. The species then becomes divided into two or more populations by some kind of geographic barrier. Maybe the Earth enters a period of glaciation, and the two populations are separated in different glacial pockets. Perhaps they occupy a lowland habitat but spread out to different sides of a mountain range. Perhaps they are a woodland species, and a grassland develops in the middle of their range. Perhaps they come to occupy different islands – a situation we will examine in more detail later. Whatever the cause, two or more populations become allopatric and unable to interbreed with each other. While they are isolated, they undergo separate genetic paths as they become adapted to local conditions. And they remain isolated long enough to become significantly different genetically and to acquire *reproductive isolating barriers*, which keep them distinct.

Reproductive isolating barriers could operate either before mating occurs or afterward. The difference is important. If two individuals mate and produce zygotes that die or reproduce poorly, they have both wasted much of their reproductive potential, perhaps all of it. So there is strong selective pressure to stop hybridization before mating can occur. The following are some isolating barriers, beginning with the premating.

habitat isolation

Two species may occupy such different habitats that they don't come into contact and thus never have a chance to hybridize. The Red Oak (*Quercus coccinea*) is adapted to swamps and wet bottomlands; the Black Oak (*Quercus velutina*) lives in drier, well-drained upland regions. Hybrids between these species are sometimes found in intermediate habitats, showing that they lack physiological incompatibilities to interbreeding and are kept apart only by their ecological specialization.

temporal isolation

Two species may breed at different times, so there is little chance of hybridization. Two closely related types of plants often release their pollen at different times, so there is little or no chance of cross-fertilization of one by the other.

behavioral isolation

Many animals engage in elaborate courting and mating rituals, which help to ensure that the wrong individuals don't mate. These behaviors are genetically encoded, so the final act of mating only occurs between individuals who share genes that give them compatible behavior patterns.

structural isolation

The reproductive structures of two species may be incompatible. The genitals of animals may not fit together properly so a male can't effectively inseminate a female of the other species. In plants whose flowers are pollinated by animals, two species of plants may become isolated by acquiring different flower colors, thus attracting different pollinators, or the flowers may develop different shapes, so they become specialized for pollination by different species of insects.

The next four barriers operate after mating.

gametic incompatibility

The gametes of the species may fail to function together. For instance, the sperm of one species may not be able to fertilize the egg of the other.

hybrid inviability

A hybrid zygote may die because it is weak or deficient in some other way. A zygote with two different chromosome sets may fail to go through mitosis properly, or the developing embryo may get incompatible instructions from the genetic programs of the maternal and paternal chromosomes, so it eventually aborts.

hybrid sterility

The hybrid may develop into a sterile adult. Sterility generally results from complications in meiosis when different chromosome sets are unable to form viable gametes. The chromosomes of even closely related species may be different enough to make meiosis in a hybrid very difficult.

hybrid disadvantage

Even if the hybrids are viable, their offspring may be inviable or have much lower fitness than the nonhybrid offspring of each species alone. Hybrids are often at a disadvantage because each species is adapted (or is becoming adapted) to a different way of life, so hybrids, with a mixture of gene complexes, generally are not well adapted to either way of life. Imagine two populations that are incompletely isolated and are becoming adapted to different niches. In each population some individuals – call them the "hybridizers" – have genes that tend to promote mating with the other population. If intermediates between the two populations have reduced fitness because they are not well adapted to either niche, the hybridizers will be putting their genes into a reproductive dead end, and genes that dispose their carriers to interbreed will be gradually eliminated from both species. The genes that remain in each population will tend to discourage interbreeding. Exceptions to this tendency, however, are quite common among plants, and successful hybridization often leads to the formation of new plant species.

after separation, the test

The next step in speciation is for the populations to expand their ranges and become sympatric again, and now we can apply the critical test: have the formerly isolated groups acquired reproductive isolating barriers or not?

One possibility is that the populations have achieved full species status and won't interbreed. So speciation is complete, and now each species has the potential of going its own evolutionary way, perhaps to divide again in the future. The other possibility is that the populations have become somewhat different but not different enough to prevent interbreeding, so they continue to interbreed. Many examples of this situation are well known. Among the most common birds of the North American woods are large, brown, ground-feeding woodpeckers called Northern Flickers. A startled bird will fly off with a roller-coaster motion, flashing a patch of white rump feathers. In the east, you will see flickers with bright yellow feathers under their wings and tails, and black mustaches adorning the faces of the males; in the west, your flickers will generally have salmon-red feathers and red mustaches. They were once called two different species, the yellow-shafted and the red-shafted flickers. However, intermediate forms occur quite often, especially in the middle of the continent: birds with orange feathers, sometimes sporting one red and one black mustache, or with some other combination of features. In other words, the various populations of flickers are still exchanging genes regularly. The red-shafted and yellow-shafted forms are not distinct species but geographic variants of a single species. They provide a fine example of animals in an intermediate or incomplete state of speciation.

Organisms such as the flickers can give biologists fits because people like to put organisms into neat boxes and give them unambiguous names. But nature isn't so simple, and this can be frustrating. One difficult situation arises when the populations are allopatric; they show some morphological differences but are clearly related, and yet we are not in a position to test their interbreeding. In this case, we call the populations *semispecies* or *allospecies*, and the whole group of semispecies is a *superspecies.* After an extended period of isolation, the semispecies may start to expand their ranges and become partially sympatric again. Then their species status can be determined. The Northern Flickers are at this intermediate stage in evolution, and the two types are still subspecies or perhaps morphs, since they are not well limited geographically.

There is no way to predict just how populations will change as they spread out into different areas. The flickers present a simple case of an intermediate stage of speciation. But some situations aren't so simple. Traveling from the southern California coast up into the mountains, you will encounter several kinds of plants known as Monkey Flowers of the genus *Diplacus.* Many of them are easy to identify and name with the aid of a field guide, but one group may give you some problems. The moist coastal areas support tall, red-flowered shrubs named *Diplacus puniceus*. The drier foothills are home to shorter bushier plants that usually have orange flowers, called *Diplacus longiflorus*. Still higher, in the very dry mountains, are very short plants with yellow flowers, named *Diplacus calycinus*. The names show that these plants are considered three distinct species. However, over a wide range *puniceus* and *longiflorus* grade into one another, so they appear to be mere varieties of a single species, and populations of plants with the form of *longiflorus* can be found in which the flowers are either red, orange, or yellow. Yet at some places in the Santa Ana Mountains, *puniceus* and *longiflorus* grow together and are clearly distinct, with no interbreeding. Are these distinct species or not? Complicated relationships between populations may develop during evolution, and different degrees of separation may evolve in different places. The difficulty of applying names to such organisms is quite unimportant compared to the lessons they hold about evolution: that organisms in different places will have genomic differences, which cause them to behave in different ways in reproduction.

The Monkey Flowers and other complex situations reinforce the point that the biological species concept, with its criterion of reproductive isolation, may run into difficulties because populations may change in complicated ways. Sometimes a species cannot be delimited neatly because we are trying to apply a simple, idealized concept where it may not fit. The Buckeye (*Junonia lavinia*), a common American butterfly, illustrates the difficult situation of a ring of races. Buckeye populations interbreed with one another around the Gulf Coast from Florida through Texas, Mexico, and Central and South America as the members of a species should. But where the ring closes in the West Indies, populations from Florida meet those from South America, and they will not mate with each other. Suddenly they are different. We don't really know how to apply names to these insects. Circles of races showing such complications are actually rather common. A similar situation exists in the North American west with the Deermouse *Peromyscus maniculatus*. In Glacier National Park, Montana, two subspecies meet with no evidence of interbreeding, partly due, no doubt, to their inhabiting different habitats. But elsewhere these populations are connected by races that interbreed with one another.

Although we catch some organisms at intermediate stages of speciation, it is clear that speciation can occur very quickly. For instance, some cichlid fishes were isolated from their parent populations in Lake Victoria, Africa, only 4000 years ago, and they have clearly become distinct and reproductively isolated in that time. Stanley describes this situation and others where speciation may have occurred in even shorter times.

evolution as opportunism and *bricolage*

George Gaylord Simpson did much to put evolution in perspective in his book *The Meaning of Evolution.* His Chapter 12, on the opportunism of evolution, is itself a paean to rationality and biological wisdom, for he begins:

> Over and over in the study of the history of life it appears that what can happen does happen. There is little suggestion that what occurs *must* occur, that it was fated or that it follows some fixed plan, except simply as the expansion of life follows the opportunities that are presented. In this sense, an outstanding characteristic of evolution is its opportunism. "Opportunism" is, to be sure, a somewhat dangerous word to use in this discussion. It may carry a suggestion of conscious action or of prescience in exploitation of the potentialities of a situation. ... But when a word such as opportunism is used, the reader should not read into it any personal meaning of anthropomorphic implication. No conscious seizing of opportunities is here meant, nor even an unconscious sensing of an outcome.

Simpson went on to point out that the opportunities available to organisms are always limited, and that the evolution of one type of organism always presents a limited range of opportunities for those of other kinds. The evolution of land plants, for instance, created a variety of new habitats for land animals to occupy.

We noted in chapter three that a critical feature of organisms is their historicity, and Simpson noted that "Evolution works on the materials at hand: the groups of organisms as they exist at any given time and the mutations that happen to arise in them. The materials are the results of earlier adaptations plus random additions and the orienting factor in change is adaptation to new opportunities." Every new structure is made by modifying existing structures, and each generation survives if its structures merely "make do," not if they achieve some ideal standard of perfection. Again and again, we see organisms operating with mechanisms that are clearly modifications of ancestral structures, that work, but which could be replaced by much better structures.

Now it is easy to read something like design or destiny or purpose into the history of life – particularly if it is viewed superficially, and most especially if it is done with an anthropomorphic attitude. An antidote to this tendency comes from an unexpected source, from the anthropologist Claude Levi-Strauss, who provided the image of primitive humans operating through what the French call *bricolage. Un bricoleur* is a workman who creates by tinkering with what he has available and coming up with a contraption that "makes do," even though someone with more resources might create a better device. All the evidence of biology is that if there is some cosmic intelligence behind biological structure and function, that intelligence operates as *un bricoleur*, not as an all-powerful inventor making the best possible design. One famous example is the panda's "thumb," as explained by Stephen Jay Gould. Pandas live exclusively on bamboo shoots, which they prepare with their hands using a kind of thumb-like extension that works against a paw with the normal five digits. The "thumb" is actually an enlarged radial sesamoid bone, one of the normal bones of the vertebrate wrist, which moves with only a slight modification of the muscles that move the true thumb in other vertebrates. Thus, pandas have become adapted for their unique diets through biological *bricolage*, by modification of the available structures to make a pseudothumb that works. A truly intelligent designer, having created the pandas and set them in the midst of a bamboo forest with instructions to be fruitful and multiply, could have supplied them with a much more efficiently designed hand.

I began chapter one by noting that North America and Europe host a multitude of very similar little sparrows and buntings, so one must wonder at their variety. Simpson observed that if this historical view of evolution is correct, one must expect to find multiple solutions to adaptational problems, and he explored the idea by reference to the wonderful variety of antelopes in what was at that time the Belgian Congo (Figure 6.2).

> Now there must be some one type of horn that would be the most effective possible for antelopes, with some minor variation in proportions or shape in accordance with the sizes or detailed habits of the animals. Obviously not all of these antelopes have the "best" type of horns, and probably none of them has. Why, for instance, with their otherwise rather close similarity, should the horns of the

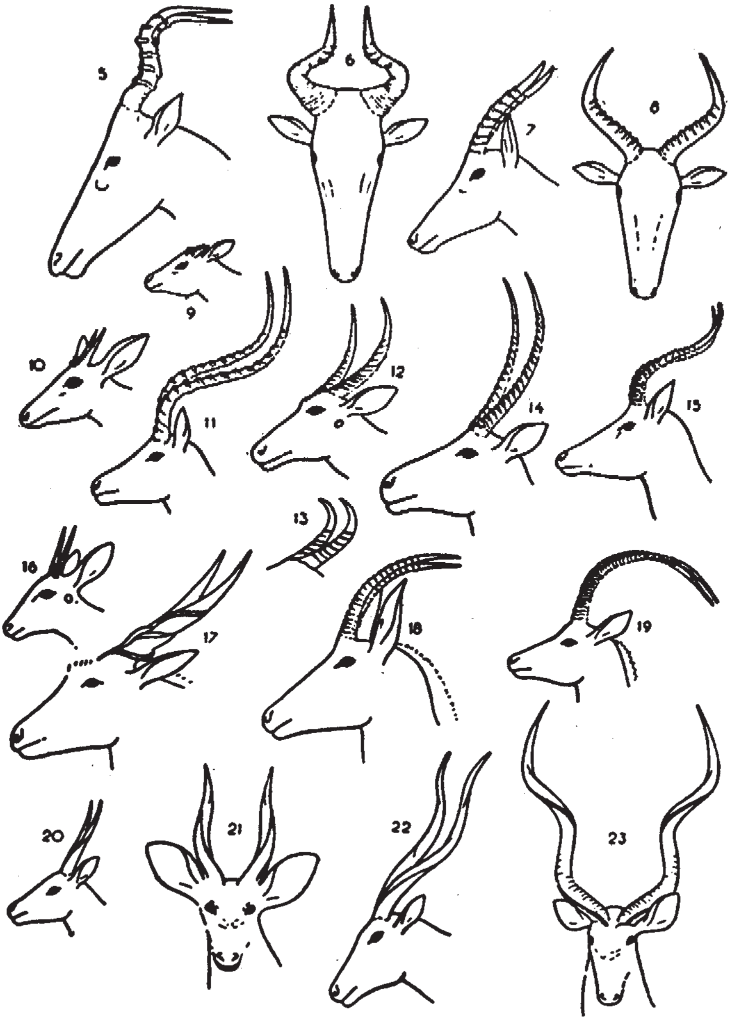


Figure 6.2 *The heads of several species of African antelopes.*

reedbuck (14 in the figure) curve forward and those of the roan antelope (18) curve backward? Do not the impala (11) and kob (15) horns with their double curve, seem to achieve the same functional placing and direction as the reedbuck horns (12 and 14) with a single curve, but to do so in a way mechanically weaker? Even though the animals themselves are small, are not the duiker horns (9 and 10) too small to be really effective, and are not the tremendous kudu horns (23) unnecessarily unwieldly?

Viewed in the light of opportunism and *bricolage*, however, this variety of antelope species makes good sense.

speciation and opportunism on islands

The Hawaiian Islands are inhabited by an unusual collection of little red and yellow-green birds, which are distinguished by an amazing variety of bills. They are now classified in a single, unique family, called Drepanididae, known as Hawaiian honeycreepers. The diversity of honeycreepers contrasts sharply with the typical birds of large land masses. Each continent has many families of birds, each one containing species that occupy very similar niches. For instance, sparrows and finches have short, conical bills and are adapted for eating seeds; woodpeckers are adapted for digging into wood to catch burrowing insects; warblers are small, nervous, insect-eaters with thin bills; and thrushes have moderately heavy bills that are used for eating fruit, insects, and other small invertebrates.

Even though the internal anatomy of the Hawaiian honeycreepers shows that they are closely related, they occupy very different niches and show enormous external differences, especially in their bills (Figure 6.3). The chunky yellow and brown chloridops uses (or used, for unfortunately many of these species are extinct now) its tough, massive bill for crushing the seeds of the naio plant. The ou looks like a parrot and feeds on fruits just as parrots do in the American tropics, using its hooked bill to scoop out the insides of the ripe ieie fruit. The koa finches and Laysan finch also fed on fruits, and the koas could split the tough twigs of the koa tree and eat grubs that lived inside them. The akialoa feeds like a woodpecker, probing its long bill into crevices in trees and sometimes peeling off bits of bark to find grubs and insects. The mamos used their long, curved bills to suck the nectar out of deep flowers, while the iiwi takes some nectar but prefers to eat the caterpillars off flowers. The apapane's narrow bill is suited for its diet of insects with a bit of nectar. As a whole, the Hawaiian honeycreepers seem to have found most of the ways in which land birds can live, and the members of a single family have diverged enough to occupy the kinds of niches that are taken by whole families of birds elsewhere.

The Hawaiian Islands lie far from any continent and have few native land birds other than the drepanids. Sometime in the past, perhaps a few million years ago, a few birds that were ancestors of

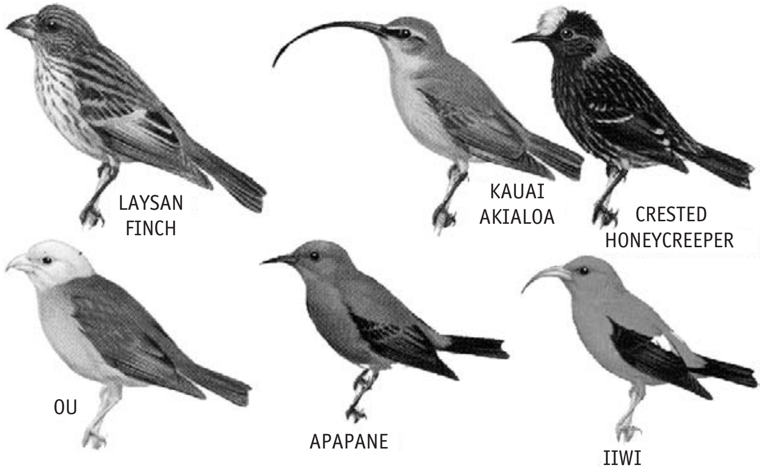


Figure 6.3 *Although they are very closely related, the species of Hawaiian honeycreepers exhibit very different morphologies as adaptations to distinct ecological niches, especially in the forms of their bills. (Plates from* A Field Guide to Western Birds, *2nd ed. © 1990 by Roger Tory Peterson. Reproduced by permission of Houghton Mifflin Company. All rights reserved.)*

the honeycreepers must have wandered to Hawaii. Finding few other birds competing for such foods as insects and nectar, they adapted to using these resources. The islands provided a particularly suitable stage for speciation, because as the founding colony multiplied, it spread out over the islands where small populations became isolated from one another. Starting with slightly different founder populations, and given isolation and time, these differences became accentuated. Thus, a colony on one island developed into seed-eaters while those on another island developed bills useful for eating insects. There is some reason to think that the founders were the red and black types that live primarily on nectar, that some of them evolved into the yellow-green insect-eaters, and that others developed later into the fruit-eaters.

