Selected Essays by

Stephen Jay Gould

Eight Little Piggies

RICHARD OWEN, England's greatest vertebrate anatomist during Darwin's generation (see Essay 5), developed the concept of an archetype to explicate the evident similarities that join us with frogs, flamingoes, and fishes. (An archetype is an abstract model constructed to generate an entire range of anatomical design by simple transformation of the all-inclusive prototype.) Owen was so pleased with his conception that he even drew a picture of his archetype, engraved it upon a seal for his personal emblem, and, in 1852, wrote a letter to his sister Maria, trying to explain this arcane concept in layperson's terms:

> It represents the archetype, or primal pattern—what Plato would have called the "divine idea" on which the osseous frame of all vertebrate animals—i.e. all animals that have bones—has been constructed. The motto is "the one in the manifold," expressive of the unity of plan which may be traced through all the modifications of the pattern, by which it is adapted to the very habits and modes of life of fishes, reptiles, birds, beasts, and human kind.

Darwin took a much more worldly view of the concept, substituting a flesh and blood ancestor for a Platonic abstraction from the realm of ideas. Vertebrates had a unified architecture, Darwin argued, because they all evolved from a common ancestor. The similar shapes and positions of bones record the historical happenstance of ancestral form, retained by inheritance in all later species of the lineage, not the abstract perfection of an ideal shape in God's realm of ideas. Darwin burst Owen's bubble with a marginal note in his personal copy of Owen's major work. *On the Nature of Limbs.* Darwin wrote: "I look at Owen's archetype as more than idea, as a real representation as far as the most consummate skill and loftiest generalization can represent the parent form of the Vertebrata."

However we construe the concept of an organizing principle of design for major branches of the evolutionary tree—and Darwin's version gets the modern nod over Owen's—the idea remains central to biology. Consider the subset of terrestrial vertebrates, a group technically called Tetrapoda, or "four-legged" (and including amphibians, reptiles, birds, and mammals in conventional classifications). Some fly, some swim, and others slither. In external appearance and functional role, a whale and a hummingbird seem sufficiently disparate to warrant ultimate separation. Yet we unite them by skeletal characters common to all tetrapods, features that set our modern concept of an archetype. Above all, the archetypal tetrapod has four limbs, each with five digits—the so-called pentadactyl (or "five-fingered") limb.

The concept of an archetype does not require that each actual vertebrate display all canonical features, but only that uniqueness be recognized as extreme transformations of the primal form. Thus, a whale may retain but the tiniest vestige of a femur, only a few millimeters in length and entirely invisible on its streamlined exterior, to remind us of the ancestral hind limbs. And although a hummingbird grows only three toes on its feet, a study of embryological development marks them as digits two, three, and four of the full ancestral complement. The canonical elements are starting points and generating patterns, not universal presences.

In the tetrapod archetype, no feature has been more generally accepted than the pentadactyl limb, putative source of so many deep and transient human activities, from piano playing to touch typing, duck shooting, celebratory "high fives," and decimal counting (twice through the sequence of "this little piggy . . ."). Yet this essay will challenge the usual view of such a canonical number, while not denying its sway in our lives.

The great Swedish paleontologist, Erik Jarvik, closed his two-volume magnum opus on vertebrate structure and evolution with a telling point about pentadactyl limbs and human possibilities.

He noted how many "advanced" mammals modify the original pattern by loss and specialization of digits—horses retain but one as a hoof; whales practically lose the whole hind limb. Jarvik noted that an essential coupling of a multidigited hand, fit for using tools, with an enlarging brain, well suited to devising new and better uses for such technology, established the basis and possibility of human evolution. If the ancestor of our lineage had lost the original flexibility of the "primitive" pentadactyl limb and evolved some modern and specialized reduction, human intelligence would never have developed. In this important sense, we are here because our ancestors retained the full archetypal complement of five and had not substituted some new-fangled, but ultimately more limiting, configuration. Jarvik writes:

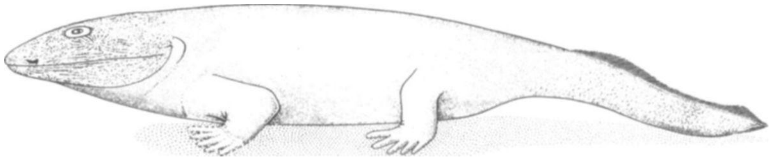
> The most prominent feature of man is no doubt his large and elaborate brain. However, this big brain would certainly never have arisen—and what purpose would it have served—if our arm and hand had become specialized as strongly as has, for instance, the foreleg of a horse or the wing of a bird. It is the remarkable fact that it is the primitive condition, inherited from our osteolepiform ancestors [fishes immediately ancestral to tetrapods] and retained with relatively small changes in our arm and hand, that has paved the way for the emergence of man. We can say, with some justification, that it was when the basic pattern of our five-fingered hand for some unaccountable reason was laid down in the ancestors of the osteolepiforms that the prerequisite for the origin of man and the human culture arose.

I don't dispute Jarvik's general point: The retention of "primitive" flexibility is often a key to evolutionary novelty and radiation. But is the five-fingered limb a constant and universal tetrapod archetype, interpreted in Darwin's evolutionary way as an ancestral pattern retained in all descendant lineages?

Erik Jarvik is maximally qualified to address this question (his rationale, of course, for raising it in the first place), for he has done by far the most extensive and important research on the earliest fossil tetrapods—the bearers and perpetrators of the five-fingered archetype in any evolutionary interpretation. (Fish fins are constructed on different principles, although the lobe-finned ancestors of tetrapods built a bony architecture easily transformable to the fore and hind limbs of terrestrial vertebrates. In any case, fish do not display the pentadactyl pattern, and this central feature of canonical design arose only with the evolution of the Tetrapoda.)

The oldest tetrapods were discovered in eastern Greenland by a Danish expedition in 1929. They date from the very last phase of the Devonian period, a geological interval (some 390 to 340 million years ago) often dubbed the "age of fishes" in books and museum exhibits that follow the silly chauvinism of naming time for whatever vertebrate happened to be most prominent. The Swedish paleontologist Gunnar Save-Soderbergh collected more extensive material in 1931 and directed the project until his untimely death in 1948. Erik Jarvik then took over the project and, during the 1950s, published his extensive anatomical studies of two genera that share the spotlight of greatest age for tetrapods—*Ichthyostega* and *Acanthostega.* Although no specimens preserved enough of the fingers or toes for an unambiguous count, Jarvik (see figure) reconstructed the earliest tetrapods with the canonical number of five digits per limb.

Our confidence in this evidence-free assumption of an initial five began to crumble in 1984, when the Soviet paleontologist O. A. Lebedev reported that the newly discovered early tetrapod *Tulerpeton,* also of latest Devonian age, bore six digits on its limbs. This find led anatomist and embryologist J. R. Hinchliffe to suggest in 1989, prophetically as we have just learned, that five digits represents a secondary stabilization, not an original state. Hinchliffe entitled his article "Reconstructing the archetype: Evolution



The standard reconstruction of *Ichthyostega* from Jarvik's 1980 book. Note the five digits on each limb. *From* Basic Structure and Evolution of Vertebrates, *vol. 1, p. 235.*

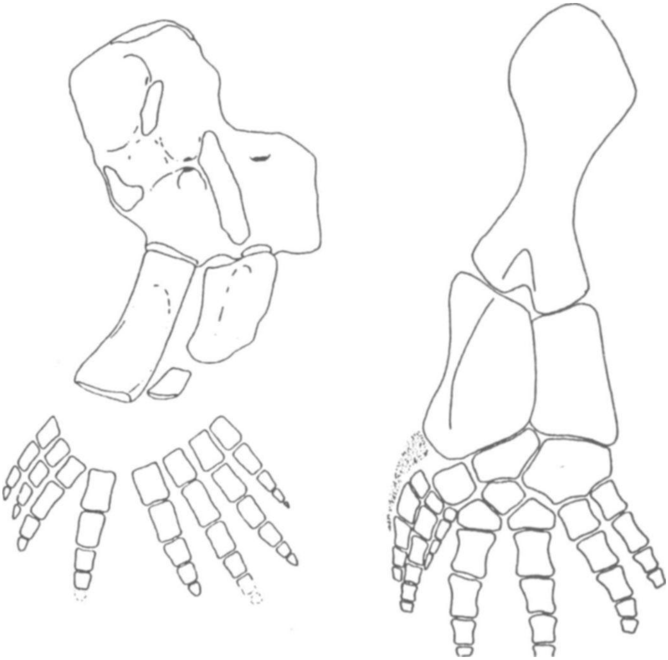
of the pentadactyl limb," and ended with these words: "Restriction to the pentadactyl form may have followed an evolutionary experimental phase."

Hinchliffe's suspicion has now been confirmed—in spades. In October 1990, M. I. Coates and J. A. Clack reported on new material of *Ichthyostega* and *Acanthostega,* collected by a joint Cambridge-Copenhagen expedition to East Greenland in 1987 (see bibliography). Some remarkable new specimens—a complete hindlimb of *Ichthyostega* and a forelimb of *Acanthostega*—permit direct counting of digits for the first time.