The Hawaiian honeycreepers are another excellent example of opportunism. The founders were faced with many opportunities for making a living, and their descendants eventually evolved ways to take advantage of many of them. By means of genetic variations that conferred particular advantages, they seized the opportunities that arose for living in new ways.

adaptive radiation and genetic drift

The pattern of evolution in the honeycreepers is called an *adaptive radiation*, because one original population radiated out in several different biological directions (perhaps also different directions geographically) as its subpopulations took advantage of new opportunities. A general way of life to which a species can become adapted is called an *adaptive zone*. In the honeycreeper case, we may characterize insect-eating, nectar-eating, and fruit-eating as three general adaptive zones, with species in each zone specialized in their own particular niches. Given the right conditions, every species has the genetic potential to divide into more species, thus creating greater diversity. The term "adaptive radiation" is applied both to small episodes of evolution, as in the honeycreepers, and to large episodes, such as the divergence of the many basic types of birds or mammals. Thus, paleontologists speak of the adaptive radiation that happened during the Cambrian era to produce so many phyla of animals, or of an adaptive radiation in the Triassic era that produced so many types of reptiles, including the various lines of dinosaurs.

As species divide and radiate out into new adaptive zones, populations may be most likely to fail during transition times. But remember the point made in chapter five that even a small change in a structure can make an important difference in fitness. We must not imagine that one of the specialized bills of a contemporary honeycreeper was useless until it acquired its modern form, nor were plants inviable while their flowers were intermediate between the forms we now see. Still, a rapid transition would seem to be advantageous. To become a successful new species, a population might have to cross a nonadaptive zone or a zone already occupied. To use the niche-spotlight model again, a population initially shares a patch of light with its parent population. A short distance away are unoccupied patches in different adaptive zones, but to reach them it must cross a darker zone.

It may therefore be important that new species are frequently founded by small populations in which *genetic drift* may occur. Genetic drift might carry a population quickly from one patch to another. The genetic make-up of a small population can change much faster by drift than by selection, and possibly in directions different from those in which selective forces would lead it. Isolated subspecies (semispecies) could acquire different habitat and niche preferences through genetic drift, and these small populations may drift to genotypes that are quite different from the typical genotype of their parent population. A special case of genetic drift is the *founder effect*: an isolated semispecies is founded by a few individuals whose genotypes are quite untypical of the main population, so the new population begins with an unusual average genotype and evolves further from there.

plant evolution through hybridization and polyploidy

For reasons that are not yet understood, hybridization is an important mechanism in plant evolution, even though it apparently plays a much smaller role in the evolution of animals. Edgar Anderson has emphasized the importance in plant evolution of *introgression*, a process in which some genes of one species work their way into the genome of another through hybridization. The hybrids between two species generally are less viable and fertile than their parents, but the progeny made by repeated backcrossing to one parent are intermediate varieties, with only part of the genome from the other parent, and they may be quite hardy and well-adapted to existing conditions. Introgression results from this sequence of hybridization, backcrossing, and selection of certain backcross types, and it is an important source of new variability in plant species. It tends to reduce sympatric species back to semispecies status, and sometimes leads to the emergence of new types.

Introgression is prominent in some of the irises, or flags, which are so abundant and diverse in the lowlands of southern Louisiana. Around 1938, Herbert P. Riley found hybridization between the elegant blue *Iris giganticaerulea* and the brilliant orange *Iris fulva*. The two species are sympatric, but *I. giganticaerulea* is adapted to the waterlogged soil of marshes and *I. fulva* grows in the drier soil of banks and woods. The two only hybridize where the habitats have been broken down by human interference, and there Riley found a number of populations that show various degrees of hybridization, as measured by seven characteristics that mark one parental type or the other. Some populations appeared to be basically *giganticaerulea* with various amounts of the *fulva* genome resulting from continuous backcrossing.

New plant species may also develop more directly by the creation of *polyploid* individuals that have more than the usual diploid number of chromosomes. *Autopolyploidy* results from an abnormality in meiosis, resulting in diploid ($2n$) gametes instead of the usual haploid ($1n$) gametes. This sometimes happens in a plant that can pollinate itself. Self-fertilization, which is rare in animals, permits an unusual $3n$ (*triploid*) or $4n$ (*tetraploid*) zygote to be made, and the apparently greater plasticity of plant development allows many of these zygotes to grow into perfectly good, fertile plants. In fact, polyploids are generally larger than their parents and produce larger fruits; many of our domestic plants, which are cultivated for these features, are polyploids. Triploids are generally sterile because their three sets of chromosomes are unable to engage in the usual processes of meiosis and produce normal, viable gametes. (Triploids such as bananas are valued by humans because they have no large seeds. And, amazingly, aquaculturists have now been able to breed triploid oysters, which don't spoil their culinary value by making large egg masses.) In a tetraploid, the four homologous chromosomes generally seem to avoid irregularities, so such plants tend to be viable and fertile.

Polyploidy may also result from a breakdown of interspecies barriers. In *allopolyploidy*, two diploid sets come from different but closely related species. This may begin with haploid pollen from one species fertilizing haploid ova from another. The diploid hybrids are sterile because their chromosome sets are too different to form viable gametes, but the plants may reproduce vegetatively (asexually). Then later one of these plants may become tetraploid as in autopolyploidy. Allopolyploids may have some advantages in nature because they combine some characteristics of both parents. They may be superior because of *heterosis* or *hybrid vigor*: for various reasons, hybrids are often superior to both of their parents in strength of growth or in general vitality. Hybrids may be suited to a slightly different niche from that of their parent species.

It has been estimated that nearly half the speciation events in the evolution of flowering plants have involved polyploidy. One documented example is the salt-marsh grass *Spartina*. *S. maritima* ($2n = 60$) grows along European coastal marshes, while *S. alterniflora* ($2n = 62$) is found along the North American coast. The American species was accidentally introduced in Britain around 1800 C.E., and it started to grow in patches mixed with its European cousin. In about 1870, a sterile hybrid between them was identified and named *S. townsendii*. It is diploid and also has 62 chromosomes (indicating some minor chromosomal alteration from the expected number of 61), but can only reproduce asexually by extending rhizoids (runners). Then around 1890 one of these plants apparently changed into a fertile allotetraploid, named *S. anglica*, which has 122 chromosomes. *S. anglica* is a very vigorous grass that is now spreading around the coasts of Britain and France, replacing its parental species.

Modern bread wheat, *Triticum aestivum*, also arose through hybridization and allopolyploidy (Figure 6.4). Because of their distinctive forms, wheat chromosomes can be traced back to those of wild grasses, involving two episodes of hybridization followed by

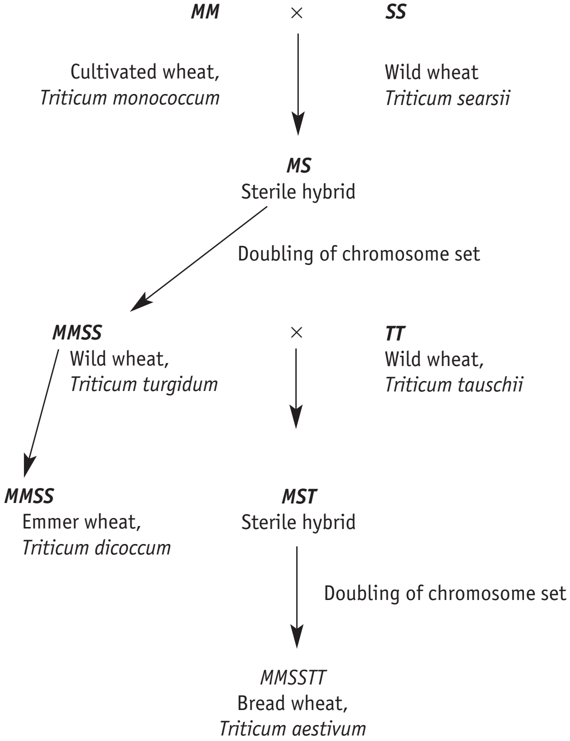


Figure 6.4 *Different species of wheat have arisen through a series of hybridizations followed by duplications of the whole chromosome set. Each of the large letters S, M, and T represents a set of 14 chromosomes characteristic of one initial species.*

duplication. The ancestral wheats have been preserved – einkorn wheat that is grown especially on poor soils in Europe and emmer wheat whose proteins make the excellent gluten needed for pasta.

These regimes of hybridization and selection can produce *sympatric speciation*, without the need for geographic isolation. New species might also arise sympatrically through strong selection for adaptations to different habitats. In Britain, a variant of the grass *Agrostis tenuis* is genetically lead-resistant and is able to live on soils contaminated by the lead-rich tailings of some mines. The original, lead-intolerant populations often grow only a few meters away on uncontaminated soil. Hybrids between the two types grow poorly on both types of soil, so the lead-resistant plants seem to constitute a new species that has arisen within the range of its parent species, perhaps because of only one or a few genetic changes.

In spite of its difficulties, the concept of a species as a group of organisms that can actually or potentially interbreed with one another seems most satisfactory. But from the viewpoint of humans who are eager to put organisms into neat boxes and give everything an unambiguous label, speciation may be messy. We must expect to find populations at intermediate stages. In general, geography seems to be the principal factor in dividing a species into new species, and speciation happens quite prominently in island groups, with their natural barriers to movement. Plants, however, commonly change through hybridization and related processes.

chapter seven

development and macroevolution

It is relatively easy to look at the differences in form of species undergoing speciation and see how those distinct species could arise. If the difference between, say, red-shafted and yellow-shafted flickers lies merely in the colors of pigments, just tweaking a gene or two could account for the distinction, and we can easily see how one gene complex could predominate in the east and the other in the west. The differences among the various Hawaiian honeycreepers are greater, of course, but we can easily accept the idea that some changes in genes for pigmentation combined with some for the length of the bill could account for these different species. But then we stand back and look at the whole animal kingdom, for instance. The obvious enormous difference between a roundworm and an insect, or between a jellyfish and a mammal, seem overwhelming. It doesn't seem to help to recognize that this evolution has occurred over about half a billion years. The great issue is not having enough time but, rather, the more fundamental questions: *How* could these enormous differences have developed? What are the mechanisms involved?

The question could not have been asked – let alone answered – in a satisfactory way until just a few years ago, because it depends upon recent progress in developmental biology and especially in developmental genetics. Every multicellular organism – plant, animal, fungus, or other – begins as a single cell, which then proliferates: it grows and divides into many cells, and this multicellular mass develops a specific shape and form. Along the way, its individual cells differentiate into a variety of more specialized cells; a complicated animal such as a mammal consists of at least a hundred different cell types, such as a variety of neurons in the nervous system, skin cells, heart muscle cells, liver cells, various kidney cells, and so on. Remarkably, each type of cell develops in the correct place. With very few rare and unfortunate exceptions, every newborn human, for instance, ends up with everything so placed that it looks like a normal human.

Evolution operates on the process of development. The change from a lobe-finned fish to a primitive amphibian involved (among other changes) small modifications of the bones in the fins, near the end of development, so they became more functional for movement beyond the water. All the evolution of complex organisms entails changes in growth to make slightly different structures. The remarkable advances of the past few decades in understanding these processes have provided some insights into their evolution in many distinct types of organisms.

As you read this chapter, please remember a point I have tried to make several times: nothing in evolution predestines success, and the existence of such a multitude of wonderful organisms, humans included, is just the result of a long series of lucky accidents. If early animals, during the first few million years of their evolution, had not hit upon certain valuable mechanisms and structures that provide enormous flexibility for future evolution, we just wouldn't have come into existence to sit here and ponder these matters.

being multicellular

The simple unicellular organisms that lived before about a billion years ago (and whose descendants we still find in our waters) differ fundamentally from the multicellular plants and animals that followed. Single cells are almost entirely at the mercy of their surroundings. They proliferate or perish according to accidental events that supply plenty of water or make a pond dry up; that supply the right amount of salt or too much; that supply organic nutrients or none at all. Unicellular organisms can regulate some movement of molecules across their cell membranes and partially control their internal conditions. Many unicells evolved mechanisms of motility – flagella, cilia, ameboid motion – so they can swim to more suitable environments, perhaps avoid droughts and search out sources of nutrition. Still, their resources for survival are limited.

A multicellular organism has potentially greater resources for survival in a hostile world. John Gerhart and Marc Kirschner have expressed this difference in the twin features of conditionality and contingency. Conditionality means that individual cells within the organism have the potential to control the conditions of their surroundings, since the entire organism is at least partially protected from its environment and from the random changes that can occur there. Contingency means the ability of cells to respond to particular conditions, both extracellular and intracellular, and thus to regulate themselves; in particular, cells have the potential to differentiate into specialized cells with specific functions. Unicellular organisms can often respond to environmental conditions by changing their physiology, even changing their forms, and these responses are subject to natural selection. Such changes within a multicellular organism give the organism as a whole much greater flexibility and potential for survival.

how to build an animal

The most obviously diverse creatures on Earth are animals. They originated sometime around a billion years ago, and (as outlined briefly in chapter three) diversified quite suddenly (in geological terms) around half a billion years ago. We now recognize about thirty distinct phyla, related generally as shown in Figure 7.1. For our purposes here, we will ignore the most primitive types (sponges, corals, anemones, and their relatives). We will try to understand how simple animals such as roundworms could have descendants as different as a fly and a mouse. Let us consider how animals are built.

A roundworm is basically a tube within a tube. The outer tube is its body wall, the inner tube an intestine running through the body from the mouth to the anus. This is a fundamental animal form, lost or modified in only a few phyla. It is made quite easily from the initial zygote. The zygote begins to divide into smaller cells: into two, then four, then eight, and so on until it becomes a small ball of cells. Then the cells on one side push inward, to start forming that inner tube; it is similar to pushing your fist into a very soft but strong balloon, and the hole your wrist lies in will be either the mouth or the anus, depending on the phylum. This indented ball will continue to elongate into a body, and eventually the hole at the other end of the intestine – anus or mouth – will break through. Although the

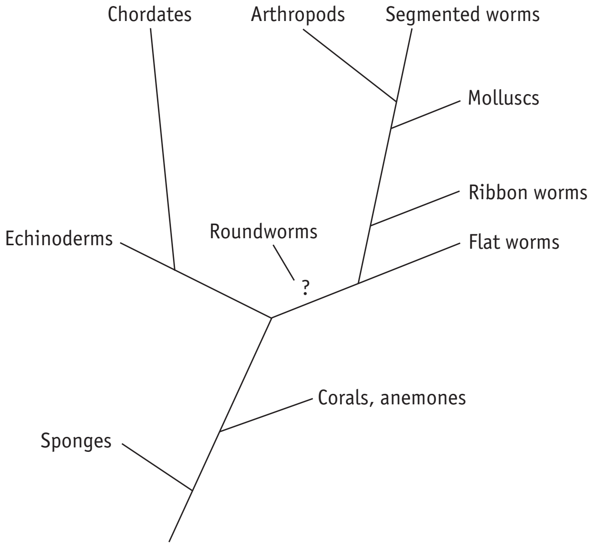


Figure 7.1 *A phylogenetic tree showing the relationships among the principal phyla of animals.*

details vary greatly, that is the fundamental way of making the basic animal form.

To be functional, the tube-in-a-tube must be modified for the typical animal way of life. Animals are predators, either on vegetation or on other animals. The animal way of life is to move around in search of food (and, incidentally, to avoid becoming food), requiring that one end, the head, must go first. The head becomes specialized for its function by acquiring sense organs (eyes, ears, receptors for taste and odor) to detect food and dangers, a mouth for ingesting the food (and perhaps chewing it up), and sometimes special appendages for grabbing the food and stuffing it into the mouth. The head also acquires some specialized nervous tissue (a brain of sorts) for processing signals from the sense organs and controlling the actions of the other parts. The process of acquiring such a specialized head end is called *cephalization.*

This animal needs two other structures, aside from its head. Although a concentration of nervous tissue in the head is important, this tissue has to serve the entire body, so a nerve cord is extended to the tail end. Also, the cells of the body need to be nourished with food and oxygen, while their wastes are removed. In the smallest animals, these exchanges can often take place through direct diffusion to and from the surroundings, but beyond that minimal size the animal needs a circulatory system, with tubes to carry blood to and from all the tissues and a heart to pump it. In the simplest animals, the blood may pick up its oxygen directly from the outside and deposit its wastes there, but the circulatory system generally acquires two appendage systems: a special place for gas exchange, such as gills, and a special place for excreting other wastes, such as kidneys (made of units called nephridia).

I don't mean to gloss over the animal's primary function from an evolutionary point of view – to reproduce itself. But that is a somewhat special business requiring that the reproductive (germ) cells be segregated off somewhere and that a simple device be made to help ensure fertilization.

Going beyond roundworms, the primary rule for making more complicated animals seems to be, "Start with identical segments." If a genome can be devised that instructs the formation of a functional piece of an animal, that piece can be repeated as many times as necessary to make the entire animal, of any length (Figure 7.2). (As an analogy, it is similar to the principle that enormous polymers such as proteins and nucleic acids are made by adding more and more similar or identical monomers.) The process is called *metamerization*, and the individual segments of the body are *metameres*. Our model is a humble earthworm, whose body consists almost entirely of very similar metameres.