In an admirable convention of scientific writing that maximizes praise for past work done well and minimizes the disturbing impact of novelty, Coates and Clack write: "The proximal region [closest to the body] of the hindlimb of *Ichthyostega* corresponds closely with the published description, but the tarsus [foot] and digits differ." In fact, the back legs of *Ichthyostega* bear, count 'em, seven toes!—with three smallish and closely bound digits corresponding to the hallux ("big toe" in human terms) of ordinary five-toed tetrapods (see figure). *Acanthostega* departs even more strongly from a model supposedly common to all; its forelimb bears eight digits in a broad arch of increasing and then decreasing size (see figure).

The conclusion seems inescapable, and an old "certainty" must be starkly reversed. Only three Devonian tetrapods are known. None has five toes. They bear, respectively, six, seven, and eight digits on their preserved limbs. Five is not a canonical, or archetypal, number of digits for tetrapods—at least not in the primary sense of "present from the beginning." At best (for fans of pentadactyly) five is a later stabilization, not an initial condition.

Moreover, in the light of this new information, an old fact may cast further doubt on the primacy of five. The naive "ladder of life" view depicts vertebrate evolution as a linearly ascending series of amphibian-reptile-mammal-human (with birds as the only acknowledged branch). But ladders are culturally comforting fictions, and copious branching is the true stuff of evolution. Tetrapods had a common ancestor to be sure, but modern amphibians (frogs and salamanders) represent the termini of a large branch, not the inception of a series. Moreover, no fossil amphibian seems clearly ancestral to the lineage of fully terrestrial verte-



Left: forelimb of *Acanthostega* with 8 digits. Right: hindlimb of *Ichthyostega* with seven digits. *Reprinted by permission from* Nature *vol. 3-17, p. 67; Copyright © 1990 Macmillan Magazines Limited.*

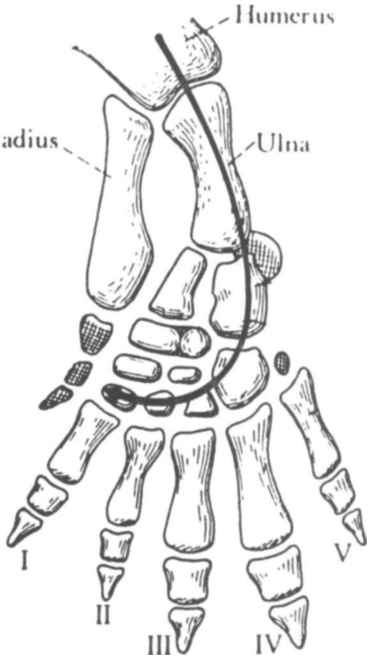
brates (reptiles, birds, and mammals), called Amniota to honor the "amniote" egg (with hard covering and "internal pond"), the evolutionary invention that allowed, in our usual metaphors, "complete conquest of the land" or "true liberation from water." (The point is tangential to this essay, but do pause for a moment and consider the biases inherent in such common "descriptions." Why is the ability to lay eggs on land a "liberation"; is water tantamount to slavery? Why is exclusive dwelling a "conquest"? Who is fighting for what? Such language only makes sense if life is struggling upward towards a human pinnacle—the silliest and most self-centered view of evolution that I can imagine.)

The first fossil reptiles are just about as old as the first amphibians clearly in the group that eventually yielded our modern frogs and salamanders. Thus, rather than a ladder from amphibian to reptile, both the fossil record and the study of modern vertebrate anatomy suggest an early branching of the tetrapod trunk into two primary limbs—the Amphibia and the Amniota (reptile, bird, and mammal).

And now, the point about pentadactyly and its limits: The Amniota do, indeed, show the canonical pattern of five toes upon each limb (or some modification from this initial state). But Amphibia, both living and fossil, have five toes on the hindlimbs and *only four* on the front limbs. Anatomists have known this for years of course, but have always assumed that this reduction to four proceeded from an initial and canonical five. This conclusion must now be challenged. If all the earliest tetrapods had more than five digits, and if amphibians have been separate from amniotes since the beginning of terrestrial life, why assume that the four toes of the amphibian forelimb descended from a primary five? All modern stabilizations probably proceeded from more than five. Perhaps the amphibian forelimb went from this higher number directly to four, without any pentadactyl stage between. If so, then pentadactyly crumbles on two grounds: (1) It does not represent the original state of tetrapods (as six-, seven-, and eight-toed earliest forms show); and (2) it may not mark the canonical state in one of the two great living lineages of tetrapods.

A key to understanding these new views may be found in a brilliant paper (see bibliography) on the embryological development of limbs, based on work done just down the hall from my office and published in 1986 by Neil H. Shubin (now at the University of Pennsylvania) and Pere Alberch (now director of the Natural History Museum in Madrid). Shubin and Alberch try to depict the complexity of the tetrapod limb as the outcome of interactions among three basic processes: branching (making two series from one), segmentation (making more elements in a single series), and condensation (union between elements). The limb builds from the body out—shoulder to fingers, thigh to toes. The process begins with a single element extending from the trunk—humerus for the arm, femur for the leg. A branching event produces the next elements in sequence—radius and ulna for the arm, tibia and fibula for the leg. The branching (to wrist bones) sets the distinctive pattern that eventually makes fingers. This key bifurcation is markedly asymmetrical, as one bone ceases to branch (and yields but a single row of segments as the limb continues to develop), while the other serves as a focus for all subsequent multiplication of elements, including the production of digits. Oddly enough, the bone that does not branch is the larger of the two elements—the radius of the arm and the tibia of the leg. The hand and foot are made by branching from the smaller element—the ulna of the arm and the fibula of the leg. (A glance at the accompanying figure should make these anatomical arcana clear.)

These basic facts have long been appreciated. Shubin and Al-



Standard anatomy of a tetrapod forelimb showing the axis of embryological development according to Shubin and Alberch. *From* Basic Structure and Evolution of Vertebrates. *voL I. p. 215.*

berch make their outstanding contribution in providing a new account of subsequent branching. The classical view holds that a central axis continues from the ulna (or fibula), and that the subsequent branches project from this axis (much like the persistent midvein and diverging lateral veins of a leaf). In this view, the roots of the digits represent different branches. Under this model, largely unchallenged for more than one hundred years, debate focused on the identity of the main axis and its position relative to the digits. T. H. Huxley, for example, argued that the main axis passed through digit three; the British vertebrate paleontologist D. M. S. Watson favored digit four, while the American W. K. Gregory advocated a position between digits one and two.

Shubin and Alberch do not deny the idea of a central axis, but they radically reorient its position. Instead of passing through a particular digit (with remaining digits branching to one side or the other), Shubin and Alberch's axis passes through the basal bones of *all* the digits in sequence, from back to front (again, a glance at the figure will make this argument clear).

The elegant novelty of this switch may not be evident in the simple change of position for the axis. Consider, instead, the question of timing. Under the old view, one might talk about a dominant digit (focus of the central axis) and subordinate elements (products of increasingly distant branching), but no implications of timing could be drawn. Under Shubin and Alberch's revision, the array of digits becomes a sequence of timing: Spatial position is a mark of temporal order. Back equals old; front is young. The piggy that "cried wee, wee, wee all the way home" comes first, the one that went to market is last. The thumb and big toe may be functionally most important in humans, but they are the last to form.

As always in natural history, nothing is quite so simple, or free from exceptions, as its cleanest and most elegant expression. Actually, the penultimate digit always forms first—ironically, the piggy that had none—and the sequence then proceeds from back to front with one exception in a reverse branch to digit five. Moreover, this generality meets a fascinating exception in the urodeles (the amphibian group of newts and salamanders, although the other major amphibian lineage of Anura, the frogs, forms digits in the usual back-to-front sequence). Uniquely among tetrapods, urodeles work from front to back (although they also follow the rule of penultimate first, beginning with digit two and then proceeding on towards five). Some zoologists have used this basic difference to argue that urodeles form an entirely separate evolutionary line of tetrapods, perhaps even arising from a different group of fish ancestors. But most (including me) would respond that embryonic patterns are as subject to evolutionary change as adult form, and that an ancestor to the urodele lineage—for some utterly unknown and undoubtedly fascinating reason—shucked an otherwise universal system in tetrapods and developed this "backwards" route to the formation of digits.

But why bring up this innovative model for embryological formation of digits in the context of new data on the multiplicity of fingers and toes in the earliest tetrapods? I do so (as did Coates and Clack in their original article) because the Shubin and Alberch model suggests a simple and obvious mechanism for a later stabilization of five from an initial lability that yielded varying numbers of supernumerary digits. If digits form from back to front in temporal order, then reduction can be readily achieved by an earlier shut-down. The principle is obvious and pervasive: Stop sooner. We can reduce population growth if families halt at two children. You can cut down on smoking or drinking by setting a limit and stopping each day at the reduced number (easier said than done, but the principle is simple enough to articulate). Evolution can reduce the number of fingers by stopping the back-to-front generating machine at five. What we now call digit one (and view as the necessary limit of an invariant archetype) may only be the stabilized stopping point of a potentially extendable sequence.

This perspective makes immediate sense of some old and otherwise unexplained data of natural history. Many lineages in all tetrapod groups reduce the original complement of five to some smaller number—sometimes right down to one, as in horses. As a general principle of reduction, known since Richard Owen's time, digit one is the first to go. Owen wrote in 1849:

> To sum up, then, the modifications of the digits: they never exceed five in number on each foot in any existing vertebrate animal above the rank of Eishes. .. . The first or innermost digit, as a general rule, is the first to disappear.

Under Shubin and Alberch's model, the reason behind this rule is obvious: last formed, first gone (the natural analog of the economic maxim: last hired, first fired).

The opposite phenomenon of polydactylous mutations (producing more than five digits) also supports the Shubin and Alberch model. In humans, most polydactylous mutations produce a sixth finger as a simple duplication (subsequent to initial branching) of one member in the usual sequence of five—a phenomenon outside the scope of Shubin and Alberch's concerns. But, in several other species, the supernumerary elements of multifingered mutants arise by extension as digits continue to form after the branching of digit number one, the usual terminus of the series. J. R. Hinchliffe writes in 1989: "Many polydactylous mutants . . . have an array of five normal digits, with the supernumerary digits added preaxially [that is, after formation of digit one]." Moreover, Hinchliffe cites some experimental data on inhibition of DNA synthesis during embryology of the lizard *Lacerta inridis.* With less material available for building body parts, digits may be lost. The last-formed digit is always the first to go. Data from both sides therefore support the idea that digits form in temporal series, back to front, and that spatial position is a mark of order in embryological timing: Extra digits are added to, and old digits are lost from, the temporal end-point of the canonical sequence—digit number one.

The pleasure of discovery in science derives not only from the satisfaction of new explanations, but also, if not more so, in fresh (and often more difficult) puzzles that the novel solutions generate. So for the Shubin and Alberch model and our new discoveries on multiplicity of digits in the earliest tetrapods. We used to think of five digits as invariant and canonical, and our chief question was always: Why five? But if five is a secondary stabilization, a stopping point in a temporal sequence with other potential (but unrealized) terminations, we must ask a very different, and in many ways more interesting, question: Why stop at this point? What, if anything, is special about five?

Since five seems to possess a certain arbitrariness under the new views, the tenacity of its stabilization in tetrapods seems all the more enigmatic. The embryological apparatus remains capable of producing more than five (at least in many species), as mutational and experimental data show. But these polydactylous mutations remain as anomalies of individuals or of small and evanescent family lines. They never stabilize within a larger group, and no vertebrate species has more than five digits generated from the back-to-front axis of the Shubin and Alberch model.

The best proof of this assertion lies in apparent (but not actual) exceptions of several tetrapod species with six functional digits. Yes, Virginia, several species do grow six fingers as a rule, not an exceptional state of mutant individuals. Yet this sixth finger is always generated in a different manner and not by the obvious (and apparently easy) mechanics of simple extension past digit one on the Shubin-Alberch series. Frogs, for example, often have six digits on their hind feet (or five on their normally four-fingered front feet). But this extra digit forms in a unique manner by extension of the unbranched sequence of bones leading out from the radius or tibia—the limb bones that never serve as foci for branches and therefore do not (in any other tetrapod species) participate in the production of digits. Anatomists have long recognized the anomalous character of these unique digits by naming them *prepollux* (for the forelimb) or *prehallux* (for the hindlimb). (*Pollux* and *hallux* are technical names for digit number one—our thumb and big toe. Prepollux and prehallux therefore designate an anomalous digit, located in front of the usual front and formed in a different manner.)

A few mammals also possess a functional sixth digit—the panda, whose false "thumb" has been a staple of these essays, and several species of moles. But these false thumbs are formed from extended wrist bones, and are not true digits at all. These facts seem to heighten the oddity (and rigidity) of stabilization at five in a sequence that was once extendable, remains so now for mutations and experimental manipulations, but seems recalcitrant in setting a maximum of five as a normal state in all tetrapod species. When six functional digits form, the extra item must be built in another way.

So why five? Of two major approaches to this question, the conventional Darwinian, or adaptationist, strategy tries to discern a marked advantage, or even an inevitability, for five in terms of utility for an organism's habitat (an advantage that might promote this configuration by natural selection). A plausible case can be made in terms of benefits for terrestrial life. Creatures that evolve from water to land face many novel challenges, none more severe than the new force of gravity and the consequent need for support in the absence of buoyancy previously supplied by water. The transition from fins to limbs provides the basis for this support, and an old argument holds that five might be an optimal configuration for weight-bearing—a central axis running through on digit three, with adequate and symmetrical buttressing on each side (one or three toes might not provide enough lateral support against wobbling, while seven toes might be superfluous and interfere with locomotion). On this argument, tetrapods have five toes because support and locomotion demand (or at least strongly encourage) this configuration as optimal.

The argument is not implausible, and surely gains credence from the probability that five digits evolved twice on hind limbs—separately, that is, in the two great divisions of tetrapods. The most obvious counterargument may also be support in disguise: Why, if five be best on land, do the earliest tetrapods bear six, seven, and eight toes respectively? A paradoxical retort holds that these first tetrapods evolved their limbs for locomotion in water and remained predominantly, if not entirely, aquatic. *Ichthyostega,* as long recognized, maintained a small tail fin and lateral-line canals on the skull. (Lateral line organs "hear" sound by sensing vibrations propagated through water, a method that does not work in thin air—see Essay 6.) Coates and Clack's restoration of *Ichthyostega* and *Acanthostega* limbs add support to this interpretation in a streamlined shape and a limit to rotation that might keep the limb horizontal, in fin position, rather than rotated downward to support a body on land (at least for *Acanthostega,* though the *Ichthyostega* forelimb seems fully load-bearing).

But strong elements of doubt also plague this adaptationist view. First, as stated above, members of one tetrapod lineage, the amphibians, grow but four toes on their front legs, and we have no evidence for an initial five—so pentadactyly may not be a universal stage in terrestrial vertebrates. Second, if five (with symmetry about a strong central toe) be the source of advantage, then why does our favorite species, the traditional measure of all things—*Homo sapiens*—retain five, require great strength in using only two limbs against gravity, but construct the end-member first toe as the main weight bearer?

The second major approach—historical contingency in my favored terminology (see my recent book, *Wonderful Life*)—argues that five was not meant to be, but just happens to be. Other configurations would have worked and might have evolved, but they didn't—and five works well enough. The obvious supports for this alternative view lie scattered throughout this essay. If five is so good, why do so many species devise such curious and devious means to produce six (prepollux or converted wrist bone)? If five is so predictable, why does one of two lineages grow but four? (I should say right up front that neither of these two positions—adaptation or contingency—really addresses the greatest puzzle of all: the recalcitrant stability of five once it evolves. I suspect that this is a question for embryologists and geneticists; phylogenetic history may offer little in the way of clues. Why should five, once attained by whatever route and for whatever reason, be so stubbornly intractable as an upper limit thereafter, so that any lineage, again evolving six or more, must do so by a different path? The inquiry could not be more important, for this issue of digits is a microcosm for the grandest question of all about the history of animal life: Why, following a burst of anatomical exploration in the Cambrian explosion some 550 million years ago, have anatomies so stabilized that not a single new phylum [major body plan] has ever evolved since?)

But the greatest boost to contingency lies in the discovery that prompted this essay in the first place—seven digits in *Ichthyostega* and eight in *Acanthostega.* If tetrapods had five at the beginning, and always retained five thereafter, then some predictability or inevitability could legitimately be maintained. (At the very least, no fuel would exist for an alternative proposal.) But if the first members of the lineage had six, seven, or eight toes, then alternative possibilities are legion, and an eventual five may be a happenstance, not a necessity.

Embryologist Jonathan Cooke, in a commentary written to accompany Coates and Clack's paper, agrees with me that possible contingency of pentadactyly is the most interesting implication of the new discovery. But he makes a curious statement in his advocacy. Cooke writes:

> But for most of us, philistine enough to accept the historically contingent nature of evolution, there is nothing specially deep about the number five. Pianists should ponder

> the challenge that our motor cortexes would have been set had Bach or Scarlatti sported eight deeply and ineffably named fingers per hand.

I love the idea, but I decry the apology and abnegation implied by the designation of "philistine" for contingency. This unnecessary humility follows an unfortunate tradition of self-hate among scientists who deal with the complex, unrepeatable, and unpredictable events of history. We are trained to think that the "hard science" models of quantification, experimentation, and replication are inherently superior and exclusively canonical, so that any other set of techniques can only pale by comparison. But historical science proceeds by reconstructing a set of contingent events, explaining in retrospect what could not have been predicted beforehand. If the evidence be sufficient, the explanation can be as rigorous and confident as anything done in the realm of experimental science. In any case, this is the way the world works: No apologies needed.

Contingency is rich and fascinating; it embodies an exquisite tension between the power of individuals to modify history and the intelligible limits set by laws of nature. The details of individual and species's lives are not mere frills, without power to shape the large-scale course of events, but particulars that can alter entire futures, profoundly and forever.

Consider the primary example from American history. Northern victory was not inevitable in the Civil War, for the South was not fighting a war of conquest (unwinnable given their inferiority in manpower and economic wealth), but a struggle to induce war weariness and to compel the North to recognize their boundaries. The Confederacy had almost succeeded in 1863. Their armies were deep into Pennsylvania; draft riots were about to break out in New York City; Massachusetts was arming the first regiment of free black volunteers—not from an abstract sense of racial justice but from an urgent need for more bodies. In this context, the crucial Battle of Gettysburg occurred in early July. Robert E. Lee made a fateful error in thinking that his guns had knocked out the Union battery, and he sent his men into the nightmare of Pickett's Charge. Suppose we could rerun history and give Lee another chance. This time, armed with better intelligence perhaps, he does not blunder and prevails. On this replay, the South might win the war, and all subsequent American history becomes radically different. The actual outcome at Gettysburg is no minor frill in an inevitable unrolling of events, but a potential setting point of all later patterns.