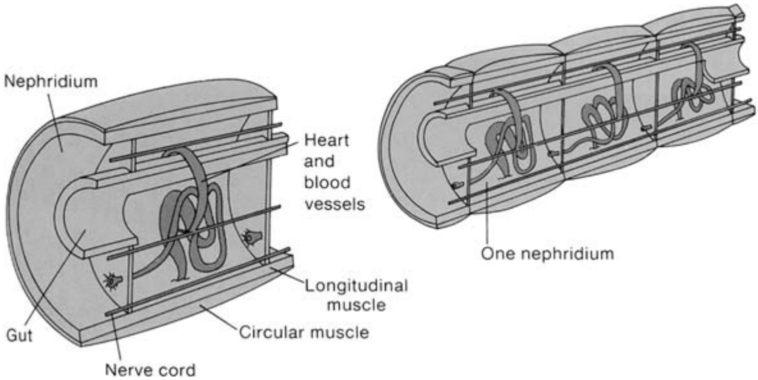


Figure 7.2 *A unit animal consists of a gut inside the body tube, with other organs such as a heart and segment of a nervous system. A whole basic animal can be made by repeating this segment several times.*

Given this basic formula for making a basic animal body, we have to consider how genes can produce it and, especially, how changes in those genes can produce functional animals of such diverse forms.

the idea of proteins that regulate genes

It has been obvious to biologists for a long time that every gene in a genome isn't expressed in every cell; "expressed" means that the gene is turned "on," so its protein product is produced. Although many genes (often called housekeeping genes) are expressed in all of the cells in the human body, each cell type is characterized by its particular proteins (which also give it a particular form). Thus, only red blood cells produce hemoglobin. Only muscle cells produce the proteins such as actin and myosin that form the tough muscle fibers, which pull on one another to produce muscle contraction. Each type of gland makes its distinctive hormones, and only specialized cells in the intestinal tract produce their particular digestive enzymes.

The story of discovering genes that regulate other genes is told in the *Genetics* book, but the general process is easily summarized. Expressing a gene means transcribing a messenger-RNA (mRNA) from it. Let me unpack that complicated sentence by reviewing some points from the section on nucleic acids in chapter three. The genes are DNA regions, located in the chromosomes in the nucleus (except in procaryotic cells, but the general principle applies to all cells). The factories where proteins are actually made are little particles called *ribosomes*, which occupy much of the cell's cytoplasm. The information is carried from the genes to the ribosomes by messengers, which happen to be distinctive RNA molecules. For a gene to be expressed, the enzyme *RNA polymerase* attaches to a region near the gene, a region called the *promoter*. RNA polymerase opens the DNA double helix and begins to move along one strand of the DNA, the so-called template strand, while it synthesizes an RNA molecule. The enzyme operates just as if it were replicating the DNA, except that it is producing RNA instead of a complementary strand of DNA. Nucleotide by nucleotide, it constructs an mRNA molecule with a sequence just complementary to that of the coding strand, and this process is called *transcription*; the resulting mRNA can then move out to the ribosomes, where its sequence is *translated* into protein molecules. Each protein is built sequentially, amino acid by amino acid, as the ribosomal mechanism reads the sequence of the mRNA.

A gene will not be expressed unless it is transcribed. Transcription can be regulated either negatively or positively, by means of other proteins. In bacteria, the regulation is often negative; a distinctive protein called a repressor binds on or near the promoter of a gene and prevents RNA polymerase from starting to act there. In eucaryotic cells, the regulation is more commonly positive: a distinctive protein, or more often a complex of several distinctive proteins, must bind to the promoter and initiate transcription. The exact method used isn't important here. The fact of there being gene-regulatory proteins is important.

Many regulatory proteins, called simply transcription factors, promote transcription by binding to promoters. But genes are also associated with regulatory regions called *enhancers*, and transcription factors may also bind to the enhancer of a gene to promote its transcription. In fact, some genes have several enhancers, and their transcription may be stimulated by various combinations of transcription factors binding to these enhancers. I mention these details only to show that there may be many ways for a gene to be turned on or off.

Every gene can easily have a distinctive promoter. Since every position can be occupied by 4 different nucleotides, there are over a million sequences of only 10 nucleotides, and using 20 nucleotides provides over 10^{12} possibilities. By means of their distinctive sequences, promoters – and thus genes – can be put into classes. So all the genes that encode specialized muscle proteins, for example, could be given a unique promoter sequence and then turned on by a unique regulatory protein that recognizes that sequence. A regulatory protein that selects certain genes to be turned on is naturally called a selector protein, and the gene that encodes it is a selector gene. We will see that the essential function of a selector gene is to confer *positional identity* on a cell; that is, selector genes tell each cell where it is in the body and therefore what it should eventually become. They say, in effect, "You lie in the middle of the thorax, and you are destined to become part of the heart."

Many selector genes have now been identified, especially in the fruit fly *Drosophila*. In general, genes are discovered and identified by means of mutations that happen to occur in them, and they are named by the characteristics of the mutants. Geneticists' senses of humor are revealed when they name new genes. For instance, a gene responsible for producing a distinctive #7 cell in the eye is called *sevenless* (*sev*); related genes found later were then named *seven-up* (*sup*), *son of sevenless* (*sos*) and *bride of sevenless* (*bos*). And you'll see some other funny names as we go along. By the way, gene names are always italicized; the names of proteins are in roman type and are commonly capitalized.

making heads, tails, and segments

The most important basic features of a typical animal are its cephalization and its metamerism. It is instructive to see how these features are created genetically in *Drosophila*, although the early development of fruit flies has some features that aren't shared by all animals. *Drosophila* eggs develop in an ovary surrounded by several nurse cells, which give it special properties well before fertilization; in most animals, the egg develops more by itself, and the head-tail axis is determined in other ways. Nevertheless, the nurse cells of *Drosophila* put two kinds of mRNA molecules into the egg: one at what will become the head end for the protein Bicoid and one at the tail end for the protein Nanos. When these mRNAs are translated, the embryo contains a gradient of Bicoid protein that is most concentrated at the head end, and a similar gradient of Nanos protein, most concentrated at the tail end. In this way, the cephalization of the embryo is determined, and the ground is laid for dividing the body into segments that will eventually take on distinct forms.

The first effect of the initial regulatory proteins is to turn on a series of *gap genes*, so called because mutations in these genes produce embryos with certain segments missing. Each of these genes, with names such as *hunchback, krüppel*, and *knirps*, identifies a region of the body, about ten regions in all. The protein products of these genes are all transcription factors, and their effect, in various combinations, will be to turn on a second set of genes, called *pair-rule* genes because the effect of a mutation in any of them is to delete either all the even-numbered or all the odd-numbered body segments. Some of the *Drosophila* pair-rule genes are *hairy, runt, even-skipped, odd-skipped*, and *fushi tarazu* (Japanese for "too few segments"). These genes lay down the basic metamerism of the body. Geneticists who study them can apply specific stains to the embryo fly to locate each type of pair-rule protein, and a stained embryo always shows a series of colored bands dividing the body

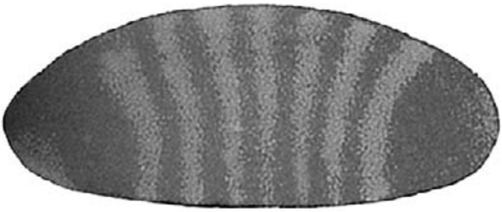


Figure 7.3 *A fruit fly embryo stained to reveal one distinctive protein involved in regulating development shows that the protein has been produced in a series of bands along the body.*

into its 14 characteristic segments (Figure 7.3). Finally, the products of the pair-rule genes activate a third set of genes, called segment-polarity genes, such as *wingless* and *engrailed*. Each body segment is divided into an anterior and a posterior half, which often have quite different structures. Each segment-polarity protein occurs in one half or the other, thus creating this division. Through a complicated logic of repression and activation of genes, this series of genes produces body segments identified by position and ready to differentiate into various structures. How does that happen?

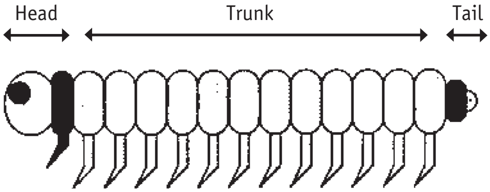
homeotic genes: producing the organs of the body

The homeotic genes were discovered through remarkable mutations that make the segments of the body very similar (*homeo-* = similar) or else substitute one structure for another; the *Antennapedia* mutation, for instance, creates legs on the head instead of antennae. As a class, they are now called Hox genes. Mutant insects lacking all the Hox genes have identical segments instead of distinct segments. *Drosophila* has eight Hox genes that determine the identities of the segments, in one cluster (*Antennapedia*) that determines head structures and another cluster (*Bithorax*) determining structures of the thorax and abdomen; remarkably, their sequence on the chromosome is identical to the sequence of their action from head to tail in the animal.

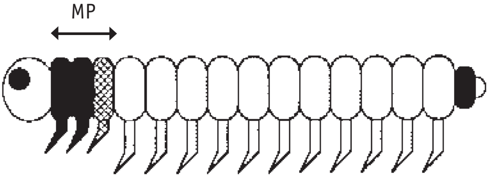
After the *Drosophila* Hox genes became known, investigators looked for similar genes in other animals. Roundworms have four of them. Mammals have four sets of Hox genes corresponding closely to the *Drosophila* set plus a few more, as if the basic set had been doubled twice: once when the first vertebrates evolved and again after the fishes had evolved. Again, the sequences of these genes on their chromosomes are identical to the sequence of their action from head to tail in the embryo.

These genes determine what specific structures will form at each point along the head-tail axis. In flies, for instance, the second thoracic segment bears a pair of wings and the third has only a pair of balancing organs, called halteres. In early experiments, Ed Lewis was able to make four-winged flies, with wings instead of halteres on the third segment, through a combination of mutations in the *Bithorax* complex. In vertebrates of all kinds, a fin or forelimb forms at the anterior boundary of the region where *Hox-c6* and *Hox-b8* are expressed. The Hox genes act as selector genes, determining in each region which other more specific genes will be turned on or off to create specific structures. The growth of a vertebrate limb, a fin or a leg, then entails complicated interactions among several genes expressed in different parts of the limb bud as it grows out of the body, and again some of these interactions involve specific Hox genes.

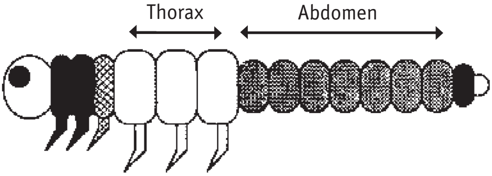
M. Akam and his colleagues have suggested how a series of duplications and diversifications of Hox genes among arthropods could account for one important line of evolution. Start with an ancestral arthropod having only three Hox genes that determine a head, several identical body segments, and a tail segment:



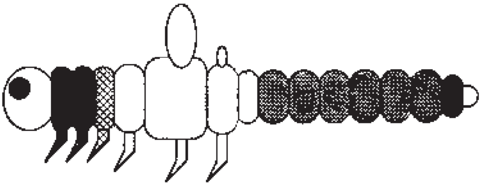
A duplication then produces a gene such as *scr* (*sex-combs reduced*), generating the maxillipeds (MP) of the myriapods (centipedes and millipedes):



Another duplication produces a gene such as *Abd* (*abdominal*), creating a primitive insect with a thorax and abdomen:



A further duplication can then produce a gene such as *AbdA* (*abdominal-A*), which directs the formation of wings, to generate a fly:



Such examples indicate how Hox genes, because of their fundamental roles in determining structure and their versatility, allow us some insights into how such a great variety of animals could have evolved. The origin of such genes in the most primitive animals seems to have opened a most fortunate series of opportunities for the later evolution of quite diverse forms.

As another example of this flexibility, the vertebrate body plan differs from that of typical invertebrates in the relative positions of major organ systems; in vertebrates, the nerve cord lies along the back (dorsal) but in arthropods and other invertebrates it runs along the belly (ventral). The two body plans are so similar that some classical zoologists debated the question of whether one type of animal could be turned into the other just by inverting one of them. In a sense, this is what has happened through interactions of the regulatory genes that determine the dorsal-ventral axis of the animal body, similar to those that determine the head-tail axis. Arthropods and vertebrates have parallel sets of genes and proteins. The *Drosophila* protein Decapentaplegic (Dpp) defines a dorsal compartment of the body and prevents the formation of nervous tissue there; in the ventral compartment of the body, the protein Sog (*short-gastrulation*) antagonizes Dpp and allows formation of the nerve cord. The vertebrate homologues of Dpp are BMP2 and BMP4, which are present in the ventral compartment of the embryo, where they block formation of nervous tissue. The vertebrate homologue of Sog is the protein chordin, which is produced in the dorsal region of the embryo, where it induces the formation of the nerve cord. So this regulatory regime has the intrinsic potential of producing quite different-looking animals by means of very similar chemical interactions.

flexibility and stability

It should be clear that evolution could not produce such a great variety of animals unless a certain flexibility were built into the operation of the genome. Mutations in regulatory genes must be able to change developmental processes to produce organisms with different forms, but the resulting changes must be viable – the resulting novel organisms must have at least some chance of survival. A common objection raised against the possibility that such complex systems could evolve is a crude analogy with a mechanism such as a watch; if you made some random change in the structure of a watch, it simply wouldn't work at all. So the actual processes of development must not be stubbornly watchlike. They must produce stable, functional structures but with a built-in flexibility.

One feature of development that creates such flexibility is compartmentalization. We have seen that the developing body is divided into distinct compartments, within which specific genes act to produce distinctive structures. Thus, the effects of many mutations will be limited to small compartments and the resulting animals will differ in small ways from their ancestors.

Another mechanism that provides potential flexibility is the combination of a single regulatory protein and its receptor. The image here may need sharpening: any molecule, which we generally call a *ligand*, might bind to a protein. The ligand might even be another protein. The binding of some ligand may then change the protein's shape so as to change its function. For instance, many enzymes have a specific binding site where some small molecule may bind to them; the enzyme alone may be active but becomes inactive when the ligand is bound, and the ligand then functions as a regulatory inhibitor. Or the regulation may work the opposite way: the enzyme might only be active when a specific ligand is bound to it, so the ligand becomes an activator. Proteins called *receptors* have the function of receiving and responding to signals. Some important receptors in animals are exposed on cell surfaces, and the ligand that binds to them may be a hormone. If a specific event stimulates a gland to release its hormone into the blood, the hormone is carried to some remote cells that bear receptors for the hormone, and the binding of the hormone to its receptor initiates some process, which stimulates the cell into a specific action.

By the way, the gene-regulatory proteins we have been discussing bind similarly, but here the "ligand" is generally a specific site on DNA and the function of the protein is to change the DNA temporarily.

Among the most important systems in this regard are enzymes called *protein kinases.* A kinase is an enzyme that can attach a phosphate ($-PO_4$) to some other molecule, and a protein kinase is one that attaches the phosphate to a specific protein. The remarkable finding is that merely attaching a simple phosphate to a protein can change its properties so drastically that it shifts from inactivity to activity (or vice versa), and it has become clear now that a great deal of cellular regulation occurs by means of protein kinases. Some regulation occurs through chains of reactions, called *cascades*, in which enzyme 1 becomes activated, perhaps by a hormone, and attaches a phosphate to enzyme 2, which then becomes activated and activates enzyme 3, and so on. Cascades are biological amplifiers, because at each stage of activation, more and more molecules are activated, producing a large final effect.

Studies of development have revealed several pairs (or trios, or more) of proteins that act as ligand and receptor. In *Drosophila*, for instance, the Hedgehog protein interacts with a receptor protein called Patched and also with protein kinase A. Each of these combinations of interacting proteins is a *regulatory module*, and such modules may be employed in several different developmental processes in a single animal. Modules afford the animal both stability and flexibility. Operating as a single regulatory unit, the module is stable. But it also provides the potential for novelty; for instance, a regulatory mutation might change the time or place for expression of the module, opening up new developmental possibilities. Remember, too, that novelty is commonly introduced through gene duplication and diversification. Genes for some of the important modules appear to have been duplicated several times, producing whole families of similar regulatory proteins with specialized roles.

Regulatory modules are used commonly in pairs to provide a kind of stability (Figure 7.4). For instance, cell 1 produces protein A

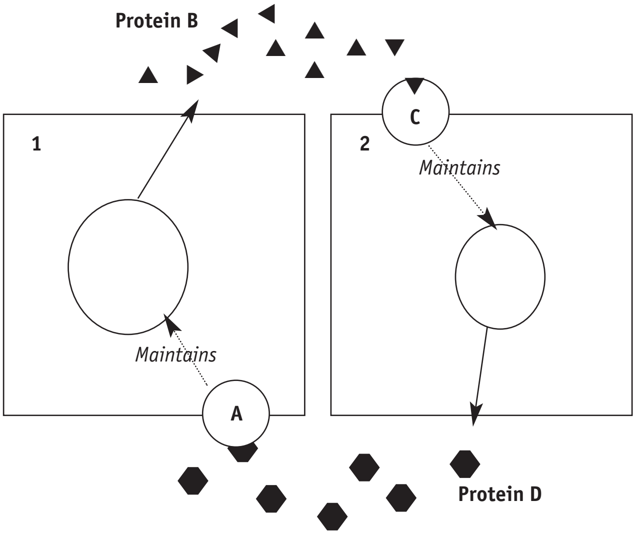


Figure 7.4 *Regulatory modules may be used to maintain two cell types in a stable condition where each cell produces a receptor for a protein produced by the other cell.*

and secretes protein B; cell 2 produces protein C and secretes protein D. But A is a receptor for D, and C is a receptor for B, and binding of a receptor to its ligand stimulates the cell to maintain its condition. So the two cell types maintain one another through their interaction. In other instances, module X activates module Y which in turn activates X, producing a wave of differentiation that may pass through a structure, as in development of the fruit fly eye.

Flexibility is also built into regulation by means of redundancy and overlapping mechanisms. If a process is controlled by two or more mechanisms, which duplicate one another in part, then removing one mechanism through mutation may have little final effect; but – like the opportunism provided through gene duplication and diversification – if one mechanism is changed, it has the opportunity to evolve in a useful direction while the unchanged mechanism continues to serve its original function.

The actual processes involved in growth and regulation are far more complicated than I have been able to show here. (The book by Gerhart and Kirschner, cited earlier, will provide some insight into their complexity.) As developmental biologists elucidate these processes, they make it easier for us to understand how such a wonderful variety of organisms has evolved in the past few billion years.

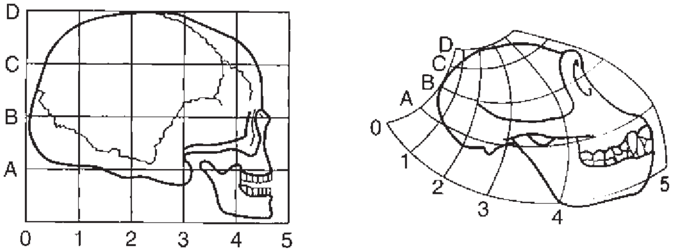
the secret is in the timing

In addition to all the genetic mechanisms outlined above, one general process allows us to explain a great deal of evolution: the timing of events. Development obviously takes time. A human infant develops for nine months before it is even born, and it then takes approximately twenty years more for a child to achieve full adult size and form. (And the changes that continue to occur – well, we won't dwell on those!) Every event in development begins at a set time and continues for a set time, and a great deal of evolution can be accounted for by means of changes in this timing. For a popularly written, comprehensive exposition of the subject, the book by Kenneth McNamara is recommended.