Never apologize for an explanation that is "only" contingent and not ordained by invariant laws of nature, for contingent events have made our world and our lives. If you ever feel the slightest pull in that dubious direction, think of poor Heathcliff who would have been spared so much agony if only he had stayed a few more minutes to eavesdrop upon the conversation of Catherine and Nelly (yes, the book wouldn't have been as good, but consider the poor man's soul). Think of Bill Buckner who would never again let Mookie Wilson's easy grounder go through his legs—if only he could have another chance. Think of the alternative descendants of *Ichthyostega,* with only four fingers on each hand. Think of arithmetic with base eight, the difficulty of playing triple fugues on the piano, and the conversion of this essay into an illegible Roman tombstone, for how could I separate words withoutathumbtopressthespacebaronthistypewriter.

Bent Out of Shape

WE ALL DREAM about retirement projects that might recapture the lost pleasures of youth, or perfect what we had, perforce, abandoned when the practicalities of making a living and supporting a family intervened. Some day, in a rosy future after the millennium, I will take out my old stamp album or sit down at the piano and finally progress beyond the first of Bach's two-part inventions and the Prelude in C Major from Book 1 of the Well-Tempered Clavier.

Charles Darwin, my hero and role model, achieved this exquisite pleasure, so I may yet have hope for emulation. His last book, published a year before his death, treated the apparently arcane, but vitally important subject of earthworms and their role in forming the topsoil of England. This wonderful and disarming book unites Darwin's end, in the calmness of old age, secure in the knowledge of accomplishment, with his more tumultuous youth, sparked by the fires of unrealized ambition. For Darwin wrote the precis of his worm book in 1838, just two years after the *Beagle* docked—a brilliant five-page article, presenting the entire argument that would fill a book more than forty years later. Darwin concluded:

> The explanation of these facts, . . . although it may appear trivial at first, I have not the least doubt is the correct one, namely, that the whole operation is due to the digestive process of the common earth-worm.

Odd juxtapositions always intrigue me. I do not grant them deep meaning, and firmly believe that they represent nothing more than coincidence. Nonetheless, we do take notice, if only because we must find patterns to tell stories. Darwin published his paper in the fifth volume of the second series of the *Transactions of the Geological Society of London* in 1838. I was reading this paper a few months ago, and couldn't help turning the last page to note the subsequent article, a four-page "Note on the dislocation of the tail at a certain point observed in the skeleton of many Ichthyosauri," written by Richard Owen.

Richard Owen, then a young man, became England's greatest comparative anatomist and first director for the Natural History division of the British Museum when the collections finally escaped the shadows of the Elgin Marbles at Bloomsbury and won their own magnificent home in South Kensington (one of the world's great Victorian buildings and an essential stop on any visit to London).

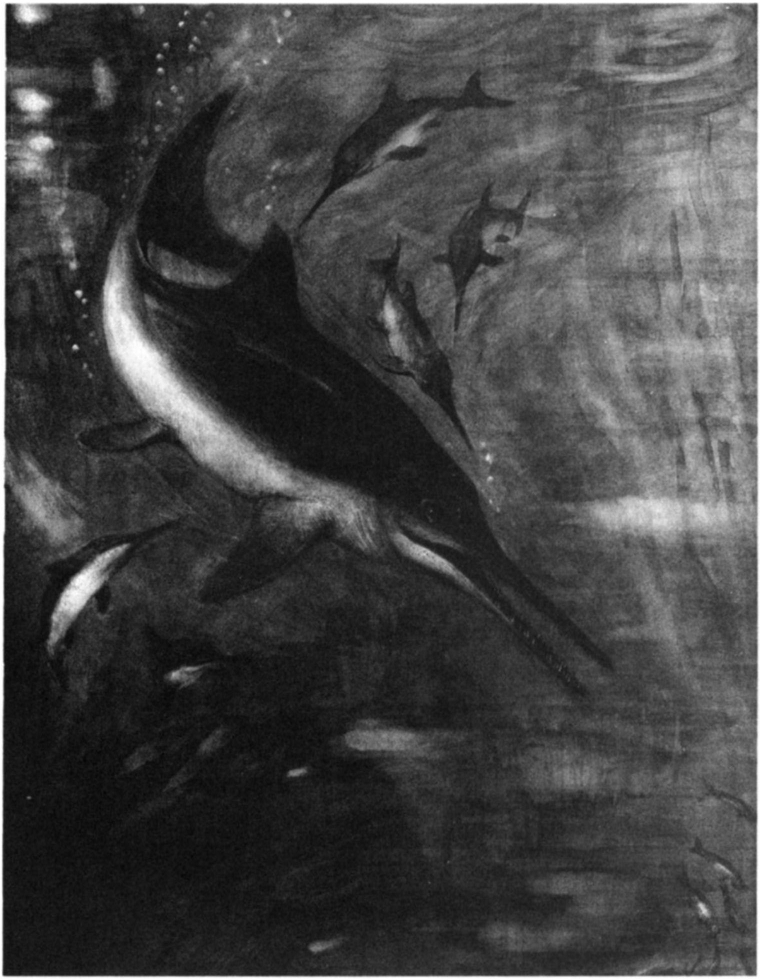
Owen and Darwin had a long and problematical relationship. Darwin originally courted Owen's friendship and support. (Owen, at Darwin's request, formally described for publication the fossil mammals that Darwin had collected on the *Beagle.* Darwin's famous *Toxodon,* for example, was named, described, and illustrated by Owen.) But the relationship inevitably soured, in part because Owen's vanity could not bear Darwin's successes. Legend holds that Owen's rejection of evolution prompted their final break, but such a falsehood only records our propensity for simplifying stories told in the heroic mode, thus making "bad guys" both nasty and stupid. Owen did reject natural selection, and with vigor, as an excessively materialistic theory depending too much on external environments and too little on laws of organic structure, but he embraced evolution as a guiding principle in natural history.

In any case, the juxtaposition of worm and ichthyosaur dates from 1838, an early period of their friendship. I couldn't help noticing another link more interesting than mere spatial proximity. Darwin wrote, as quoted above, that his subject seemed trivial but really unleashed a cascade of implications leading to substantial importance. Owen then made the very same point, arguing that an apparently broken tail in an ichthyosaur might seem entirely devoid of interest, but that close study yielded generalities of more than passing concern. Since the conversion of detail to wide message, through links of tangential connection, forms the stock-in-trade of these essays, I could hardly avoid such a double invitation to discourse at greater length on the tail bend of ichthyosaurs.

Ichthyosaurs are a group of marine reptiles with bodies so fishlike in external form that they have become the standard textbook example of "convergence"—evolved similarity from two very different starting points as independent adaptive responses to a common environment and mode of life (wings of birds and bats, eyes of squids and fishes). Ichthyosaurs are not closely related to dinosaurs, though they arose at about the same time and became extinct before the great wipeout that ended the dinosaurs' reign some 65 million years ago. (The god-awful spelling of their names, with its unpronounceable sequence *chth,* only records an orthographic convention in converting Greek letters to Roman. This four-consonant sequence represents two Greek letters, *chi* and *theta,* one transliterated *ch,* the other as *th.* Both belong to a five-letter Greek word for fish, and ichthyosaur means "fish lizard." We meet the same orthographic problem in such words as ophthalmology. But never despair and remember that things could always be worse. What would you do if that four-letter sequence came right at the beginning of a word—as it does in a common barnacle with the most forbidding name of *Chthamalus.)*

In considering the convergence of ichthyosaur upon fish, we marvel most at the form and location of fins and paddles—the machinery of swimming and balancing. The fore and hind paddles are, perhaps, least remarkable, for ancestral structures are clearly present as front and back limbs of terrestrial forebears—and these can be modified, as whales and dolphins have done, to forms better suited for sculling than for walking. But the dorsal (back) and caudal (tail) fins are boggling in their precision of convergence with analogous structures in fishes. For the terrestrial ancestors of ichthyosaurs obviously possessed neither back nor tail fin, and ichthyosaurs therefore evolved these structures from scratch—yet they occupy the position, and maintain the form, that hydrodynamic engineers deem optimal for propulsion and balance.

Yet just as ichthyosaurs themselves developed these fishlike



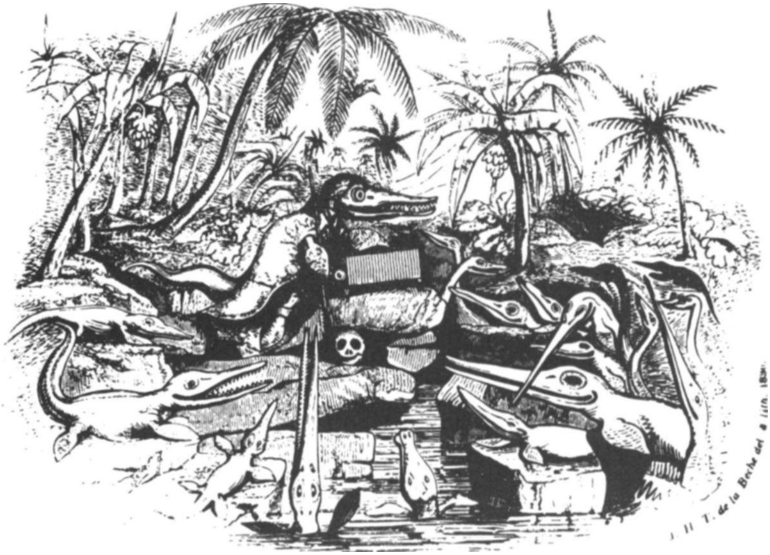
The classic painting of an ichthyosaur by Charles R. Knight. Note the fish-like position of the fins. *Courtesy of Department of Library Services. American Museum of Xatttrat History.*

features in a graduated transition from terrestrial ancestors, so too did our understanding of their extensive convergence grow piece by piece. To be sure, the basic similarity with fishes had never been doubted. In fact, the first two published references, both in 1708, mistook ichthyosaur vertebrae for the backbone of a fish. Both the celebrated Swiss naturalist J. J. Scheuchzer, in his *Querelae Piscium* (Complaints of the Fishes) and the German J. J. Baier, in his work on fossils from the area of Nuremberg, presented figures of ichthyosaur vertebrae for a most interesting purpose: to maintain that fossils are true remains of creatures that once lived, and not some manifestation of a plastic force inherent in rocks and ordained to establish global order by eliciting parallel forms in the organic and inorganic realms (an idea that strikes us as absurd today, but that made lingering sense within a neo-Platonic ideology not yet fully dispersed by the causal theories of Newton and Descartes).

Both Scheuchzer and Baier argued that these "fish" fossils recorded the devastation of Noah's flood. Scheuchzer's work is written as a humorous conversation among fossil fishes annoyed at humans who do not recognize their organic nature and affinity with living relatives. As for Baier, I recently had the pleasure of purchasing a copy of his rare work, without the slightest expectation that I would soon, or ever, have any practical or immediate use for this beautiful book. What a pleasure, then, to read his two page discussion of "ichthyospondyli" (fish vertebrae), with its conclusion that we must view them *"pro piscibus vere petrificatis . . . pro universalis Diluvii reliquiis"*—as truly petrified fish, remains of the universal Hood.

Better evidence, primarily from bones of the skull and paddles, revealed the reptilian nature of ichthyosaurs by the early nineteenth century, but strong convergence upon fishes remained the prevailing theme of most writing. Nonetheless, though skeletons revealed the streamlined body and fishlike paddles, two missing pieces conspired to prevent any full appreciation for the true (and awesome) extent of convergence—for the back and tail fins, as soft structures, had not been discovered. All the early reconstructions—by Buckland, Conybeare, de la Beche, Hawkins, and other worthies of early English geology—showed a slithering serpent without back or tail fins, not the reptilian embodiment of a swordfish. How, then, did the two key pieces fall into the piscine puzzle?

Richard Owen's note of 1838 stands as the chief document in this resolution. Thanks largely to keen insight and uncanny field work from Mary Aiming, and to support from the demented and



Caricature of ichthyosaurs by Henry de la Beche, made in the early nineteenth century before the back and tail fins had been discovered. *Courtesy of Department of Library Services, American Museum of Natural History.*

eccentric Thomas Hawkins (whose monographs of 1834 and 1840 must rank as the craziest documents ever written in paleontology), many good skeletons of ichthyosaurs were collected in England during the early nineteenth century. Owen had noticed an apparent peculiarity in one fine specimen—a sharp downward bend in the sequence of rear vertebrae at about two-thirds the distance from the back flippers to the end of the tail. Owen gave little thought to this tailbend, reasoning that it only represented an anomaly (probably a postmortem artifact) of a single specimen. But when skeleton after skeleton showed a tailbend in the same position, Owen realized that he had stumbled upon a phenomenon worthy of explanation. Owen wrote:

> Having recently examined many saurian skeletons now in London, the greater part of which have been disencumbered of their earthy shroud by the chisel of Mr. Hawkins, a

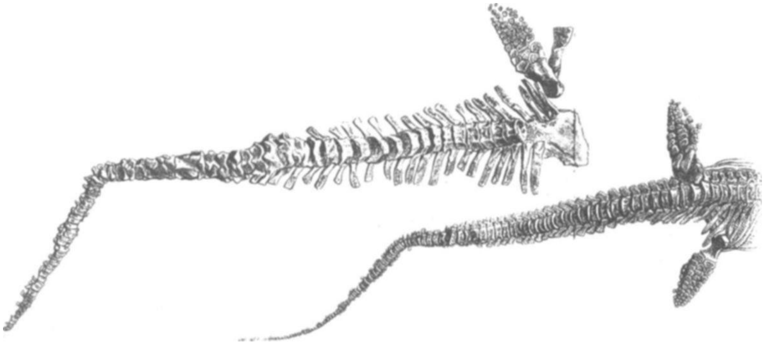


Illustration of ichthyosaur tail bends taken from Richard Owen's 1838 article. *Courtesy of Department of Library Semices, American Museum of Natural History.*

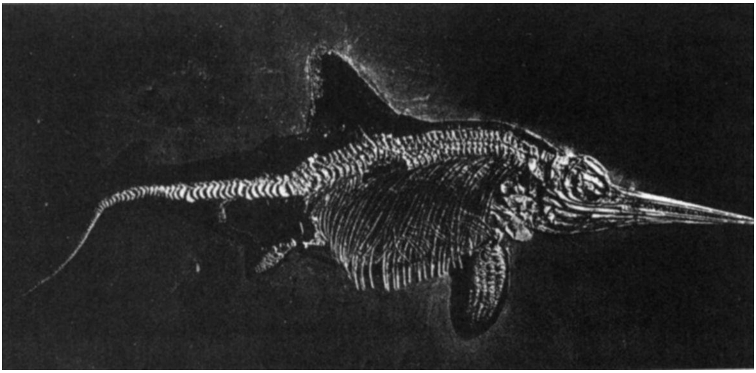
> condition of the tail which, on a former occasion, in a single instance had arrested my attention, but without calling up any theory to account for it, now more forcibly engaged my thought, from observing that it was repeated, with scarcely any variation, in five instances [boy, did they love to write back then, as in Owen's "disencumbered of their earthy shroud" for our modern "dug out of the rock"]. The condition to which I allude is an abrupt bend or dislocation of the tail . . . the terminal portion continuing, after the bend, almost as straight as the portion of the tail preceding it. In short, the appearance presented is precisely that of a stick which has been broken, and with the broken end still left attached, and depending [that is, hanging] at an open angle.

Owen then drew the right conclusion for the wrong reason and correctly inferred the existence of a tail fin. He argued that the constant position of the tailbend must record an attachment of some structure at this point. He rightly conjectured that this organ must be a tail fin, and he even predicted its vertical position (as in fishes) rather than a horizontal orientation (as in whales). But he wrongly assumed that the bend must represent a dislocation (probably after death) of an originally straight vertebral column—perhaps because the tail fin bloats with gas as the animal begins to decay, thereby fracturing the vertebral column at the front border of the fin. Owen then added other conjectures, and wrote:

> The appearance in the tail of the *Ichthyosaurus* . . . is too uniform and common to be due entirely to an accidental and extrinsic cause. I am therefore disposed to attribute it to an influence connected with some structure of the recent animal; and most probably to the presence of a terminal . . . caudal fin, which, either by its weight, or by the force of the waves beating upon its extended surface, or by the action of predatory animals of strength sufficient to tug at without tearing it off, might . . . give rise to a dislocation of the caudal vertebrae immediately proximal to its attachment.

The puzzle finally achieved its solution in the 1890s when the perennial, but rarely granted, prayer of all paleontologists was answered by the powers that be. Ichthyosaurs with preserved soft parts were discovered in the Holzmaden deposits near Stuttgart. These sediments are so rich in organic oils and bitumen that they actually burn. (One fire raged beyond control from 1668 to 1674 and another from 1937 to 1939). Details of internal organs are not retained in these bitumen beds, but body outlines remain intact as black films upon the light gray rock. (Most of the fine specimens displayed at museums throughout the world come from the Holzmaden beds, and many readers are no doubt familiar with ichthyosaur body outlines preserved as blackened films on the rock under and behind the bones.)

The Holzmaden ichthyosaurs finally proved the extent of external convergence upon the stereotypical form of a free-swimming fish. The dorsal fin, with no bony support at all, was revealed for the first time. And the caudal fin, correctly inferred by Owen from the tailbend, now stood out for all to see. The fin was vertical, as Owen had surmised, and composed of two nearly equal and symmetrical lobes. The vertebral bend did mark, again as Owen had conjectured, the anterior border of the fin—but as an item of normal anatomy, not a postmortem artifact or dislocation. The vertebral column bent naturally down to follow the lower border of the lower lobe of the tail right to the animal's rear end. No other vertebrate displays this orientation. In fishes, the



A tossil ichthyosaur with characteristic and excellent preservation from the Holzmaden deposits. Note the outlines of back and tail fins, and also the bending of the vertebral column into the lower lobe of the tail. *Courtesy of* Natural History.

vertebral column either stops at the inception of the tail or extends, as in sharks, into the upper border of the upper lobe. No wonder that the ichthyosaur tailbend had provoked such confusion for more than fifty years.