What is the difference between a tall and a short person? It is primarily in the lengths of the limbs, especially the long bones of the legs. These bones begin to grow early in embryonic development, and throughout childhood they elongate as new tissue is laid down at growth points near the ends of the bones. The genes that determine the timing of these events can shut off growth early or late, producing people of different heights. Now consider the neck of the giraffe. All mammals have seven cervical (neck) vertebrae, and giraffes are no exception. Giraffes do not differ in having more vertebrae but in having much longer vertebrae, bones that were allowed to grow considerably in length before their growth was terminated.

Many anatomical features can be accounted for through extension of this idea. The biologist D'Arcy Thompson pointed this out years ago by showing how one can lay a grid over a drawing of one animal and then, by systematically shifting the grid, convert it into a drawing of a different, but easily recognizable animal (Figure 7.5). Thompson showed that in this way he could account for the forms of related species of fish, for instance, merely by assuming that growth in one species had changed in a simple, systematic way. Here, then, is another general factor for evolutionary forces to "play" with. As this line of inquiry in development grows over the next few years, we can expect to learn how significant changes in form can be made merely by letting a structure grow for a longer or shorter time.

Developmental biologists are just now revealing the intricate genetic mechanisms that regulate the growth of a fertilized ovum into a mature organism. Already, though, we can see many points at



Human skull

Chimpanzee skull

Figure 7.5 *A rectangular grid is drawn over one anatomical drawing and then transformed. The process shows how the skull of a modern human can be derived from that of an earlier primate simply through regular changes in the growth of each region, by relatively greater growth toward the back of the skull.*

which organisms with distinctive forms can be made by mutation or by the production of a new gene through duplication and diversification. Readers who are ready for a challenge may plunge into the intricacies of the matter through some of the books cited in the list of further reading.

chapter eight

human evolution

Victorians who were shocked by Darwin's ideas might have been willing to accept them if only they did not apply to us. As one well-born lady is reported to have said, "Descended from the apes! My dear, we will hope it is not true. But if it is, let us pray that it may not become generally known!" Contradicting the Bible was bad enough, but implying that God's noblest and finest creation, the human being (or at least the well-born male European human being), was not created specially and lovingly as the centerpiece of his Universe, well, it was just ... just too much.

The fact, however, is that *Homo sapiens* is a mammal and a primate, a member of the Class Mammalia and the order Primates that includes the monkeys, apes, and their kin. Desmond Morris called us the "naked ape." We share over 98 per cent of our DNA sequences with chimpanzees, who are clearly our closest living relatives. And although no fossil record is ever quite as complete as a paleontologist might wish, we have quite an extensive fossil record showing how the evolution of certain primates over the past ten million years or so produced humans. This record resides in many precious skeletons and fragments of tooth and bone in museums around the world. The forces of evolution that operate on other kinds of organisms have shaped humanity just as inexorably, and they continue to do so today, however slowly.

To understand humans and human evolution, we need to stand back and take a historical and ecological look at ourselves. An animal's structures say something important about the kind of life it is fitted for; we are not primarily fitted for swinging bats and tennis racquets, poking computers, and driving little vehicles around city streets. We will understand human anatomy and physiology in the light of our ancestors' lives.

primates

Writing about the order Primates, the British anthropologist W. E. Le Gros Clark noted that:

> It is peculiarly difficult to give a satisfying definition of the Primates, since there is no single distinguishing feature which characterizes all the members of the group. While many other mammalian Orders can be defined by conspicuous specializations of a positive kind which readily mark them off from one another, the Primates as a whole have preserved rather a generalized anatomy and, if anything, are to be distinguished from other Orders rather by a negative feature – their *lack* of specialization.

The earliest mammals were quite restricted ecologically, while terrestrial niches were so strongly occupied by reptiles. Le Gros Clark considered that early mammals were probably already adapted to an arboreal (tree-dwelling) life and that primates have retained and emphasized adaptations for this niche, while other orders have taken up various ways of life on the ground, or flying or swimming. Many mammals have highly specialized extremities; hoofed mammals are superbly adapted for running, but they can do little else with their hooves. The marvelous flippers and fins of aquatic mammals, like whales and seals, make them excellent swimmers, but they lead a restricted aquatic life. But for their generally arboreal ways, primates have remained quite generalized mammals. They are characteristically frugivorous (fruit-eating) or omnivorous and are best adapted for living on leaves and fruits among the small branches at the extremities of trees, where their major competitors are bats and frugivorous birds. Later, a few species, such as humans, became adapted to life on the ground.

For their arboreal and largely omnivorous life, primates have evolved several critical features.

arms and hands

The primate hand retains basic mammalian features but has an *opposable thumb*, which moves more freely than the other digits and can be pressed against the fingers to make a fine grasping tool. (Most primates also have an opposable big toe.) All primates can use their hands in a *power grip* for climbing and grasping tree branches – the grip you use to hold a hammer; later-evolved primates, such as apes and humans, also have a more delicate *precision grip* for manipulating small objects – the grip you use to hold tweezers. Chimpanzees and humans use their precision grip to make and use tools; it is a key factor in cultural evolution. Primates also have flat nails instead of the claws of ancestral mammals. This leaves a bare, protected working surface at the ends of the digits, a surface rich in nerve endings that make it very sensitive and contributes to manual dexterity.

Primates typically have very long arms, useful for reaching to the extremities of trees to grasp fruit – another use for an opposable thumb. The primate arm also rotates very freely. With a flip of the wrist, primates, especially humans, can rotate the hand at least 180° relative to the upper arm, while also rotating the upper arm bone (humerus) in the shoulder socket. Just watch a gibbon swinging from the bars in a zoo or a child on a jungle gym, and you'll see the value of these features for a tree dweller.

teeth and jaws

Much of the story of mammalian evolution can be told through teeth. A paleontologist searching for our ancestors has the advantage that jawbones and teeth are among the most common finds in fossil beds, and they show diagnostic dental patterns and other features of hominoid evolution.

We mammals have four types of teeth: *incisors* in the front of the jaw that are specialized for cutting; *canines* just behind them, which are generally sharp tearing instruments; and then *premolars* and *molars* behind, which often have large surfaces for crushing and grinding, but may become specialized for cutting in the more carnivorous mammals. Anatomists describe the dental pattern of a mammal with a set of four numbers, the number of each type of tooth in order for half of the upper jaw, over another four for half of the lower jaw. (The left and right halves are identical, of course.) The generalized mammalian formula is 3.1.4.3/3.1.4.3. Early in primate evolution, the incisors were reduced from three to two in each jaw. New World monkeys have the pattern 2.1.3.3, as did the oldest primates; the formula of Old World monkeys, apes, and humans is 2.1.2.3. Primate premolars and molars have retained their forms for crushing and grinding, although some of the premolars have been lost. On the whole, primate dentition remains quite unspecialized, as befits their omnivorous eating habits.

In differentiating humans from their apelike ancestors and relatives, the structures of teeth and jaws become critical. The jaws of apes are U-shaped, with parallel sides containing the canines, premolars, and molars, connected by a rounded front bearing the incisors; in strong contrast, humans have parabolic jaws, wider at the hinge than at the chin, in which all the teeth lie on a gentle curve (Figure 8.1). The canines of apes, particularly upper canines, are large and pointed; human canines are quite small. When apes' jaws are closed, the large upper canines overlap the lower teeth, accommodated by small gaps in the lower tooth row. This locks the jaw for holding prey but does not allow a sideways movement useful for grinding vegetation. The modern apes also have a distinctive *simian shelf*, a plate of bone across the lower jaw in the region of the canines. A feature that becomes interesting in examining the fossils of young animals is a difference in times of eruption: the canines of apes only erupt after the second molar does, while human canines erupt before the second molar.

The structures of molars and premolars are especially complex. Their biting surfaces have small cusps or cones. A generalized mammalian molar has five cusps. The ape lower premolar has one large cusp, but in humans it has become a bicuspid tooth with two. The

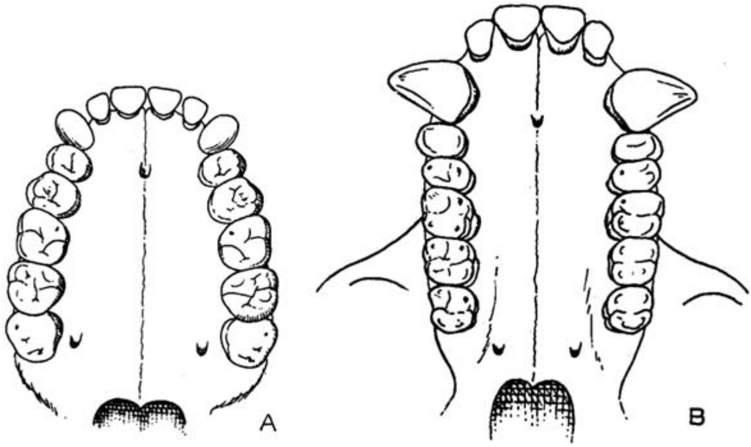


Figure 8.1 *The palate and upper teeth of a primitive hominid (an australopithecine), left, compared with that of a gorilla, right.*

molars of apes are generally high, and they do not wear down, but human molars generally wear down to an even grinding surface. Also, the early ancestors of apes had only four molar cusps; a fifth cusp evolved later.

vision

Primate vision is one of the strongest adaptations for an arboreal life. Think of the challenges facing an animal that has to move quickly through a maze of limbs and branches, deciding instantly where to grab a handhold, how to swing Tarzanlike from a branch here to a limb there. Such an animal needs stereoscopic vision and depth perception, which is achieved by locating the eyes on the front of the head where they can focus on the same object from slightly different angles. (Horses and mice, with their eyes directed to the side, have little or no depth perception; it isn't essential for their ways of life.) In addition to the light-receptors called rods, the retina of a primate's eyes have cells called cones for color vision and greater visual acuity, with a *fovea*, a central area about a millimeter square in humans, that is the point of clearest vision. The fovea contains only cones, not rods, and the lens of the eye focuses an image directly on it. Moreover, the other cellular layers that normally lie over the retina are displaced to the side in the fovea so light striking there doesn't have to pass through them. Portions of the primate brain that process the high-resolution information coming from the eyes are enlarged, as are other areas that control the sensitive hands and process the information coming from them. The sense of smell (olfaction) is less useful to primates, however, and their olfactory brain centers are diminished.

posture and bipedalism

A major trend in primate evolution has been toward more upright posture. Even monkeys sit in upright, human postures, and all higher primates hold their heads high, presumably a general adaptation for getting a better view of their surroundings. Upright posture not only affords a wider range of vision but also is a prerequisite for bipedalism – walking on two legs – which frees the sensitive and dexterous front limbs for carrying things, such as tools and babies. Because bipedalism is such an important and uniquely human trait, we will return to questions about it later.

large brains

Intelligence in mammals is correlated with the ratio of brain mass to body mass, and primates on the whole are big-brained. The increase in brain mass becomes most obvious in the evolution of humans, but all primates have relatively large brains, probably to process all the information needed to move through the trees with such agility.

Finally, primates have fewer offspring than do many other mammals, and their young are dependent on the parents longer. Some of the arguments about the evolution of bipedalism relate it to juvenile development. A relatively long, intense period of adult – child interaction is essential for the evolution of culture as a way to transmit survival skills, a practice that is most strongly developed in humans, who transmit culture via language throughout an extensive childhood.

anthropoids and apes

The order Primates is divided into two suborders:[1] Prosimii includes the little tarsiers and lemurs, and Anthropoidea includes the simians: monkeys, apes, and humans. In his huge, brilliant study *The Life of Vertebrates*, J. Z. Young commented,

> The outstanding characteristic of the anthropoids might be said to be their liveliness and exploratory activity, coming perhaps originally from life in the tree-tops necessitating continual use of eye, brain, and limbs. With this is associated the development of an elaborate social life, based not, as in most mammals, on smell, but on sight.

The anthropoids include separate families of Old-World and New-World monkeys, and a superfamily Hominoidea that includes the families Hylobatidae, the gibbons; Pongidae, the orangutan, gorilla, and chimpanzee; and the human family, Hominidae. (So "hominid" means a member of the Hominidae and "hominoid" is a broader term encompassing the whole superfamily.) We and the pongids share ancestors that lived about 20–10 Myr ago. From these common ancestors, one line of evolution led to several extinct species of prehumans; only a single species of modern humans, *Homo sapiens*, has survived.

Anthropoid apes are distinguished from monkeys by having a short tail or none at all, by distinctive tooth structure, and by a somewhat more upright posture than monkeys. Apes commonly move through the forest by *brachiation*, swinging from branch to branch with their arms overhead, a movement made possible by their long arms with extremely mobile swivel joints. Brachiation has resulted in a reduction in size of the hind limbs and somewhat reduced thumbs on the hands, so that the hand becomes less a grasping instrument and more like a hook that can be slapped over a limb and then released quickly.

The largest apes, however, spend much of their time on the ground. They are clumsy walkers, since the form of the ape pelvis requires them to swing the leg outward to move forward and gives them a crouching, bent-over posture. The hominid pelvis, in contrast, provides full upright posture and permits a bipedal gait – that is, walking erect on two legs. But apes do walk. Chimpanzees and gorillas get around by *knuckle-walking*, putting some weight on the knuckles of their hands from time to time, and this posture allows them to run while carrying things in their hands.

early anthropoid evolution

The geological time-scale for charting hominoid evolution begins in late-Oligocene time, before 24 Myr ago, and continues through the Miocene period from 24 to 6 Myr ago. The Pliocene era extends from 6 to 2 Myr ago, at which time the Pleistocene era starts. The end of the Pleistocene is placed somewhat arbitrarily at 10,000 years ago.

The Fayum beds of Egypt have yielded some remarkable simian fossils of Oligocene age, around 38 Myr ago, including the bones of *Parapithecus* and *Apidium*. These were generalized anthropoids, about the size of a small monkey, with three premolars like more basal primates and New World monkeys. Somewhat larger apes from the later Oligocene, named *Propliopithecus*, were about the size of a modern gibbon and had teeth similar to those of a gibbon, with the 2.1.2.3 dental pattern. They also had certain other dental features that make them appear quite hominoidlike: lower molars with the five cusps of hominoids and incisors set vertically rather than jutting forward. *Aegyptopithecus zeuxis*, very likely an early hominoid, had teeth very much like those of a modern ape, with large molars increasing in size from front to back, elongated front premolars, and large canines. Living in typical arboreal ways in tropical forests, these

Oligocene primates were probably frugivorous or omnivorous. The infamous "coming down out of the trees," which popular thought associates with human evolution, was several million years off. However, the animals that came down out of the trees were not humans but the ancestors of a large part of the hominoid branch.

As the Miocene climate grew cooler and drier, tropical forests in Africa and Asia gave way to subtropical forests and to extensive steppes (large grassy plains) and savannas (plains with scattered trees). The first horses appeared that were adapted for grazing in grasslands rather than browsing leaves. In early-Miocene times, some hominoids also moved into a new adaptive zone, living on the ground in the grasslands, out of competition with arboreal primates, replacing (or supplementing) their diet of fruit and leaves with tough foods such as nuts and roots. (Modern chimpanzees, though basically tropical forest animals, have a similarly varied diet, and some are as omnivorous as humans.) These were the *dryopithecine apes*, *Dryopithecus* and its relatives, whose fossils have been found over a vast area from southern Europe through East Africa, India, and China. Dryopithecines were generalized apes ranging in size from a small gibbon to a large modern ape. Though lacking the huge, protruding canines of later simians, they had strong jaws with more heavily enameled teeth, attached to the skull so as to permit the rotary grinding motion – instead of chomping – useful in chewing tough foods such as roots. The dryopithecines on the whole present a difficult complex of features. David Pilbeam has divided them into two groups: the dryopithecids, whose dentition and other anatomical features suggests their ancestry to various great apes, and the ramapithecids, whose dentition suggests they might have been hominid ancestors. In spite of their food habits, the teeth of some ramapithecines show less wear than do those of *Dryopithecus* and modern apes, suggesting that their permanent teeth emerged later, as in modern humans, and implying a longer period of development. The lack of wear also suggests that they used their hands a great deal, rather than tearing all their food with their teeth, and thus the beginnings of a more upright posture.

These Miocene ape fossils extend from about 20 to 10 Myr ago. The first definitive hominids, dating to about 6 Myr ago, walked fully upright. During that period of about 4 Myr, still largely dark to us, transitional hominids were acquiring bipedalism and other features of later australopithecines. A few fragmental fossils from this period are starting to emerge.

australopithecines, the "southern ape-men"

In 1924, the skull of a hominid child was discovered in a limestone quarry at Taung, South Africa. The anatomist Raymond Dart immediately recognized it as something special and named it a new species, *Australopithecus africanus* ("southern ape man from Africa"); he noted that the skull had many of the features of a bipedal hominid: the rounded shape, relatively large cranial capacity for its overall size, shape of the jaw, and position of the foramen magnum, the large opening at the base of the skull where it attaches to the spine. During hominid evolution, the foramen magnum has moved forward to a more central position, so the skull rests with better balance on the vertebral column as the animal sits or stands upright.

The many australopithecine fossils discovered since clearly reveal hominids with protruding jaws and heavy brow ridges. Comparing the skulls of a typical australopithecine and even a semimodern human of the genus *Homo* will show how different they must have looked and how paleoanthropologists can distinguish skulls, even skull fragments, of the two genera. Don't think of australopithecines as looking like primitive – perhaps rather hairy – humans. They still had the long, sloping faces of apes: broad across the eyes, but narrowing to jaws that we might even call muzzles. Their skulls contrast sharply with *Homo* skulls, which have a generally flat, vertical face with a protruding nose, like modern people. It is more accurate anatomically to think of them as erect, bipedal apes, not humans. (Several recent books about human evolution have excellent drawings of the various hominids, but those in Colin Tudge's *The Variety of Life* convey a striking sense of the changes in our ancestors and cousins.)