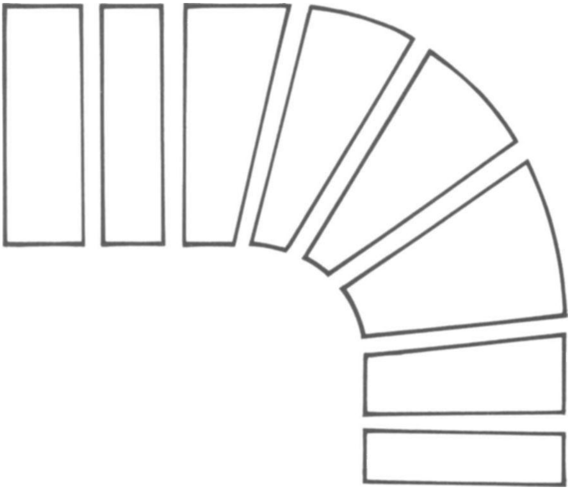
Nearly a century has passed since the Holzmaden discoveries revealed the true nature of the ichthyosaur tailbend by exposing its enclosure within the caudal fin. Yet the tailbend continues to provoke commentary and controversy for two main reasons as outlined by Chris McCowan of the Royal Ontario Museum, Toronto, and the world's leading expert on ichthyosaurs (my thanks to Dr. McCowan not only for his many illuminating articles, but especially for enduring a long phone call of inquiry during my research for this essay). First, and positively, the location, angle of downturn, and length of the vertebral column after the bend specify both the size and form of the caudal fin (only the Holzmaden ichthyosaurs preserve the fin itself as a carbonized film; all other specimens are bones alone, and the tailfin must be inferred from the vertebral column).

Second, and representing yet another dubious triumph of expectation over observation (perhaps the most common of human foibles), many classic specimens have been reconstructed on the assumption that tailbends must be present. I raise no issue of fraud or delusion. In many specimens, the vertebrae (particularly the small items at the rear end) lie scattered over the rock surface. The wonderfully expert and professional Holzmaden preparators adopted the custom of removing these bones entirely from the matrix and then resetting them in the inferred position of the living animal—that is, with a tailbend. We have no doubt that several ichthyosaur species developed a pronounced tailbend, since perfect specimens with preserved body outlines clearly show the tail vertebrae extending into the lower lobe of the caudal fin. But perhaps other species (particularly the earliest forms) lacked a tailbend, and perhaps preparators have tended to exaggerate the amount of inclination in reconstructing their specimens.

If the actual tailbends of most specimens on display are thus infected with doubt, how can we be confident about the existence and form of the caudal fin in most species? And, since this information is crucial to our understanding of swimming and maneuvering in ichthyosaurs, how can we hope to reconstruct the ecology of these fascinating animals? Obviously, we need a criterion of confirmation separate from the bend itself. Fortunately, McGowan has been able to establish such a criterion and to devise an ingenious way of putting it into practice.

How can an angular bend be produced in a basically linear structure (like the vertebral column), built from a sequence of disks that must follow, one behind the other, without large spaces between? As the accompanying sketch shows, tailbends imply a change in the shape of the crucial vertebral disks at the bend itself—from their usual form (with upper and lower borders of equal width) to a wedge with a wider border on top and a narrower edge below. A succession of wedge-shaped disks will inevitably cause the tail to bend, and the greater the difference in width between upper and lower borders, the more pronounced the bend. In fact, by a simple construction akin to the problems we all worked in high-school plane geometry, the angle of the bend can be inferred from the number of wedge-shaped disks and their intensity of wedging.

But how can this wedging be assessed? The vertebrae of most skeletons are at least partially embedded in rock, and both ends are rarely exposed to reveal the extent of wedging (while mu-



Shape of vertebral disks in ichthyosaurs with tail bends. Note the necessary wedge shape at the bend itself. *Ben Camit.*

seums rarely look kindly upon requests for sufficient mayhem upon their specimens to dig the vertebrae out of the enclosing matrix). McGowan solved this problem with a boost from modern medical technology—computed tomography as provided by a CT-scanner. These marvelous, donut-shaped x-ray devices can take a photographic slice right through a human body in any orientation (so long as the body fits into the donut-hole of the machine). Well, an ichthyosaur in its matrix is often about the same size as a human body. Why not take a CT-scan of vertebrae at the tailbend, thus producing a photographic image of the vertebral disks while still embedded in their matrix? (McGowan didn't initiate the application of CT-scanning to paleontological material. Several successful attempts have been made in the past few years, including the resolution of cranial capacities and form of unerupted teeth in some important skulls of the human fossil record.)

McGowan used a CT-scanner to affirm that *Leptopterygius tenuirostris,* an early ichthyosaur with an uncertain tailbend currently subject to hot dispute, did grow a series of six wedge-shaped vertebral disks in the crucial region—not strongly wedged to be sure (none producing more than a five degree bend), but yielding in their ensemble a modest tailbend of some 25 degrees (see McGowan's article, "The ichthyosaurian tailbend: A verification problem facilitated by computed tomography," in the bibliography). Somehow, I feel a great sense of satisfaction in the affirmation of this continuity in human striving for knowledge through time—to think that a discussion beginning in two Latin treatises written in 1708, proceeding through the keen observations of England's greatest anatomist in the 1830s, and on to the discovery of preserved body outlines in a famous German locality during the 1890s should be resolved, as we begin our last decade's countdown towards the millennium, by the latest device of medical machinery!

Yet, however satisfying the particular resolution, this tale (and tail) would convey no message or meaning (to those outside the tiny coterie of ichthyosaurian aficionados) if the problem of the ichthyosaur tailbend did not illuminate something central in evolutionary theory. Ichthyosaurs are most celebrated for their convergence upon the external form of superior swimmers among fishes. Since English traditions in natural history place primary emphasis on the concept of adaptation, these similarities of fish and marine reptile have won the lion's share of written attention—for we know how the threefold combination of flippers, backfin, and tailfin work in efficient hydrodynamic coordination, and we are awed that two independent lineages evolved such uncanny resemblance for apparently similar function. This awe even predates evolutionary theory, for an earlier attribution to God's benevolent care inspired as much admiration as our current respect for the power of natural selection. William Buckland, Owen's close colleague, had a special affection for ichthyosaurs. He also wrote the greatest paean of the 1830s to adaptation as proof of God's benevolence. In *Geology and Mineralogy Considered with Reference to Natural Theology,* written in 1836, Buckland invoked the precise convergence of ichthyosaur and fish as a proof of God's goodness. Buckland acknowledged that an ordinary reptile would be in severe trouble at sea, but ichthyosaurs have been granted by divine fiat (read "endowed by natural selection" for a modern version of the same argument):

> . . . a union of compensative contrivances, so similar in their relations, so identical in their objects, and so perfect in the adaptation of each subordinate part, to the harmony and perfection of the whole; that we cannot but recognize throughout them all, the workings of one and the same eternal principle of Wisdom and Intelligence, presiding from first to last over the total fabric of the Creation.

Yet, in our complex world of natural history, almost any profuse enthusiasm also elicits its mitigating opposite. (Such a cautionary splash of cold water may then emerge as a primary theme with more enlightening implications in itself.) Yes, ichthyosaur convergences are remarkable; only a soulless curmudgeon could fail to be impressed by the fishlike form of this descendant from ordinary terrestrial reptiles. Only the most militant denigrator of Darwin and the entire English tradition could fail to utter the word *adaptation* with both confidence and admiration.

But another perspective demands equal attention—and Owen, the much misunderstood proponent of a continental tradition that viewed adaptation as superficial, and sought regularities of form underneath a garb of immediate design, discussed ichthyosaurs primarily in the light of this alternative. What are the limits to adaptation imposed by the disparate anatomical designs underlying a convergence (fishes and reptiles in this case)? To what extent must the ichthyosaur remain in the thrall of its past, quite unable to mimic the form of a fish exactly because the historical legacy of a reptilian body plan precludes a large set of favorable options? To what degree, in short, must an ichthyosaur remain an easily identified reptile in marine drag?

For a primary statement of this alternate theme (limits imposed by inherited design), we must look to the largely forgotten work of the great Belgian paleontologist Louis Dollo (1857-1931). Dollo gave his name to an evolutionary principle known as *irreversibility* (often called Dollo's Law). In one of the cruel ironies often imposed by history, many fine thinkers win their posthumous recognition only by eponymous linkage with a principle so widely misunderstood that true views turn into their opposite. Many evolutionists interpret Dollo's Law as an antiquated statement about inherent, directional drives in evolution—a last gasp of a mystical vitalism that the Darwinian juggernaut finally defeated. In fact, Dollo was a convinced mechanist, and a Darwinian in basic orientation (with some interesting wrinkles of disagreement).

To Dollo, irreversibility epitomized the nature of history under simple conditions of mathematical probability (Dollo had obtained an extensive education in mathematics and attributed his formulation of irreversibility to this training). Evolutionary transformations are so complex—involving hundreds of independent changes—that any complete reversal to a former state becomes impossible for the same reason that you will never flip 1,000 heads in a row with an honest coin. No mysticism, no vitalism, only the ordinary operation of probability in a complex world. A simple change (increase in size, mutation in a single gene) may be reversed, but the standard transformations that form the bread and butter of paleontology (origin of flight in birds, evolution of humans from apelike ancestors) cannot run backwards to recover an ancestral state exactly.

History is irrevocable. Once you adopt the ordinary body plan of a reptile, hundreds of options are forever closed, and future possibilities must unfold within the limits of inherited designs. Adaptive latitude is impressive, and natural selection (metaphorically speaking) is nothing if not ingenious. A terrestrial reptile may return to the sea and converge upon fishes in all important aspects of external form. But the similarity can only be, quite literally, skin deep and truly superficial. The convergence must be built with reptilian parts, and this historical signature of an evolutionary past cannot be erased. Dollo explicitly linked his principle of irreversibility with a concept that he called "indestructibility of the past."

When we look again at the three great convergences of ichthyosaurs—the flippers, the dorsal fin, and the caudal fin—but this time from the alternate perspective of limits imposed by irrevocable starting points, we find that these features beautifully illustrate the three most important principles of irreversibility as a signature of history.

1. *The flippers, or you must use parts available from ancestral contexts little suited to present environments.* The flippers, by external form, are well adapted for swimming and balancing. But their internal bony structure reveals a terrestrial reptile under the marine adaptation. The front flipper begins with a stout humerus, followed by

a shortened and flattened radius and ulna, side by side. The carpals and metacarpals (hand bones) and phalanges (finger bones) follow in a similar flattened modification. In an interesting change (still related to an irrevocable ancestral state), the phalanges are multiplied into long rows that mimic the rays of fish fins. Humans have three phalanges per finger (two for the thumb); ichthyosaurs can grow more than twenty per finger.

2. *The dorsal fin, or you can* V *get there from here.* The dorsal fin of fishes generally contains a strengthening set of bony rays. Similar structures might well have benefited ichthyosaurs, but their terrestrial ancestors built no recruitable body parts along the back. Ichthyosaurs therefore evolved a boneless dorsal fin (that would have eluded us altogether if we had never discovered the Holzmaden specimens).

3. *The caudal fin and its tailbend, or you must always build a converging structure with some distinctive difference, due to irrevocable ancestry, from the original model.* The vertebral column of fishes, as noted above, either stops at the inception of the tail or extends into the upper lobe. Only in ichthyosaurs do the vertebrae bend down into the lower lobe of the tail. We do not know why ichthyosaurs developed this strikingly different and unique internal structure (I would need another essay to discuss the interesting structural and functional explanations that have been proposed), but all convergences evolve with distinctive differences based on a thousand quirks of disparate ancestries.

Louis Dollo has long been one of my private heros. I meant to cite his views on irreversibility as a centerpiece of this essay, but I didn't know, until a chance discovery in the midst of my research, that he had written an entire paper on the caudal fin of ichthyosaurs—and at a most interesting time, in 1892 just after the discovery of fin outlines in the Holzmaden specimens. Dollo rejoiced that these beautifully preserved specimens had resolved *"la cuneuse dislocation de la colonne vertebrate, signalee depuis longtemps"* (the curious dislocation of the vertebral column, recognized for so long). And he proposed an explanation rooted in uniqueness imposed by irrevocable history. I doubt that he was right in detail, but his conjecture is ingenious, and entirely in the spirit of an important and insufficiently appreciated principle of historical reconstruction. He argued that the tailbend arose because the two-lobed caudal fin of ichthyosaurs evolved from a skin-fold along the back (source of the dorsal fin as well), which extended itself in a posterior direction to form the upper lobe of the tailfin and then pushed the vertebral column down to form the lower lobe. Since several modern reptiles maintain such a skin fold along the back, but never along the belly, new fins could only evolve along the dorsal edge of the body, and the vertebral column could only be pushed down to form a two-lobed tailfin. But ancestral fishes maintained a fin-fold along both back and belly, and a two-lobed tailfin could evolve as a lower lobe pushed the vertebral column up.

Richard Owen, in contrast with his adaptationist colleague Buckland, appreciated the primacy of maintained reptilian design as the main lesson of ichthyosaur convergence. He wrote in his great monograph on British fossil reptiles (published between 1865 and 1881, and anticipating Dollo's concerns):

> The adaptive modification of the Ichthyopterygian skeleton, like those of the Cetacean [whale] relate to their medium of existence; | but | they are superinduced, in the one case upon a Reptilian, in the other upon a Mammalian type.

At about the same time, and in a more pointed commentary on the same theme of irrevocability in history, W. S. Gilbert (in *Princess Ida)* then penned a crisp epitome to remind his audiences of evolution's major lesson:

> Darwinian man though well behaved
> At best is only a monkey shaved.

An Earful of Jaw

THE MOST SUBLIME of all beauties often proceed from the softest or the smallest—the quadruple pianissimos of Schubert's "Scheme Mullerin," as sung by Fischer-Dieskau (and penetrating with brilliant clarity to the last row of the second balcony, where I once sat for the greatest performance I ever witnessed) or the tiny birds of brilliant plumage depicted in the marginalia of medieval manuscripts. But even the most refined and intellectual character may succumb without shame to the sheer din employed now and then by great composers to overwhelm the emotions by brute force rather than ethereal loveliness—Ravel's orchestration of the "Great Gate of Kiev" at the end of Moussorgsky's *Pictures at an Exhibition,* or the last scene of Wagner's *Die Meistersinger.*

I once had the privilege of singing with the Boston Symphony at Tanglewood in the midst of *numero uno* among musical dins—the *Tuba mirum* of Berlioz's *Requiem.* I had listened to the piece all my adult life; we had rehearsed (without orchestra) for weeks. I knew exactly what was coming as the dress rehearsal began. The four supplementary brass choirs enter one after the other, building and building to a climax finally joined by the timpani—eight pair, I think, although they seemed to extend forever in an endless row before the choral risers. And against this ultimate crescendo, the basses alone (including me) must sing the great invocation of the last judgment:

Tuba mirum spargens sonum
Per sepulchra regionum
Coget omnes ante thronum

(The wondrous sound of the trumpet goes forth to the tombs of all regions, calling all before the throne.)

So it should go, and so it went—but not for me. I had devolved into tears and spinal shivers—not in ecstasy at the beauty, but in awe at the volume. (Forewarned is forearmed; I was fine at the performance itself.) Great composers have every right to exploit the physiology of emotional response in this way, but only sparingly, for timing is the essence (and most of Berlioz's *Requiem* is soft).

My memory of this extraordinary incident in my emotional ontogeny focuses upon a curious highlight of mixed modalities. The sound of the brass assaulted my ears, but the thunder of the timpani followed another, unexpected route. It entered the wooden risers under my feet and rose from there to suffuse my body; sound became feeling.

I am no disciple of Jung, and I do not believe in distant phyletic memory. Yet, in an odd and purely analogical sense, I had become a fish for a moment. We (and nearly all terrestrial vertebrates) hear airborne sound through our ears; fish feel the vibrations of waterborne sound through their lateral line organs. Fish, in other words, "hear" by feeling—as I had done through a set of wooden risers with a density closer to water than to air.

For an optimal combination of fascination with excellent documentation, no saga in the history of terrestrial vertebrates can match the evolution of hearing. Two major transitions, seemingly impossible but then elegantly explained, stand out at opposite ends. First, at the inception of terrestrial life: How can creatures switch from feeling vibrations through lateral lines running all over their bodies to hearing sounds through ears? How, in other words, can new organs arise without apparent antecedents? Second, at the last major innovation in vertebrate design: How can bones that articulate the upper and lower jaws of reptiles move into the mammalian ear to become the malleus and incus (hammer and anvil) in the chain of three bones that conduct sound from the eardrum (the tympanum in anatomical parlance, recalling my Berlioz story in the singular) to the inner ear? How, in other words, can organs switch place and function without destroying an animal's integrity as a working creature? How can we even imagine an intermediary form in such a series? You can't eat with an unhinged jaw. Creationists have used this difference between reptiles and mammals to proclaim evolution impossible a priori—I mean, really, how can jawbones become ear bones? Get serious! Yet, we shall see, once again, that the domain of conventional thought can be much narrower than the capabilities of nature—although ideas should be able to extend and soar beyond reality.

The key to the riddle of both these transitions lies in the major theme of my Berlioz story—multiple modalities and dual uses. You can pat your head and rub your stomach, walk and chew gum at the same time (most of us, at least), feel and hear sound, chew and sense with the same bones.

Nature writing in the lyrical mode often exalts the apparent perfection and optimality of organic design. Yet, as I frequently argue in these essays, such a position plunges nature into a disabling paradox, historically speaking. If such perfection existed as a norm, you might revel and exult all the more, but for the tiny problem that nature wouldn't be here (at least in the form of complex organisms) if such optimality usually graced the products of evolution.

I recently made my first trip to Japan to deliver a lecture at the opening of an annual series that will bring one American scholar to Japan and a Japanese counterpart over here to speak on a common topic. I was both pleased and intrigued by our assigned theme for this initial year (largely at Japanese request)—creativity. (Some Japanese apparently fear—although my superficial impressions included nothing to sustain such anxiety—that their scholars and industrialists excel at efficiency and alteration, but not at innovation.)