During the 1970s, Donald Johanson and his associates unearthed an extensive series of australopithecine fossils, 3.8–3.0 Myr old, in the Afar Triangle of eastern Africa, including the now-famous skeleton of a young female that they named Lucy. Johanson and Timothy D. White established a new species, *Australopithecus afarensis*, to include these fossils and specimens that had been found to the south, at Laetoli, by Mary Leakey. When first described, *A. afarensis* was remarkable because it showed clearly that hominids were bipedal and stood fully upright almost four Myr ago, even though their brains were still small (about 400–500 ml). They were probably no taller than 1.2 m and weighed 25–30 kg. Their jaws and teeth were similar to ours, except for their larger, sturdier molars, and the hinge between jawbone and skull permitted the rotary chewing motion that had begun with the dryopithecines. Evidence from the pattern of dental wear and from animal bones associated with their bones indicates they were omnivores and may have eaten some meat, as modern apes do. The rest of the australopithecine skeleton shows adaptations for bipedalism. Their arms may have been somewhat less mobile than ours, but their ankle bones – intermediate between human and typical ape forms – seem suited for bearing weight in bipedal walking. The general structure of their thighs and hips seems well adapted for erect standing, walking, and running, but also for an arboreal life of climbing by grasping trunks and large branches. Their pelvic structure may be an exaptation, which evolved initially as an adaptation for climbing trees and was just incidentally suited to bipedalism. Australopithecines probably divided their time between the ground and trees, perhaps sleeping in trees at night as modern chimpanzees do. Like chimps, they probably lived in small groups – extended families perhaps – of a few dozen individuals.

A. afarensis undercut the formerly popular view that large brains evolved along with erect posture, based on the idea that bipedalism evolved to free the hands for tool use, which would require a larger brain. But bipedalism clearly evolved in hominids with rather small brains. Modern human brains range from about 1200 to 1800 ml, with an average of about 1400 ml. This large organ supports all the complex activities that humans engage in, and its development from the australopithecine brain was a major feature of hominid evolution. Australopithecines had brains of about the same size as a modern gorilla's brain, but remember that intelligence is correlated with the ratio of brain size to body size, and the gorilla is a much larger animal.

As more evidence that the australopithecines were bipedal, a team led by Mary Leakey described a series of footprints in volcanic ash at Laetoli apparently made by a male and a female of this species walking side by side about 3.7 Myr ago. These tracks are particularly poignant, as they capture for posterity two of our ancestors, probably a mated pair, engaged in a simple activity that men and women still share today. So while they lacked the appearance of humans, in behavior and perhaps in their mental life they may have been very human.

A. afarensis was apparently ancestral to at least two distinct australopithecines that coexisted between about 3 and 1.5 Myr ago, along with some early representatives of *Homo*. But just how many species there were is a matter of controversy. Paleoanthropologists studying these fossils have tended to be "splitters" rather than "lumpers"[2] and to assign more distinct species names – and even generic names – to their subjects than other paleontologists do; the several distinct "species" may or may not deserve the names. Some dated between about 3 and 2 Myr ago are known as "gracile" australopithecines, in contrast to "robust" forms that appeared later. The gracile fossils have been named *A. africanus* and *A. aethiopicus*, the latter sometimes assigned to a genus *Paranthropus*. *A. africanus* appears to have been very similar to *A. afarensis*, although perhaps a little taller and with less sexual dimorphism. Robert Broom and Louis and Mary Leakey later described robust forms – designated *A. robustus* and *A. boisei*, but sometimes assigned to *Paranthropus* – whose fossils are dated between about 2.3 and 1.5 Myr ago. They were taller (up to 1.5 meters), had more massive teeth, and were probably vegetarians.

In 1995, Alan Walker and Maeve Leakey found fossils dating from 4.2 Myr ago, which they described as a new species, *Australopithecus anamensis*. These were small hominids; they had jaws of the typical U-shaped ape form but had more humanlike teeth with thicker enamel. Perhaps most significantly, their tibias show the features associated with bipedalism. In 1992, White discovered fossils dated 4.4 Myr ago that pushed the hominid line back still farther. He gave the species defined by these fossils the name *Ardipithecus ramidus*, deeming it worthy of status as a separate genus, and bones assigned to the same genus have been found in strata back to 5.8 Myr ago, virtually to the point sometime between 10 and 5 Myr ago where the hominid and ape clades diverged. *Ardipithecus* was described as "the most apelike hominid ancestor known." (However, some anthropologists are skeptical of its status as a hominid.) Although fossils aren't yet available that would show whether *Ardipithecus* walked upright, the jaw and arm fragments are clearly those of a very early hominid that retains many features of a typical ape. The thin enamel covering on its teeth, for instance, suggests a diet like that of modern chimpanzees. Although no anthropologist talks seriously about "the missing link," some were willing to say, jokingly, that *A. ramidus* comes about as close as one could wish to being such a link.

why did our ancestors stand upright?

I said that the discovery of *A. afarensis* put to rest a previously popular view that bipedalism evolved along with large brains as the use of tools, made possible by that brain, required the hands to be free. It is clear that quite small-brained hominids were fully bipedal. Then the mystery remains: why did they stand up on two legs?

In his book *Lucy*, Donald Johanson presents quite an extended argument from C. Owen Lovejoy to explain the origin of bipedalism. You might want to consult it, for its detailed, illustrated explanation, but I want to examine it here, too. The argument contains an interesting point about the idea of causality in science. If you stroke a cue ball against another billiard ball so it takes a predictable path and drops into a pocket, it is easy to talk about the motion of your cue stick and the cue ball being causes of the motion of the other ball. But an animal is a complicated critter with many structures and features; it interacts with its environment in complicated ways, and the course of its evolution must be determined by many intertwined factors and forces. So in evolution it is difficult, and probably simplistic, to pick out single factors and say, "This is the cause of that." Rather, a complex of several features evolve together to meet certain ecological requirements and to shape a species for a certain ecological niche and way of life. In spite of the following argument about reproductive strategies, another possible explanation for the advantage of bipedalism is that it provided better heat balance under the hot tropical sun. And perhaps other factors were important, too.

Organisms exhibit two general strategies of reproduction. One is to produce enormous numbers of potential offspring, even though only a few will actually survive; the other is to produce only a few offspring and invest much time and energy in protecting and nourishing them. Primates clearly use the second method. Each female produces only one or a very few young at one time and spends a long time nurturing them to independence and maturity. Hominids were pushed toward this method by the evolution of larger brains, which required infants to be born early, before their brains and skulls had grown too large for the birth canal; such very immature young require a longer period of development overseen by their parents. Now, Lovejoy sees this way of reproduction as a potential ecological trap: that the survival of a species is tenuous if it reproduces itself so slowly because parents can raise few offspring at a time. However, the primate way of life could have changed to improve the chances for survival. One way would be to enhance a mother's ability to nourish her infant without leaving it exposed to predators. A female ape cannot carry her young around with her very well as she forages for food in the trees; its hands are growing into good devices for brachiating through the trees but are not well adapted for holding on to her body. So if she is to forage for food, she must leave it alone on the ground for a while, where a predator could easily grab it. There are at least two ways around this dilemma. One is for the species to develop a much stronger social structure, so individuals share food with one another and so the infant can be left in the care of other members of the troop – female relatives, perhaps – while the mother is out gathering food. Another is for males and females to become increasingly bonded to one another, to form the sort of strong pair bonds that characterize human relationships, so the father has reason to bring food to the mother and infant.

Another way to enhance a species's survival is to increase its rate of reproduction, and this can be done by changing the strictly sequential way of primate reproduction to an overlapping way. Primate females have estrus cycles, so they are only fertile and receptive to mating for limited times each year. To reproduce, such a female must be impregnated by a male during this critical time; she then carries the baby to term and nurtures it for a time after birth. And during that time, she is infertile and not receptive to mating. Only after she weans her newborn does her estrus cycle start again, so she can conceive again. If this is a kind of reproductive trap, one way out is to gradually extend her fertile period until she is fertile much of the time – in other words, to transform the restrictive estrus cycle into the human menstrual cycle, which makes a woman potentially fertile most of the time.

The change to the human type of reproductive cycle means that a female is receptive to mating during almost the entire year, except perhaps during her menses. This has the particular advantage of promoting pair-bonding between one male and one female; the pair-bond develops and is maintained by frequent copulation combined with the male giving his mate gifts of food. This complex of behavior patterns is common in many species of birds and mammals, and it is sensible to postulate its evolution in hominids, too.

The picture that emerges from these considerations is one of females having more than one infant to nurture at a time, as human mothers commonly do, and thus needing to use her hands to hold them and care for them; and at the same time, for males having a need to use their hands to carry food to their mates and offspring. This provides a reason for the evolution of an increasingly upright posture with bipedal movement and freeing of the hands.

the first members of *Homo*

From somewhere in the sea of australopithecines, the earliest members of the genus *Homo* emerged between about 2 and 1.5 Myr ago. Although the situation is somewhat confused at present, the skeletal remains of these hominids are often associated with tools.

People make things. It may be our most significant non-anatomical feature. We are not the only tool-making species; one of Jane Goodall's most interesting discoveries was that chimpanzees fashion simple tools, such as probing sticks with which they fish for termites. Now and then, a bird is observed to use rocks or other objects in a tool-like manner, but these are rare. No other species makes tools so consistently or of such complexity as we do. As we begin to talk about our own genus, we naturally look for evidence of primitive tools and the evolution of tool-making.

Human evolution has been characterized by anatomical changes and by the development of an extensive culture, culminating in the use of language. But language – and most of culture in general – does not fossilize and cannot be dug out of the rocks. What we can dig up are tools. Appearing first in strata of about 2 Myr ago, they become more common, varied, and complex up to the present. Until quite recent times, they are the sole remnants of hominid culture. Each collection of tools and other artifacts, along with the ways they are made – a *tradition* or an *industry* – is named for a locality where typical remains are found. However, since we don't unearth hominid hands grasping those tools, we have to infer who the tool-makers were, based on their associations with hominid remains.

In Olduvai Gorge, south of Lake Victoria in Tanzania, Louis Leakey discovered primitive stone tools that represent the oldest known tradition, the Oldowan. The original Oldowan tools seem to be little more than chipped pebbles, and some of the evidence for their being tools is that they must have been carried to the stratum where they were found. In fact, these pieces are apparently just the cores from which flakes, the actual cutting tools, were chipped. Anthropologists experimenting with this technique, in which a flint rock is just hit with another rock, have shown that the large flakes that fall off the core really make quite efficient scrapers and knives. In 1964, Mary Leakey found bones of the species now called *Homo habilis* (literally, "handy man") at Olduvai. The Leakeys placed these animals in the genus *Homo*, for their bodies appeared to be smaller than those of their contemporary australopithecines, coupled with astonishingly human teeth and a large brain capacity (650–700 ml). This find dates to about 1.75–2 Myr ago, about the same age as the Oldowan tools, making *H. habilis* a likely artificer of the Oldowan tradition. In 1972, Richard Leakey reported a new series of fossils from Koobi Fora, east of Lake Turkana (formerly Lake Rudolf) in Kenya. The prize of this collection, a skull numbered KNM-ER (for Kenya National Museum-East Rudolf) 1470, became something of a celebrity among human fossils. It was originally identified as a *H. habilis* skull, but with a brain capacity of 750 ml. Its anatomy is very human. Furthermore, the KNM-ER 1470 bones were associated with artifacts that are more advanced than those of the Oldowan tradition. Some paleoanthropologists who have analyzed these and more recent finds in the Koobi Fora region have judged them to show too much diversity for a single species, so they have assigned some fossils such as KNM-ER 1470 to a species *Homo rudolfensis*. By this definition, *H. habilis* had a narrower face and a brain capacity of 500–700 ml, compared with 700–800 ml for *H. rudolfensis*. Whether one species of *Homo* or more existed at this time, they were distinguished from australopithecines by having larger brains, the foramen magnum quite centrally placed in their skulls, and pelves that permitted an easier upright stride. With hands similar to ours, they were developing greater manual dexterity. They made simple tools. There is no evidence that any australopithecine made tools, perhaps indicating a difference in intelligence that explains why *Homo* eventually won out.

Specialists in hominid anatomy and evolution must be the ones to define early hominid species, but part of learning to think about evolution is maintaining a certain broad perspective. First, keep in mind just how variable a population can be; our own modern species shows enormous variation, even in brain size. Furthermore, think about the process of speciation as discussed in chapter six. Some early representatives of the genus *Homo* were clearly living over a broad area of Africa during a period of several hundred thousand years. Had we observed these early humans, we might have been inclined to call them different subspecies or different semispecies living in neighboring regions, but we probably would not call them separate species. We would certainly look at them ecologically with Gause's principle in mind and would wonder just how many ecological niches might have been available in the Africa of 2 Myr ago for an intelligent, tool-using, bipedal hominid. More than one? In any case, classification of the sketchy *Homo* fossils of this period is still controversial.

To add to the *habilis-rudolfensis* issue, a remarkable, almost complete skeleton named the Turkana Boy was unearthed from a 1.6-Myr deposit west of Lake Turkana. He was judged to be about nine years old when he died; apparently he fell into a swamp and was buried, so his body was not disturbed by predators, as was so typical of other hominid fossils. This fossil is now taken to represent a species called *Homo ergaster*, although many anthropologists consider the *H. ergaster* fossils merely to be early African representatives of *Homo erectus.*

Muddy as the current picture may be, there is evidence for two to four types of hominids coexisting in Africa between about 2.5 and 1.5 Myr ago: one or two types of australopithecines evolving from the *africanus* to the *robustus* type and at least one species of early *Homo*, whether it is named *habilis*, *rudolfensis*, or *ergaster*. The stage was set for the development of the next human species.

Homo erectus arrives

About 1.5–1 Myr ago, *H. habilis* and whatever other "species" may have coexisted with it were replaced by *Homo erectus.* Eugene Dubois described the species in 1891 from specimens he discovered in Java, and named it Java man or *Pithecanthropus erectus*, meaning "ape man that walks erect," for features that were considered remarkable at the time. *H. erectus* people stood about 1.5 meters tall, with a skeleton much like ours, but a skull more like that of earlier hominids. Their cranial capacity of 800–1100 ml approaches the modern human range, but they retained massive teeth and characteristic heavy eyebrow ridges. *H. erectus* was widely distributed throughout Africa and Western Asia. Fossils assigned to *erectus* may reach back to almost 2 Myr ago but certainly to 1.5 Myr ago; the youngest specimens are as late as 300,000 years ago. Similar fossils dating from around 600,000–250,000 years ago are found in Europe, and anthropologists commonly assign them to a separate species, *H. heidelbergensis*, named after a fossil jaw discovered at Heidelberg, Germany. The argument is that the *heidelbergensis* skull is more "inflated," that its heavy brow ridges are more individually arched above the eyes, and the back of the skull is more rounded, along with certain facial features. But, to avoid becoming tedious on the subject of defining hominid species, I'll refer to them all as "erectus" people.

The *erectus* people left clear records of a developing culture. They were omnivorous hunters and gatherers. Large herds of animals, which must have provided plentiful food, roamed the extensive steppes and savannas of their middle-Pleistocene world. The campsites of these people contain vast bone remnants of deer, antelope, and large, ferocious animals such as bears and elephants. They may have killed these animals with pointed wooden spears and probably depended upon techniques used by contemporary aborigines. A hunter can stealthily creep up on his prey, and bipedalism allows him to dog his prey at a steady trot for hours or even days, until it is too exhausted to resist. Primitive hunters may also have used the aboriginal American technique of stampeding herds of animals over a cliff to their death.

The *erectus* people left extensive collections of stone tools that define the Acheulean culture, characterized by both core and flake tools. Crude as they are, the choppers and tear-shaped hand-axes of this culture are clearly an improvement over those made by previous hominids because they are carefully worked into functional devices, rather than just being chipped along one edge. They must have been used for domestic purposes such as fashioning wooden tools or cleaning and cutting the carcasses of animals. This stone tradition defines a long period, the Lower Paleolithic (Old Stone Age), that lasted until about 200,000 years ago in Africa, and to perhaps 150,000 years ago in Europe and Western Asia.

Like contemporary tribes of hunter-gatherers, the *erectus* people were probably nomads who roamed widely in small bands and returned to the same base camps periodically. At some point, they also learned to use fire, for evidence from both Hungary and China clearly shows that they were cooking with fire 500,000 years ago.

The *erectus* humans lasted for nearly a million years, at least 40,000 generations, and during that time both they and their environment changed. At first, while the climate was still relatively warm and they were quite unskilled, they probably went naked and lived in the open. But the Pleistocene climate was growing colder, and by 600,000 years ago a series of ice ages began, during which extensive areas of Eurasia and North America were covered by glaciers. The people of these times began to clothe themselves with animal skins, and some moved into caves. By domesticating fire, they could heat those cold, damp spaces and keep wild animals out.

The development of language is a key aspect of human evolution, since human culture could not have developed far without speech. Language offers a great selective advantage, as it is applied to developing a social structure and hunting cooperatively, since social solidarity depends upon named classes of relations that cannot exist without language. Familial relationships, for instance, are passed from one generation to the next by language, whereas nonlinguistic primates must reestablish dominance relationships every generation. The primate brain had been evolving linguistic capacities for a long time. Contemporary apes have considerable linguistic ability; gorillas are reported to communicate with 22 distinct sounds, and chimpanzees have an even larger natural vocabulary and are highly communicative. (Whether chimps can learn to use an artificial language as humans do is a controversial issue, but at least they can communicate well, if not creatively.) Clues from artifacts and from skull morphology, which shows the size and shape of various brain areas, indicate that *H. erectus* probably used a kind of rudimentary language.

With culture, a new mechanism of natural selection appeared that could shape behavior much faster and more effectively than purely genetic selection. Cultural requirements also put a premium on a larger brain for storing and processing information, so it is no wonder that in less than a million years of evolution the human brain increased so enormously.

Neanderthal and later humans

By 250,000 years ago, the human skeleton was well established and was modified very little in further evolution. Between 250,000 and 150,000 years ago, *H. erectus* was replaced as the dominant hominid by people much like us, generally designated *H. sapiens*. The earliest fossils define Neanderthal humans, named after the Neander Valley in Germany where the first fossils were found. They have been named a subspecies, *H. sapiens neanderthalensis*, but were they our ancestors? Are there Neanderthal genes in the modern human genome? The answer, according to analyses of mitochondrial DNA (mtDNA), now seems to be No. Some investigators have obtained samples of mtDNA from Neanderthal fossils and compared it with modern human DNA; they are clearly quite distinct, and one group of investigators estimated that Neanderthals must have diverged from the ancestors of *Homo sapiens* between 365,000 and 850,000 years ago. Also, studies by Brian Sykes and his colleagues on the diversity of mtDNA in modern human populations show only small differences, consistent with common ancestors about 30–40,000 years ago, but certainly no more than 80,000 years ago. This work leaves no room for Neanderthal genes that might have been combined with *sapiens* genes. So it is reasonable to designate them a separate species, *H. neanderthalensis.*

Although they were not our ancestors, the Neanderthals are fascinating. Averaging about 1.7 m in height, they were considerably more robust than our ancestors but had large cranial volumes, averaging about 1600 ml. The major anatomical differences between Neanderthals and *H. sapiens* lie in facial features, since a classic Neanderthal skull has a markedly receding chin, heavy brow ridges, and a sloping face and forehead, in contrast to the slight brow ridges, higher foreheads, vertical face, and more angular chin of *H. sapiens.* Some anthropologists, however, regard the classical, heavy-browed western Neanderthalers as a subgroup whose facial features may have been an adaptation to the cold, like the heavy brows and flat noses of contemporary Arctic peoples such as Eskimos. Over most of their range, from western Europe through the Mediterranean, the Middle East, and East Africa, most Neanderthals were of the "progressive" type, with skulls much more like ours.

Some time before 250,000 years ago, as *erectus* humans were being replaced by later humans, the Acheulian tradition in toolmaking was being replaced by the Mousterian. Hand-axes that had been made by striking chips off a core were now made more carefully by striking a wooden tool held against the core to remove flakes. This method produced sharper, more symmetrical tools. The resulting flakes were delicately shaped into tools such as scrapers and spear points. The invention of a long wooden spear with a sharp stone tip must have been a major advance in hunting. Among Neanderthal artifacts are the bones of many animals. Neanderthal people possessed the knives to butcher animal carcasses and the fire to cook the meat. The cold climate must have placed a premium on these fires for warmth and on animal hides for crude clothing.

modern humans

Virtually all the skeletons dated later than about 35,000 years ago are those of *sapiens* people. Until the issue of Neanderthal genes was settled, the genetic evidence was consistent with various ideas about our origins. But today we are left with the "out of Africa" model: that modern *sapiens* people emerged from a single African source sometime around 100,000 years ago and spread through Europe and Asia, eventually replacing indigenous humans in each area.

The recent discovery of very small human skeletons on the Indonesian island of Flores shows that other species of humans may have been living quite recently along with *Homo sapiens*, although their designation as *Homo floresiensis* raises the usual questions about the definition of a species and the legitimacy of such names. These little people, who lived as recently as 13,000 years ago, stood only about three feet tall when fully grown and had anatomical features unlike those of pygmies, who belong to *H. sapiens* in spite of their small size.

Over the last 35,000 years humans have become a truly cosmopolitan species spread across the face of the Earth, with only small genetic differences among contemporary races. Physical evolution in humans has not stopped, but it is of secondary importance to cultural evolution, which has wrought remarkable changes in a short time.

The first modern *sapiens* humans are known as Cro-Magnon, from the cave in southern France where their remains were found. In the Upper Paleolithic period, from about 35,000 to 8000 B.C.E., they created the foundations of our culture. With ever more refined methods, they learned to shape stones and then bones into excellent tools. We find spearheads and fishing hooks like those made by modern hunter-gatherers, and needles show that they must have tailored clothing out of animal hides. They were probably our equals in intelligence and humanity. They carefully tended their dead, which were sometimes painted with red ochre and buried with various artifacts – evidence of some thought about an afterlife.

They also expressed themselves through painting and sculpture. Some of their carvings rival our own in delicacy and realism; others are clearly exaggerated representations of pregnant women that probably figured in fertility rites. (Fertility was important to people who were constantly threatened with injuries and death; their rate of infant and childhood mortality must have been enormous, and no more than 10 per cent of them lived to the age of 40.) Paintings from at least 12,000 years ago in some French and Spanish caves still inspire awe and admiration. These people had learned to make paints from clays and animal fats colored with charcoal and metal oxides; their painted scenes emphasize the animals they hunted, perhaps for rituals and magic to ensure successful hunting or the return of migrating herds, or to boast about past successes.

Contemporary with the Cro-Magnons, similar Upper Paleolithic cultures of hunter-gatherers were thriving in Asia and Africa. But by about 10,000 years ago many had started to settle in permanent communities where food was abundant. At this time, there was a general warming of the Earth, a retreat of the glaciers, and a transition to the so-called neothermal conditions in which we now live. All ecosystems had to adapt to these changing conditions, and people of this time were intimately entwined in their ecosystems. Northern European people, for instance, had long been largely dependent on herds of reindeer, but with warming conditions these herds had to adapt to new food plants and to the encroachment of forests into the European plains. There is also good evidence of very dry periods about this time. These factors forced people to find new food sources. Some tribes settled on lake and ocean shores where they created transitional cultures, known as Mesolithic, with efficient industries for catching fish and molluscs. While these European peoples continued to subsist by hunting, fishing, and gathering, others to the east were inventing something that would change the face of the Earth: agriculture. And at this point we abandon the realm of anthropology and evolution, and move into human history.

notes

1. In another modern classification, the order is divided into two different suborders defined on the basis of nasal structure, but the more traditional classification will be more useful for us here.
2. Among taxonomists, splitters are those who tend to divide taxa into smaller groups, and lumpers are those who tend to combine smaller groups into larger ones.

chapter nine

probability and entropy

This chapter explores a kind of argument often heard from people who have doubts about evolution, including scientists who express what they think are legitimate scientific doubts. The argument is twofold, or perhaps it rather mixes two scientific concepts in a confusing way. The gist of the argument is that it is impossible to imagine anything as complex as even a simple organism arising by chance, and that evolution as commonly described violates the second law of thermodynamics. These arguments raise complex issues. Their advocates don't understand either the concept of natural selection or the principles of thermodynamics, but conclude that there must be an Intelligent Designer who is responsible for the wonderful complexity and diversity of organisms. That is a conventional conclusion, a version of natural theology advanced in many forms over many years by theologians of various stripes. But those who conclude that life is a miracle in the traditional sense – a supernatural phenomenon outside the realm of science – miss a more exciting conclusion: that life is a miracle (though I hesitate to use the word) in a scientific sense. There is a kind of grandeur, a freeing and elevating of the human spirit, in recognizing that the wonderful complexity and diversity of life, which we see in ourselves and in our surroundings, has been produced solely by the interplay of natural forces over long times, without the need for foresight, planning, or intelligence.

the improbability of life

To address the probability argument first, remember that a typical protein is made of a couple of hundred amino acids – 300 is a good average. Since a protein can be made by placing any one of 20 types of amino acids at each position in the chain, there are 20^{300} possible proteins of this size, or approximately 10^{390}. Numbers like this are so absurdly huge that we can only make them meaningful with science-fiction stories. For instance, suppose you had a machine for putting amino acids together in any desired sequence, and suppose it could assemble a protein of 300 amino acids in one second. Suppose you set it to work at the instant the universe originated, around 15 billion years ago, programed to assemble every possible sequence of 300 amino acids one by one, and you waited until it made just one protein of this size with a biologically useful sequence – an enzyme, perhaps. The machine wouldn't have to produce all 10^{390} combinations before it hit on a good one. Maybe it would only have to make half that number. How long would it take to do that, just by chance? One year is about 3×10^7 seconds, so in 15×10^9 years the machine could make 4.5×10^{17} different proteins. That's a pitifully small number in comparison with 10^{390}. (Remember, please, that 10 raised to a power x is only one-tenth of 10 raised to the power $x + 1$, so the difference between 10^{17} and 10^{390} is enormous.) Well, suppose you made a million machines, or a billion, or a trillion, and you had each one making different sequences. A trillion is 10^{12}, so those trillion machines could make 4.5×10^{29} proteins. Still nowhere near the number needed.

Several people, particularly critics of evolution, have made this kind of calculation and have then asked, "Suppose you had a lot of amino acids (or any other random 'parts' of an organism or a machine) on some primitive planet, and you let them assemble themselves by chance. What is the probability that they will form a functional organism, or even a single functional molecule?" Given the kinds of numbers I've just been playing with, the probability is so incredibly small that the scenario is beyond belief. The conclusion is that organisms could not be created by chance; there must have been an intelligent creator to assemble all the parts in a functional way.

Before addressing the probability issue, let's examine this word "functional." Our bodies are made of organs with distinct functions, such as pumping or filtering blood. Their functions depend on having constituent cells with particular functions, such as contracting rhythmically or moving certain atoms and molecules here and there. The cells, in turn, operate as they do because they are built of certain proteins (and other molecules) that interact chemically with one another or with small molecules in their vicinity. The word "functioning" is most meaningful at this chemical level. We easily mislead ourselves if we think that the only functional molecules are those that do the kinds of operations that go on in our bodies, or in the bodies of other living things that we know of. This attitude is terribly myopic. Remember that modern organisms, ourselves included, are historical objects whose functions, whose mechanisms, have been derived from the mechanisms used by their ancestors. There is no obvious limit to the range of chemical processes that could have biological functions. Every protein, assembled at random, will interact in *some* way with the molecules around it, because every chemical structure has *some* affinity for other molecules and interacts with them. Thus, every primitive protein molecule, no matter how randomly it was slapped together by unknown forces, could have had a function. If the proteins of our ancient ancestors had interacted differently with their surroundings, evolution would have taken a different path and we would have quite different metabolisms.

Advocates of the probability argument just don't understand natural selection. I have called natural selection a kind of *editing* process, and that is a key to understanding it. Of course, it would be impossible simply to produce a perfect functional protein *de novo*, out of nothing. But that isn't what actually happens. The process always starts with a structure, which then gets modified. A really satisfying rejoinder to this probability argument would go back to the barest glimmerings of life in the most primitive biological structures and show just how genetic editing could produce a more completely functional structure. But, as discussed in chapter three, the processes that produced the first barely functional molecules, probably RNAs and proteins, are obscure and hard to reason around. So I will skip ahead to the point where some kinds of functional organisms have started to evolve. In fact, we don't even need whole organisms; just some barely functional proteins or RNAs will serve as long as their structure is specified by primitive genomes. Any such molecule will have at least the beginning of a function; or, better, among a collection of molecules produced randomly, there will be some that have the bare beginnings of *functions*, plural. All that means is that they will interact *somehow* with other molecules.

So a primitive organism whose genome specifies any protein with any function at all will have some ability to persist, to function, and to reproduce itself. Its offspring may include some mutants that have variations on the structure. One or more variants may have slight improvements on the original, or maybe slightly different functions. Of course, other variants will be worse versions, and the organisms that make them will be discarded. Further reproduction of the surviving versions will create another generation of variants. Again, many will be discarded, but some may be improvements, and they are selected. The process continues generation after generation, gradually producing better and better versions and more variants with other functions. So natural selection is a process that inherently creates better functions, merely by chance. Richard Dawkins has written about this as a *cumulative* process, one that builds one slight improvement upon another, and it is this kind of process that has generated the wonderfully complex structures we see in ourselves and in the rest of the biological world. So organisms intrinsically are things with an inherent capacity for bootstrap uplifting.

All those variants that are discarded as being worse are important to the process. Garrett Hardin has written "in praise of waste" to emphasize the importance of producing all those inferior versions, which are just thrown away. The process depends on "tinkering," producing random changes with no foresight; then it happens, merely by chance, that some improvements are produced. But tinkering produces waste, and the waste is necessary.

Let me try an analogy here that might help. The situation I've been analyzing is similar to the famous scenario of putting a million or a zillion monkeys to work pecking randomly at typewriters, with the assurance that, given enough time, one of them will eventually type the works of Shakespeare. In a modified version, suppose each monkey is *genetically disposed* to type a certain random sequence and that one of them keeps typing the sequence, "To be or nox to be, tham is the questiop. Whether tis nobles in the dharieaspjeoiesj;rlskjewa;lisejss ..." and the rest is gibberish. We single out this monkey as being on the right track and let it reproduce in an environment that encourages mutation. Then one of its offspring might correct the "nox" to "not," or one of them might change the first bit of gibberish to "mind" and thus get closer to the right sequence. In the next generation, we breed one of the monkeys that types an improved version, and one of its offspring may be a mutant that types a still better version. Of course, given the number of letters and punctuation marks in English and the length of Shakespeare's works, the probability of a monkey producing them by chance is even lower than the chance of making that random good protein; but I've changed the scenario by making the system *genetic* and by introducing selection – not natural selection, but selection by rationally examining what each monkey produces and picking the best sequences. And – at the risk of stressing this too much – notice how critical it is for the system to be genetic.

entropy

The second kind of argument that gets mixed in with the probability argument is about thermodynamics – the science that deals with energy – and the concept of entropy. Entropy is a rather subtle and tricky concept. It can be illustrated in various ways, and I will try a couple of different approaches.

You know about energy. It is the ability to do work, and work means moving anything any distance by applying a force. Suppose you need to do some work – say, moving a piano up to the third floor of a building. If the building has a large elevator, you can use its strong cables and powerful motor to hoist the piano up. If not, you can get a few husky guys to move it. The elevator motor uses electrical energy, which is converted into the mechanical energy of raising the piano. The electricity came from some distant source, such as water falling down through a dam or coal being burned or perhaps the heat generated by radioactive material. If you have to use strong men, they will be expending the energy stored in their bodies to power their muscles – energy that came originally from the food they ate.

In transition from the source to the motor, a lot of energy will be lost. Regardless of its source, the electricity generated will have less energy than there was in the source. At every step of changing one form of energy into another, some energy will be lost as heat. The motor running the elevator will be hotter than it was before. The husky guys will have less energy stored in their muscles than there was in the food they ate; and while sweating and straining, they have produced a lot of body heat. As energy is converted from one form to another, the total amount remains constant – that is the *first* law of thermodynamics. But some *must* always be wasted. The "must" reflects another law of nature. The energy that can be conserved and used for further work is called *free energy*; the wasted energy is heat. The *second* law of thermodynamics says that in every real process, less free energy will be available afterward than there was before, and more heat will be generated. A quantity called *entropy* measures how much energy is wasted. The entropy change in any process is actually the heat generated divided by the temperature at which the process happens.

Besides relating entropy to wasting energy as heat, the idea of entropy can also be understood in relationship to probability. That conception will help enhance the previous argument about the probability of making a functional organism. It is best illustrated with some simple examples.

Example 1: Your bedroom is a little messy. Although you do have some neat piles of clothes, books, and papers, you have others scattered about randomly. If you don't make any effort to straighten the room, do you expect to see the piles degenerating into random messes, or do you expect to see the random messes making themselves into neat piles?

Example 2: You have a shallow, open box with a checkerboard pattern printed on it. You stand across the room with a lot of checkers and throw them one at a time into the box. When you look into the box, do you expect to see (1) all the checkers arranged in a few neat rows on one side of the box or (2) the checkers lying randomly on the pattern?

Example 3: Make a tank that will hold water, divided in two by only a thin barrier. Fill one side of the tank with hot water and the other with ice water. Which of the following do you expect to observe? (1) Heat flows from the ice water into the hot water, so the ice water gets cold enough to freeze and the hot water gets hot enough to boil. (2) Heat flows from the hot water into the ice water until both tanks come to the same medium temperature. (Without getting into a long lesson in physics, it will help to know that when water – or any substance – is hot, its molecules are moving faster. Molecules in a liquid or gas move around randomly, constantly colliding with one another. When a fast molecule and a slower molecule collide, the fast one gives up some of its energy to the slower one, so their energies afterward are more average.)

The answers to these questions are quite obvious. The examples show that the natural course of events is for everything to achieve a less organized, more disorderly condition – in other words, a condition with high probability. Neat, orderly conditions have a low probability of occurring. You know that things tend to become messy as we move around and use them, and it takes special effort to make them orderly again. If you threw your clothes into the room, the probability of them landing in neat piles is essentially zero. In the checker toss, you also expect to see the checkers lying randomly on the squares. It is very unlikely that they would all fall on only a few squares in an orderly arrangement. Similarly, the probability of all the water molecules with high energy – the hotter molecules – moving in the direction of the hot water is practically zero. Instead, the molecules all move randomly in different directions and end up all mixed with each other. Heat simply doesn't flow spontaneously *toward* a hot thing – it flows *away* from a source of heat, and things tend to achieve medium-range temperatures. This is our common experience of the world.

Entropy can be measured by its relationship to heat, and it can also be related to probability. A condition with low probability has low entropy; one with high probability has high entropy. Another statement of the second law is that any system left to itself will run toward a condition of maximum entropy, which means maximum disorder.

the entropy of evolution and of living

Now let's return to evolution. A second kind of argument made against evolution is that it violates the second law of thermodynamics. Critics say, "The laws of thermodynamics say that systems ought to be getting worse and worse – more and more random and run down. The evolutionists claim that organisms are getting more and more complicated and well organized. That simply can't happen." How to answer such an argument? (By the way, remember that the idea of evolution as progress is an illusion, and many lines of evolution have produced simpler creatures rather than more complex ones.)

One answer to the argument is that it just isn't true as stated. The second law says that the entropy of every *closed* system will reach a maximum. A closed system is one that cannot exchange energy with its environment, but an organism is just the opposite of closed. It's quite obvious that if someone tried to make you into a closed system by keeping you from getting any more energy from food, you would rather quickly turn into a system with high entropy – a rather disgustingly high-entropy system that would have to be cremated or interred in a cemetery. You maintain your relatively low entropy through a continuous input of more energy. And the whole world of living organisms also maintains itself only through a constant input of energy, ultimately light from the sun.

Let me amplify that by examining an organism to see how the laws of thermodynamics will affect it as it reproduces. Any old organism will do, but it is most instructive to take a small, simple asexual organism like a bacterium. Here's one. Observe this bacterium as it sits in a flask full of nutrients (sugar and other organic compounds). It grows larger. It divides in two. It reproduces. So do all its offspring. The two divide into four, the four into eight, and so on. After several hours, the flask is getting cloudy with bacteria. Are any laws of physics being violated so far? Well, we might be concerned that the second law is being violated even if no evolution is going on. After all, the flask contained molecules of sugar and a few salts, and now those molecules have been converted into some highly organized biological structures! That, in itself, seems to be a violation. If it is true that matter naturally tends to become less organized and more disordered, how is it possible for the stuff in the flask to become more organized? Isn't life itself a violation of thermodynamics?

This has been an issue in physics, and we have to resolve it before moving on to the larger question of evolution. The general answer is No, the ordinary processes of growth and reproduction don't violate the laws of thermodynamics. Quite a bit of energy is stored in the bonds of the sugar and other organic compounds, the energy source for the bacteria. Quite a bit of energy is also stored in the bonds of the complicated molecules of the bacteria. But a comparison of the two shows that the sugar contained more energy than is now built into the bacteria; in fact, most of the energy that was in the sugar has gone off in the form of heat, wasted energy. Less than half is still in the bacteria. So when we compare free energies before and after, we find less free energy after bacterial growth, and that satisfies the second law of thermodynamics.

Still, a kind of nagging doubt is trying to make itself heard. Yes, we might agree, simply measuring energy will show that there is less in the bacteria than there was in the sugar. But the molecules of the bacteria are a lot more *orderly* than those of the sugar, aren't they? And wasn't an important part of the concept of entropy about order – about bedrooms getting messy instead of orderly, about checkers falling in a messy instead of an orderly pattern? Isn't there still something wrong here?

There seems to be. To solve this puzzle, let's go back to the messy bedroom and think about how we can make it orderly again. Ah, here's a sweater on the bed; pick it up, fold it, and put it in the closet on the sweater pile. Here's a pair of pants thrown over a chair; it looks dirty and needs to go into the laundry. Here are several papers. Ah, this one needs to go into the pile of correspondence to be answered, the next one can be thrown into the recycling basket, the next one needs to go into a certain file in the filing cabinet, and another one needs to go into a different file. That book on the floor needs to go into a certain space on the shelf. Little by little, piece by piece, we can put the room back in order. When we are finished, we will have expended some energy in our muscles and we will have created some order in the room. But how did we know where to put everything to create the order? We needed some *information* – information about the structure of the room and where each item is to be stored. The key to understanding this situation is to understand information, and now let me remind you that genetic systems are all about information: the genetic information encoded in genes. To explore that idea further, let me go on an apparent digression to another situation involving entropy, one similar to the chamber with hot water on one side and cold water on the other side.

When the science of thermodynamics was developing in the nineteenth century, the great physicist James Clerk Maxwell made up an instructive story. He imagined a chamber filled with gas molecules, divided in two with a little gate in the division and a little demon operating the gate. The demon can watch the gas molecules as they move around randomly. The demon watches each molecule as it approaches the gate; if a fast (hot) molecule approaches from the right, he lets it go into the left chamber. If a slow (cool) molecule approaches from the left, he lets it go into the right chamber. Otherwise, he keeps the gate closed. Little by little, he allows fast (high-energy) molecules to accumulate on the left and slow (low-energy) molecules to accumulate on the right. Thus, the left chamber gets hot and the right chamber gets cold.

The demon is violating the laws of thermodynamics. It is decreasing entropy, but the natural course of events is for entropy to increase or at least stay the same. But how can the demon do that? It does so only by obtaining *information* about the gas molecules – by discriminating among them on the basis of their energy. If the demon operates by magic – outside the physical laws of the universe – then it can violate the second law of thermodynamics and reduce the entropy of the chambers. But if it operates within the laws of physics, it must expend more energy to get information about the speed of the molecules than the energy it stores up in the gas, and this makes it physically impossible.

Now we can reconsider the organism that seems to be violating the laws of physics. I said that it has less energy in its structure than in the sugar it uses as an energy source; it seems to be violating the second law by making considerable order out of a chaos of little molecules. The answer again lies in information. First, the information for the structure of the whole organism is encoded in its genome. That genetic information gets transformed into *structural information*, information in the orderly structure of each protein molecule, and those proteins, in turn, are the agents that create the greater order of growth. And now I can reveal the great secret that makes this all understandable: *information is negative entropy.* The physicist Leon Brillouin used the abbreviated form *negentropy*. Leo Szilard, the brilliant Hungarian physicist who was involved in the development of atomic energy, pointed out the relationship between entropy and information in an obscure paper in a German journal in 1929, but, as Brillouin wrote, he was misunderstood. Claude Shannon, whose early work in information theory laid the foundation for much of modern computer science, discovered the relationship again in 1949, although he wrote about entropy in a somewhat confusing way. The interested reader with a background in mathematics and physics can get the details of the idea from Brillouin's book. Like any physical concept, this idea can become very complex, but for our purposes it is enough to reflect on what we have already seen: highly structured objects, containing information, can establish greater order in the world they interact with. Your highly structured brain, for instance, contains some information (in what form, we don't know yet) about where various objects belong in your room, so you can use your brain to create order. DNA is a highly structured object, and the organisms it surrounds itself with (to borrow a biological metaphor from Richard Dawkins) contain other structures that transform the information in DNA into more of their own order. Each protein molecule, being formed with a particular shape to perform a certain function in an organism, creates order as it performs its function.

Evolution can be told as a story about storing up structural information, functional information, in the form of complicated organisms. Because evolution operates in organisms with genomes, which store information that makes for successful reproduction, it becomes a kind of mechanism for organisms collectively to lift themselves by their bootstraps. The instruments – organisms – involved in evolution are intrinsically information-bearing structures, and this gives them a special place thermodynamically. Now, of course, none of this contradicts the second law of thermodynamics. As I emphasized before in joining Garrett Hardin to praise waste, producing every generation of successful organisms wastes a lot of structures (a lot of material and energy) that don't survive. This is the cost we pay for maintaining those that are at least as successful as the previous generation and perhaps even a shade better at surviving the exigencies of life.

I mentioned earlier that Jacques Monod begins his book *Chance and Necessity* with a quotation from Camus's *The Myth of Sisyphus.* Sisyphus, Camus's central figure, was condemned for eternity to roll a huge rock up a hill, only to have it roll back down each time. Camus wrote, "Sisyphus ... too concludes that all is well. This universe henceforth without a master seems to him neither sterile nor futile. ... The struggle itself toward the heights is enough to fill a man's heart. One must imagine Sisyphus happy." So, too, in a world that needs no intelligence to explain its beauty and intricacy, we creations of chance and necessity may look back on our long history with happiness, with even a kind of pride – if the word is not too much – that we have achieved our condition through the operation of the purposeless forces of nature.

chapter ten

the problem of creationism

creationism in historical context

Darwin wrote his great books on the origin of species and the "descent of man" against a background of Christian orthodoxy, with its belief that the world, and all life on it, had been created quite recently as described in the Bible. Although many people quickly saw the logic of his ideas and were won over to them, the immediate reaction in English and American society, including the society of scientists, was shock and disbelief. Several writers (see Further Reading) have summarized this history very well. Briefly, during the latter part of the nineteenth and the early part of the twentieth centuries, the idea of evolution evoked antagonism among the faithful, but not the strong, aggressive reaction that emerged later. The first strong reaction arose during the 1920s among evangelists such as Billy Sunday and their followers. Influenced by their evangelical railing against modern ideas, several states in the U.S. passed laws prohibiting the teaching of evolution in the public schools. The famous Scopes Trial in Tennessee in 1925 was a response to these laws, a testing of the law; unfortunately, although the verdict went against Scopes, the case was dismissed on a technicality, so there was no opportunity to carry the issue to a higher court and thus test the constitutionality of the anti-evolution laws until much later.

The general mood in public education during the 1930s and 1940s, even into the 1950s, was to quietly ignore evolution, largely out of fear of creating a public uproar and violating some of the existing laws.

But this mood ended abruptly in 1959, largely because of Sputnik. Americans had faith in the superiority of American science; Americans knew that their scientists had invented the atomic bomb (quietly ignoring the whole development of modern physics in Europe and the key roles of leading European scientists in the atomic bomb project) and were now creating a beautiful new world of plastics and antibiotics. They had faith in the superiority of American public schools. So the public was shocked when the Soviet Union demonstrated its technical superiority, at least in one arena, by launching the first satellite to circle the Earth. Congress reacted quickly, pouring money into programs sponsored by the National Science Foundation and others to improve science education in the U.S. This new emphasis on science included the production of modern science textbooks for high schools, and the biologists who wrote and consulted on these books naturally emphasized evolution, since it is a foundation concept of modern biology.

The contemporary creationist movement was largely a reaction to this new emphasis on evolution. Though the various creationist viewpoints differ in emphasis, they are all characterized by a horror of evolution, both for strictly religious reasons and for a complex of social-political reasons. Modern Christians, of many denominations, have reacted with alarm to the social changes in contemporary American society: increasing violence, decreasing moral values as shown particularly by more and more blatant sexuality, increasing access to abortion and acceptance of it, and growing lack of respect for traditional values among youth. To traditionalists, it became obvious that subversive elements, including international communism, were destroying American society and its values; these forces had even won a prohibition of prayer and the teaching of religious values in schools, and were generally turning American youth away from family and faith, toward a crude, materialistic culture. Religionists blamed these changes on the emergence of a collection of ideas that they labeled "secular humanism," identifying it as a secular religion that opposes all traditional religious values. And they saw evolution as a kind of sour frosting on this bitter cake.

Although the U.S. Supreme Court has ruled unconstitutional the teaching of creationism in the public schools, under the guise of so-called "creation science," the teaching of evolution is under renewed attack. In opinion polls, about half the adult population profess their disbelief in evolution, making it easier for creationists to win their battles. Many citizens are alarmed by this situation, and organizations such as the American Civil Liberties Union and Americans United for the Separation of Church and State have been waging continuous battles over this and related issues.

Eve and Harrold (Further Reading) have distinguished among types of creationists. The central and most common belief is young-Earth creationism, which maintains that the Earth is only a few thousand years old, and that the world and all life were created as described in Genesis. In contrast, old-Earth creationists accept the dating of geologic events but still insist on divine creation rather than evolution. They may do this, for instance, by noting that the Hebrew word *yom*, which is translated as "day" and used to describe the periods of creation in Genesis, does not necessarily refer to a 24-hour day, so the "days" of Genesis could have been as long as geologic periods. The old-Earth creationists have maintained that by rejecting all the sound scientific evidence for the age of the Earth, young-Earthers are in danger of making the whole idea of creationism look ridiculous. Still, the old-Earthers reject evolution, especially the idea of human origins through evolution.

Eve and Harrold apply the designation "theistic evolutionists" to those who accept the scientific account of evolution but maintain that life was originally divinely created. Theistic evolutionists show clearly that there is no necessary conflict between science and religion in their proper spheres, and no reason for anyone to oppose the teaching of evolution. Some may believe that the purpose of evolution was to create humans and that God chose to do it in this way; a general anthropocentrism has been hard to maintain since the development of modern science, and yet this may be a personal belief to which people are entitled. As a philosophical position, theistic evolution stands outside science, so no empirical evidence can be adduced to support it or oppose it. It is a position held on faith, as are religious beliefs in general. But theistic evolutionists in general are not opposed to the scientific account developed in this book.

beliefs of "scientific creationism"[1]

Leaders of the young-Earth creationists include a small group who have been devising a so-called creation science as an alternative to mainstream contemporary science. Particularly because they propose their science as a legitimate alternative that ought to be given equal time in the public schools, it is important to deal with their claims. People in an open society are free to believe anything they want to. But principles of the various sciences are so closely intertwined that those who try to develop an alternative to mainstream biology are forced to attack other principles of modern science. Thus "scientific creationists" run into serious problems when they come up against modern physics and geology.

Moreover, since creationists claim that everything originated about 4000 B.C.E., it is enlightening to put some historical perspective on this discussion, for they are in conflict with history and archeology as well as the natural sciences. There is good evidence that sheep were domesticated in northern Iraq around 9000 B.C.E., that wheat and barley were domesticated in southwestern Iran around 7000 B.C.E. There was an extensive settlement at Jericho around 7500 B.C.E. Writing began in Sumer and Egypt around 3300–3100 B.C.E. The Akkadian civilization dates from 2800 B.C.E., and the empire of Sargon I lasted from 2350 to 2250. Advancing human civilization was not being disrupted by events that creationists must place during historical times, including unbearable heat and huge glaciers, as discussed below.

the age of the Earth

Young-Earth creationists claim that the Earth is only about 6000 years old, rather than about 4.5 billion. To account for this huge difference, scientific creationism must try to discredit the methods used to determine the age of the Earth and its geological layers. The most important of these methods (chapter two) are radiometric, based on the rates of decay of various radioisotopes. Now radioactive decay is just one phenomenon covered by modern physics, especially quantum mechanics. This fundamental science underlies all the rest of modern science, and its foundations are secure, even though any subject of ongoing research is always open to reexamination. Radioactivity is explained by the so-called strong and weak forces, the forces that hold an atomic nucleus together and allow some particles occasionally to decay into two others. The theory of quantum mechanics established during the 1920s and 1930s holds together with remarkable coherence, and anyone who proposes to attack any part of it has to find some fundamental defect in the theory. No one has tried to do this. It would require a profound knowledge of modern physics, and it would be foolhardy at best for anyone lacking that knowledge.

To try to attack quantum mechanics, some creationists have pointed to something they can understand – the speed of light, one of the primary physical constants governing the universe. They have tried to show that it isn't really constant or that its value isn't really well established; then the fabric of physics will have a small hole in it, and the whole thing may be weakened. If, for example, the speed of light can change, then perhaps other constants related to radioactive decay could change. However, attempts to cast doubt on the speed of light have been quite unsuccessful. More and better measurements in the last few years have just made this constant more precisely known and more certain.

Some creationists have tried to attack the speed of light by reference to the redshift observed by astronomers. This is similar to a Doppler effect but an effect of light rather than sound. You experience the Doppler effect regarding sound when you hear a police siren or a train's horn as the vehicle approaches you or leaves you. As it approaches, the sound waves are pushed closer together, shortening their wavelength and thus raising the pitch of the sound; as it leaves you, the sound waves are stretched out, and the pitch falls. Astronomers of the 1920s discovered a significant shift in the light coming from distant stars, a shift toward the longer light waves at the red end of the spectrum. This redshift is evidence that the stars are all rushing away from the Earth – in other words, that the universe is expanding. This is now a fundamental concept of astronomy.

Creationists have attacked this phenomenon by arguing that the conventional interpretation of the redshift would require the universe to be expanding faster than the speed of light, in violation of relativity. So they have argued that the universe is actually very young and that rapid changes in the speed of light have simply given the illusion of old age. However, this attack shows a misunderstanding of physics. Even though the redshift is analogous to the Doppler phenomenon in sound, the redshift in light reflects the fact that, as Donald Wise has put it, "these wavelengths represent a kind of tape measure embedded in space itself." The light started long ago from the stars, with characteristic wavelengths. But while it has been traveling, the universe has been expanding, so the wavelengths of the embedded light have been stretched, and the longer wavelengths we measure are in effect a measure of how much the cosmos has been expanding in the long term. The point is rather subtle, but it carries the lesson that the coherence of modern science, the interdependence of its various concepts, makes it very difficult to reject a part of science in the name of some special cause without running into difficulties somewhere else.

sedimentary deposits and continental drift

We saw in chapter two how the idea of evolution developed through the combined growth of biology and geology, so "creation science" runs into strong conflicts with geology as well as biology. Some of the principal "creation scientists" have earned Ph.D. degrees in geology, yet without losing their faith in an Earth created according to Genesis. These geologists have to ascribe all the events of sedimentation and fossilization to the Noachian flood and its consequences, and since the Bible says the flood lasted for about a year, they have to cram events into that short time that actually took place over many millions of years. This creates some problems.

Sedimentation occurs as minute rock particles and minute organisms with hard shells fall out of water to form a mud that gradually turns to rock under heat and pressure; limestones are made from calcareous mud – that is, mud made rich in calcium carbonate (calcite) by organisms that make their shells from this mineral: single-celled organisms such as radiolarians and foraminifera, and by animals such as molluscs. The sediments form distinctive layers, one on top of another, to eventually create beds of rock hundreds of feet thick. These beds contain the fossilized remains of animals showing the successive appearance of different types, from small invertebrates through fishes to terrestrial vertebrates such as reptiles, birds, and mammals. Creationists have to explain this. One of their attacks has been to claim that the sedimentation is really much more chaotic than that – that geologists have distorted the stratigraphic record to make it appear regular and defend established ideas about Earth history. (Interestingly, the petroleum industry has no doubts about traditional stratigraphy and continues to pour billions of dollars into exploring the geological column with core drilling.) The best answer to that charge is actually to watch geologists at work, to see how carefully they interpret the layering in each area, and to wonder why the adherents of a whole science would want to delude themselves so badly.

George McReady Price proposed one creationist explanation for the layering of fossils in 1923: that as the flood came on, terrestrial vertebrates (including humans) rushed up the mountains, so they were buried last, while all the simpler aquatic invertebrates were buried in the lower levels. The obvious question is why the aquatic creatures were killed and fossilized at all! The flood must have expanded their potential habitat enormously, giving them plenty of space to live in, and even as the waters slowly receded at the flood's end, the animals could slowly retreat without dying en masse. And why should they have died with the layering we observe? Why weren't fish skeletons or amphibians mixed with invertebrates in the lowest layers? Why do the lowest sediments contain the remains of species such as trilobites that are so different from any animals alive today? And why are there no fossils of all the humans who must have been killed in the flood? There must have been a lot of them, and one would expect at least a few of their skeletons to have shown up in the sediments. (The fossils of early hominid species described in chapter eight were clearly not modern humans who died in a flood.)

Sedimentary beds can be incredibly thick, showing what long times were required to deposit them at the very slow rates of about 1–3 cm per 1000 years that have actually been measured in the deep sea. The chalk cliffs of Dover, for instance, are 1000 feet thick, made of the shells of foraminifera that lived briefly and then settled to the bottom of the ocean. At the lowest rate, 30 million years would be needed to deposit a bed 30,000 cm (about 1000 feet) thick. That is a good approximation to the actual rate, since the cliffs are dated to the Cretaceous period, between about 144 and 65 Myr ago. However, if the Dover chalk beds were actually deposited during a single year, they must have grown at the rate of about 80–90 cm – nearly a meter – per day, which is beyond belief. Imagine standing in the shallow water near the shore of an ocean brimming with minute organisms that are dying and falling so fast that your feet are being buried as you stand there.

Similarly, the Kaibab limestone visible in the Grand Canyon of southeastern United States is 150 m thick. If it had been deposited during the flood year, the organisms that produced it would have made calcareous mud at the rate of 40 cm per day.

To get around the problem of sedimentation rates, the creationist geologist Steven Austin has devised another scenario. Austin postulates that during the 1500 years between the creation and the flood, the atmosphere had a much higher level of carbon dioxide than it does now. During that time, he believes, organisms formed their carbonate shells very rapidly and abundantly, depositing calcareous mud in the depths of the oceans. He then postulates that continental drift – explained in the next paragraph – occurred at speeds of 1–10 km per hour, and these forces hurled mud deposits onto the continents during the flood. He apparently does not explain how all that mud turned to rock very quickly.

While rejecting the bulk of geology, creationist geologists actually believe in tectonic plates and continental drift. It is now well established that the continents rest on huge plates of crust that are floating on a bed of magma, and over very long times they have been changing their positions, at rates in the order of 1–2 cm per year. They were once clustered together in a gigantic continent, Pangaea, which then broke up into a large northern supercontinent and another large southern supercontinent. The northern mass then broke up as North America drifted away from Eurasia, and the southern mass divided into South America, Africa, India, and Australia. As the tectonic plates separate, they create more ocean floor, whose gradual formation is visible in trenches between the continents, as in the middle of the Atlantic Ocean, both north and south. Where one plate pushes against another, the edge of one is generally forced downward, a process called subduction, while the plate on top is folded into mountain chains. This has happened, for instance, where the plate bearing India has pushed into the plate bearing Asia, raising the Himalayas. Even the slow movement of 1–2 cm per year requires enormous forces, but the friction between adjoining plates is so high that they cannot slide past each other smoothly; instead, they build up pressure that is released in sudden starts, which we experience as earthquakes.

The creationist contention that all these continental movements occurred in a very short time naturally leads to some absurdities. You may have been wondering where all the water of the flood went, and the creationist Henry Morris suggested that it all drained away into the ocean basins as the continents moved apart. But if this happened during the last half-year of the flood, the continents must have moved at incredible speeds. The Americas are about 4000–5000 km from Africa and Europe at various points, and to move even 4000 km in, say, 200 days, they were moving at 20 km per day or half a mile per hour! Perhaps realizing that such a speed defies belief, another group of creationists led by J. R. Baumgartner has proposed that after the Earth's core formed (only 6000 years ago!), the convection and friction from the moving plates of crust changed the Earth's mantle from the consistency of rock to the consistency of Jell-O, and the continents, riding on this base, were able to move at speeds of meters per second. One result was that plumes of steam emerged from some unknown source in the Earth and then condensed and created the flood. This scenario ignores the heat of the Earth's formation, which must have raised the temperature of the planet by 2500°C, so it is beyond belief to imagine that it happened within the last few thousand years. Furthermore, if the masses of steam were released that created the flood, their cooling released additional heat. Just how Noah and his family and all the creatures on the Ark survived this heat is not explained. But somehow it was all used to melt the Earth's mantle to the Jell-O consistency so the continents could be moving, though all this was happening underneath the flood waters that for some reason were not boiling away. Finally, at the end of the flood year, all this heat dissipated miraculously, leaving the Earth at its present temperature with no evidence of the heat and with very few hot springs, which we might have expected from the heat in the Earth.

These creationist arguments were obviously devised out of desperation. They are terrible examples (or perhaps excellent examples!) of special pleading, imagining special, unique circumstances that might explain the facts but defy common sense. Austin must assume extremely high CO_2 concentrations in the atmosphere, for which there is no other evidence. He must explain how plants and animals, including humans, that were adapted to those conditions could live in the atmosphere following the flood (and why, by the way, did it change?) with much lower CO_2 levels. He must assume that his high level of CO_2 caused animals to grow and die and produce calcareous muds at unheard-of rates and that the huge tectonic plates on which the continents rest were able to move at unheard-of speeds. Finally, even granting that such incredible movements could have generated the forces to throw ocean sediments onto the continents, he must explain how the sediments were deposited with fossils so neatly arranged in the order we find them.

coal deposits

Creationists don't do any better when they try to explain the formation of coal beds during the flood. According to traditional geology, the carboniferous strata that we mine for coal were formed from the gradual accumulation of 20–30 m of vegetation in swamps; bacteria living in this vegetation removed oxygen from it and left high concentrations of carbon, which then gradually turned into coal under the pressure of overlying rock. The oldest strata are around 320–280 Myr old; others were laid down in Mesozoic or even Cenozoic rocks. In Austin's doctoral thesis on a coal bed in Kentucky, he concludes that the bed had been a mat or logjam of floating vegetation that turned into coal very quickly. So creationists propose that all coal beds had been formed this way during the flood. However, the coal beds of Pennsylvania and West Virginia cover 20,000 km^2, and they are highly structured from sands and lake beds up through the overlying vegetation. Creationists still have to explain how a logjam of that size could have been formed, how it could differentiate into the observed structure, and finally how it could possibly turn into coal within only a few hundred years to, at most, a few thousand years.

the ice ages

Geologists have adduced overwhelming evidence for four ice ages during the Pleistocene era of the last two Myr. Observers in the nineteenth century began to realize that powerful forces had been moving huge rocks around when they saw that these rocks, some of them weighing many tons, were far removed from their places of origin. At first, their movement was ascribed to the rushing waters of the Noachian flood, but in 1802 John Playfair, a professor of mathematics at Edinburgh, suggested that they had been moved by glacial ice. This hypothesis explained the large scratches on these boulders as well as the huge moraines (deposits of gravel) that must have been deposited ahead of glaciers as they pushed down from the north. Other scientists presented evidence that the glaciers had covered large parts of Europe and North America. In 1840, Louis Agassiz published a study of the glaciers and developed the idea that there had been a rather recent ice age. Then in 1854, Adolphe Morlot discovered fossils of plants between layers of glacial deposits and interpreted this as evidence that there had been two warm periods between three distinct cold periods. The evidence is that subtropical vegetation was overrun by advancing ice sheets, laying down distinct soil horizons. Around 1900, Albrecht Penck and Eduard Brückner studied the Alpine glaciations and established that there had been four major glaciations, which they named Günz, Mindel, Riss, and Würm. Later investigations showed that some of these periods were divisible into subperiods of partial warming and partial retreat of glaciers. The glaciations have been dated in multiple ways. Ice cores cut down through the polar glaciers show thousands of distinct annual layers. Also, the decay of ^{14}C (see Table 1, chapter two) is used to date relatively recent geological events, and measurements of ^{14}C decay of the CO_2 in air bubbles trapped in the ice can be correlated with ^{14}C dating of trees and the patterns of tree rings, and with sedimentation in glacial lakes and the patterns of sedimentation in deep-sea cores. There is also good evidence for much older ice ages, including one in the Precambrian.

Of course, creationists ignore all this evidence. Austin's model for continental drift postulates that the heat released during this process warmed the ocean waters. (I mentioned earlier that the heat would have been so intense as to boil all the water away, but never mind.) Austin then postulates that the warmer oceans would have warmed the atmosphere and, for some unknown reason, facilitated transfer of moisture to the poles. He then introduces another postulate for which there is no evidence: that geologic activity during the flood produced volcanic ash, which reflected the sunlight, cooled the Earth, and produced a very brief ice age, which ended around 2000–2500 B.C.E. Leaving aside all the special assumptions, Austin does not explain how there could have been an ice age during historic times, when there is plenty of evidence for the beginnings of human civilizations without any massive ice sheets.

The creationist geologists have tried to develop other arguments to defend their beliefs, such as their interpretation of the sedimentary layers visible in the Grand Canyon. (The creationist influence has become so pervasive that visitors to the Grand Canyon can now purchase creationist literature giving their own version of how the sediments and the canyon itself were formed.) But by now you should be able to see that creationists can only defend their view of Earth's history by absurd assumptions and special pleadings, which are quite at odds with well-established principles of geology and physics, and with well-established history. Yet this is the kind of "science" they would like the public schools to teach our children.

"intelligent design theory"

Many people who would like to be creationists for religious reasons gave up on naïve creationism long ago, realizing that it is simply incompatible with all of modern biology with evolution as one of its central tenets – indeed, with modern science as a whole, as I have shown above. But the religious tendency made another foray into evolution and biology a few years ago in the form of so-called "intelligent design theory."

Intelligent design (ID) must be understood in its larger context, and for this purpose the collection edited by Pennock is invaluable. In her opening paper in this collection, Barbara Forrest explains that ID is a central factor in a program with much larger goals; in the words of Phillip E. Johnson, the inventor of ID, "we should affirm the reality of God by challenging the domination of materialism and naturalism in the world of the mind. With the assistance of many friends I have developed a strategy for doing this. ... We call our strategy the 'wedge.' " The movement began when Johnson, a Professor of Law at the University of California, Berkeley, underwent personal traumas after a divorce and became a born-again convert to Christianity. Focusing on evolution and creation as a central issue, Johnson gathered a group of sympathetic academics to advance his program. But their goal is not merely to overthrow the idea of evolution; it is to replace the entire naturalistic philosophy and methodology of science with an alternative philosophy, which Johnson dubs "theistic realism": "A theistic realist assumes that the universe and all its creatures were brought into existence for a purpose by God. Theistic realists expect this 'fact' of creation to have empirical, observable consequences that are different from the consequences one would observe if the universe were the product of nonrational causes." With evolution as its focus, Johnson and his followers have been energetically promoting their "wedge strategy," primarily through the Center for Renewal of Science and Culture, a part of the Discovery Institute, a Seattle-based think-tank.

The most articulate proponent of ID, as a would-be science, is William A. Dembski, who has developed some complex arguments based on an extensive historical review. His book *Intelligent Design* is subtitled, "The Bridge Between Science & Theology," and his fundamental motivation, clearly, is to promote theistic realism, though he does not use this phrase. Dembski dismisses scientific naturalism, as I outlined in chapter one, as an ideology that is not essential to science, and he would happily admit supernatural forces, such as gods, into science. (Evidently this is justified by a 1993 Gallup poll of the opinions of Americans about evolution.) But he does not realize – or at least admit – that such a move destroys the essence of science.

Naturalism entails the determination to restrict science to things and phenomena that can be investigated empirically. No one has ever seen electrons, but we can posit their existence because we can perform experiments that determine that they exist and have specific properties. But we cannot (scientifically) posit the existence of a god because there is no way to test such an idea empirically; you can imagine a god who has any characteristics you choose – one who loves beetles or hates homosexuals or prohibits the eating of milk and meat together – and belief in such a god can only be sustained through revelation, authority, and faith, not through investigation.

Dembski tries to develop a modern, sophisticated version of natural theology. The natural theologians of the nineteenth century put forward arguments for the existence of God based on their observations that the natural world is wonderfully complex and orderly; as the Anglican minister William Paley put it, if one found a watch in a field, one could immediately infer from its complexity that it had been designed, and by the same argument, the beauty, harmony, and order we observe in the world leads us to conclude that it must have had a designer – God. Dembski willfully misunderstands the genetic nature of organisms and the process of natural selection – he calls it an oxymoron. He denies that useful information can be generated by natural forces, though this is precisely what does happen as a result of mutation and natural selection – Monod's chance and necessity. He argues that the only explanation for the wonderfully organized, complex creatures we see around us, including ourselves, is design. Design then implies an Intelligence, a deity with the knowledge and power to have created everything. He develops a sophisticated argument that we can recognize design in nature by certain criteria, principally complexity and what he calls "specification." His notion of specification is difficult and far from clear, but the argument becomes more substantive when he relates it to the arguments of the biochemist Michael Behe.

In his book *Darwin's Black Box*, Behe argues that many biological systems are characterized by what he calls *irreducible complexity*, by which he means that they consist of essential parts so interrelated that removing a single part will destroy the function of the whole. His examples of such complex biochemical systems include the blood-clotting mechanism of vertebrate blood, the immune system, and the little motor mechanism that drives bacterial flagella, which I used as an example in chapter one. Behe doesn't have to dig very far for complicated mechanisms on which to base his arguments; organisms in their chemical detail are incredibly complicated. From this observation of complexity, Behe reasons that such systems could not have come into existence through a gradual evolution but must have been created in their fully functional form by an intelligence.

The scientific aspects of the issue raised by Behe and Dembski are far too complicated to examine here; my role is to guide the interested beginner into the fray, with a warning that it is intellectually taxing and not to be entered lightly. The counterargument to Behe, that even the most complex structures can be explained plausibly by means of known evolutionary processes – and perhaps similar processes yet to be discovered – has been developed by several writers, notably Richard Dawkins in such books as *The Blind Watchmaker*, whose title is a direct challenge to arguments of the Paley type. The issue, scientifically, comes down to a set of questions that need to be answered empirically and theoretically: for each specific biochemical mechanism, can one designate a plausible scenario for its evolution through ordinary evolutionary processes, without any need to invoke design or a designer? Though some investigators have given positive answers to the question in certain cases, it remains fundamentally open, a challenge for continued work.

Although Dembski and his colleagues propose to pass off their ideas as legitimate scientific theory, ID fails as science. Johnson, in the quotation above, expects theistic realism to have "empirical, observable consequences" that are different from those predicted by classical biological theory. Well, such consequences exist, but unfortunately for ID, the observations favor classical theory and call for the rejection of ID. I noted in chapter one and again in chapter six that all the evidence favors the random formation of new species and structures by opportunism and *bricolage*. Organisms actually have all kinds of defects in their structures and operations; had they been created by an intelligent designer, they would be designed much better than they are. Dembski and Behe evidently postulate an intelligent designer who is very good at making complicated biochemical systems but who makes all kinds of silly mistakes in constructing other systems, such as eyes and the pharyngeal apparatus that sometimes confuses breathing and swallowing. One ID response to such criticism is a version of the theodicy argument, that we simply do not know the mind of God, and what appears to us to be ugly, dysfunctional, and nonideal is perfect and beautiful from God's point of view, with his cosmic perspective. But if ID purports to be science, this argument takes it outside the boundaries of science. ID fails the empirical test: it no longer has implications for observations or experiments that could challenge it. It becomes unfalsifiable.

But the ID argument fails as science in a second way. Science is an open-ended program of determination to seek answers to questions of Why and How about the universe. The Behe–Dembski program represents abandoning that quest, giving it up. That is one of its fundamental difficulties. (I'll get to its other, more serious difficulty in a moment.) We see some extremely complicated mechanism operating in an organism, and the spirit of the scientific quest demands that we seek an answer to its origin: explain how, step by step, protein by protein, this mechanism could have come into existence through ordinary biological processes. That is an open challenge, and evolutionary biologists must meet it in instance after instance. But the ID proponents write a period where there ought to be a question mark; they shut the door on scientific inquiry by giving a pat, unsatisfactory answer: "God designed it. That's the answer, so forget it and go about your business."

I have shown that "scientific creationism" is a pseudoscience because it must pervert science to conform to an ideology, Christian fundamentalism. But ID is a pseudoscience of a much more dangerous sort, because it would not only pervert a limited arena of science but would pervert science as a whole, as a human enterprise, to satisfy the same ideology. Dembski's book *Intelligent Design* purports to be developing a richer science and to be creating a link between science and religion; but the science Dembski would create by rejecting naturalism would be distorted and ultimately unrecognizable as science, an enterprise subservient to the Christian theology so prominent in his book. Dembski, Johnson, and their colleagues make no secret of their strategy to gradually wedge Christian theology into science. However, we now have a history – a sad and frightening history – of sciences perverted and repressed by ideologies, extending from the persecution of Galileo by the Catholic Church to the long suppression of genetics in the Soviet Union in the name of communist ideology. In the past few years, critics have cited instances of science being perverted and ignored in the U.S. by the current administration whenever it conflicts with the administration's political ideology. The last thing any secular democracy now needs is a pseudoscience based on the belief "that the universe and all its creatures were brought into existence for a purpose by God."

The ID supporters expect to extend their ideology into the operation of American society, and eventually world society, by making

ID a part of public school science education. Thus their program is a real danger to all secular, democratic societies since it threatens to replace democracy with theocracy. Unfortunately, ID is very seductive to those who are scientifically and philosophically unsophisticated, including most educators, who cannot have had extensive study in science and philosophy on their way to becoming teachers and administrators. Then, given a public already skeptical about evolution and school boards made of equally ignorant citizens whose personal agendas often include introducing religion into the schools, the wedge cohorts have potentially fertile ground for their program. Although the U.S. Supreme Court has ruled against the outright teaching of creationism in the public schools, the battle to keep education free of ID will depend upon articulate and philosophically sophisticated advocates to argue before courts that may be unable to comprehend the subtleties of the issue.

Those who still believe in democracy rather than theocracy will have to be constantly vigilant of their legislatures and their local school boards. Fundamentalist legislators may introduce bills mandating the teaching of creationism or ID in their states' schools; though such bills may make little headway in the busy legislative process, citizens need to keep an eye on them and be ready to oppose them. I hope this book can serve as a citizen's handbook for those who need to marshal their arguments before legislatures and school boards. As the judiciary that might stand against this movement becomes more politicized, we cannot rely on it as an ally in the fight for democracy and rationality. Only a highly educated, activist citizenship can ensure the health of democracy as we know it.

notes

1. Much of the argument in this section is taken, with the author's permission, from Donald U. Wise's paper "Creationism's Geologic Time Scale." I thank Dr. Wise for giving me permission to use his paper so extensively.

references and further reading

Note Books are listed under the chapter in which they are first mentioned, but some are relevant to more than one chapter.

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