I had no words of wisdom on Japanese life (I would not dare, not even by the old criterion that experts are folks who have been in a country either more than twenty years or less than two days); nor do I understand the sources of creativity in the human psyche of any culture. So, following the fine maxim that a shoemaker must stick to his last (a wooden model of a foot, not a final goal), I spoke on the evolutionary meaning of creativity—specifically, on the principles that permit major transitions and innovations in the history of life. I don't know that my message was well received in this land of supreme artistry in the efficient use of limited space, for I held that the watchwords of creativity are sloppiness, poor fit, quirky design, and above all else, redundancy.

Bacteria are marvels of efficiency, simple cells of consummate workmanship, with internal programs, purged of junk and slop, containing single copies of essential genes. But bacteria have been bacteria since life first left a fossil record 3.5 billion years ago—and so shall they probably be until the sun explodes. Such optimality provokes wonder but provides no seeds for substantial change. If each gene does one, and only one, essential thing superbly, how can a new or added function ever arise? Creativity in this sense demands slop and redundancy—a little fat not for trimming but for conversion; a little overemployment so that one supernumerary on the featherbed can be recruited for an added role; the capacity to do several things imperfectly with each part. (Don't get me wrong. Bacteria represent the world's greatest success story. They are today and have always been the modal organisms on earth; they cannot be nuked to oblivion and will outlive us all. This time is their time, not the "age of mammals" as our textbooks chauvinistically proclaim. But their price for such success is permanent relegation to a microworld, and they cannot know the joy and pain of consciousness. We live in a universe of trade-offs; complexity and persistence do not work well as partners.)

To build a vertebrate along the tortuous paths of history, evolution must convert the poet's great metaphor into flesh and bones. "I hear it," writes Yeats, "in the deep heart's core." I don't mean to be excessively literal, but if creatures couldn't occasionally hear with their lungs (as some snakes do) or with their jaws (as our immediate reptilian ancestors probably did), we would not now have ears so cleverly wrought that they fool us into the attractive but untenable vision of organisms as objects of optimal design. Consider the first and last major steps in anatomical construction of the mammalian middle ear—for we know no better or more intriguing story in the evolution of vertebrates.

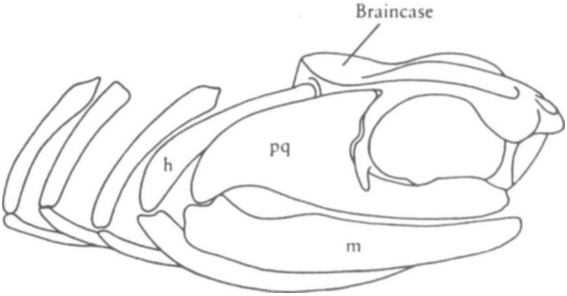
1. *The origin of hearing bones in the first terrestrial vertebrates.* The hearing of sound in thin air poses a major physical problem: How can low-pressure airborne waves be converted into high-pressure waves suitable for transmission by fluids in the cochlea of the inner ear? Terrestrial vertebrates use two major devices to make the necessary conversion. First, on the "stiletto heel" principle (quoting a metaphor from my colleague T. S. Kemp), they collect sound on the relatively large area of the eardrum but eventually

transmit the waves into the inner ear through a much smaller opening called the *fenestra ovalis* (oval window). Second, they pass the vibrations from eardrum to oval window along a bone or series of bones, called in mammals, the malleus, incus, and stapes, or hammer, anvil, and stirrup to honor a truly uncanny resemblance. These bones act as levers to increase the pressure as sound waves travel toward the brain.

Fish have an inner ear, but no eardrum or middle-ear bones; they "hear" primarily through their lateral line organs by detecting the movement of water produced by sound waves in this dense medium. How then could middle-ear bones arise in terrestrial vertebrates, apparently from nothing?

The first vertebrates had no jaws. Modern lampreys and hagfishes survive as remnants of this first vertebrate radiation; their formal name, Agnatha (or jawless), embodies their anatomy (or partial lack thereof)- In agnathans, a series of gill openings lies behind the boneless mouth—and this arrangement foreshadows the evolution of jaws. In the first jawed fishes, gills are supported by a series of bones, one set for each gill slit. Each set includes an upper and lower bar, pointing forward and hinged in the middle. Obviously, this arrangement, although evolved for supporting gills, looks uncannily like the upper and lower jaws of a typical vertebrate. We do not know for certain whether jaws arose from a functioning gill arch that moved forward to surround the mouth or whether jaws and gill arches just represent two specializations, always separate, but generated from the same system of embryological development. In either case, we do not doubt that gill supports and jaws are homologous structures (that is, evolved from the same source and representing the "same" organ in different forms—like arms and legs or fingers and toes). The evidence for homology is multifarious and overwhelming: (1) the embryo builds both jaw precursors and gill arches not from mesoderm, the source of most bones, but from migrating neural crest cells of the developing head; (2) both structures are made of upper and lower bars, bending forward and hinged in the middle; (3) the muscles that close the jaw are homologues of those that constrict the gill slits.

If vertebrate jaws represent an anterior gill arch, then another crucial element of the skull also derives from the gill supports just behind. The upper bar of the next gill arch in line becomes the



A classic figure of homologies between gill arch and jaw bones, taken from R. L. Carroll's *Vertebrate Paleontology and Evolution.* The upper and lower jaws (pq and m) have the same position and form as all the gill arches behind them. Note also that the upper element of the gill arch just behind the jaws articulates with the braincase. This bone becomes the hyomandibular (h) and later the stapes in terrestrial vertebrates. *Courtesy of Department of Library Sennees. American Museum of Natural History.*

hyomandibular of jawed fishes, a bone that functions in support and coordination by linking the jaws to the braincase.

All this detail may seem distant from the origin of hearing bones, but we are closing in quickly (and shall arrive before the end of this paragraph). Mammals have three middle-ear bones—hammer, anvil, and stirrup, or stapes. And the stapes is the homologue of the hyomandibular in fishes. In other words—but how can it happen?—a bone originating as a gill support must have evolved to brace the jaws against the braincase, and then changed again to function for transmission of sound when water ceded to air, a medium too thin to permit "hearing" by the lateral line.

As usual in a world of encumbrances, we must flush away an old and conventional concept before we can understand how such an "inconceivable" transition might actually occur without impediment in theory or practice. We must forget the old models of horses and humans mounting a chain of improvement in functional continuity—from small, simple, and not-so-good to larger, more elaborate, and beautifully wrought. In these models, brains are always brains and teeth always teeth, but they get better and better at whatever they do. Such schemes may work for the improvement of something already present, for a kind of stately continuity in evolution. But how can something original ever be made? How can organisms move to a truly novel environment, with needs imposed for functions simply absent before? We require a different model for major transitions and innovations, for King Lear was correct in stating that "nothing will come of nothing."

We need, in other words, a mechanism of recruitment and functional shift. Evolution does not always work by enlarging a rudiment. It must often take a structure functioning perfectly well in one capacity and shift it to another use. The original middle-ear bone, the stapes, evolved by such a route, changing from a stout buttressing bone to a slender hearing bone.

If each organ had only one function (performed with exquisite perfection), then evolution would generate no elaborate structures, and bacteria would rule the world. Complex creatures exist by virtue of slop, multiple use, and redundancy. The hyomandibular, once a gill support, then evolved to brace jaw and braincase. But this bone happens to lie right next to the otic capsule of the inner ear—and bone, for reasons incidental to its evolution, can transmit sound with reasonable efficiency. Thus, while functioning primarily as a brace, the hyomandibular also acquired other uses. Skates and rays take in water through a round opening, called the spiracle, located in front of the other gill slits. The hyomandibular then helps to pump this water into the mouth cavity, and thence out and over the gill slits. Closer to our phyletic home, the hyomandibular may help to ventilate the lungs of modern lungfishes.

I have wanted to write about the origin of middle-ear bones ever since I began this series, for we have no finer story in vertebrate evolution. But I like to wait for a handle in new information, and one recently came my way (see J. A. Clack, in bibliography, on finding the oldest stapes). The first known tetrapods (four-legged terrestrial vertebrates) hail from eastern Greenland in rocks 360 million years old (see Essay 4). They have been known for some time under the names *Ichthyostega* and *Acanthostega,* but their stapes had not been well resolved before. Clack found six stapes of *Acanthostega,* four preserved in their life positions.

Clack suggests not only a dual but a triple function for the stapes of these first land vertebrates. The bone is stout and dense, not slender and delicate as in stapes adapted largely for hearing. This original stapes must still have functioned in its earlier role as a brace (other early tetrapods, including mammalian ancestors, also had stout stapes). Clack also advocates a supplementary role in respiration. Finally, she makes a key observation based on the stapes's location: "The stapes is likely to have had some auditory function because of the close association between the footplate [a part of the stapes] and the otic [ear] capsule."

Such a multifarious bone nearly bursts with evolutionary potential. The stapes may have braced for a hundred million years, but it also worked for respiration and hearing if only in an incipient or supplementary way. When the cranium later lost its earlier mobility, and the braincase became firmly sutured to the skull—as occurred independently in several lineages of terrestrial vertebrates—the stapes, no longer needed for support, used its leverage and amplified a previously minor role in hearing to a full-time occupation.

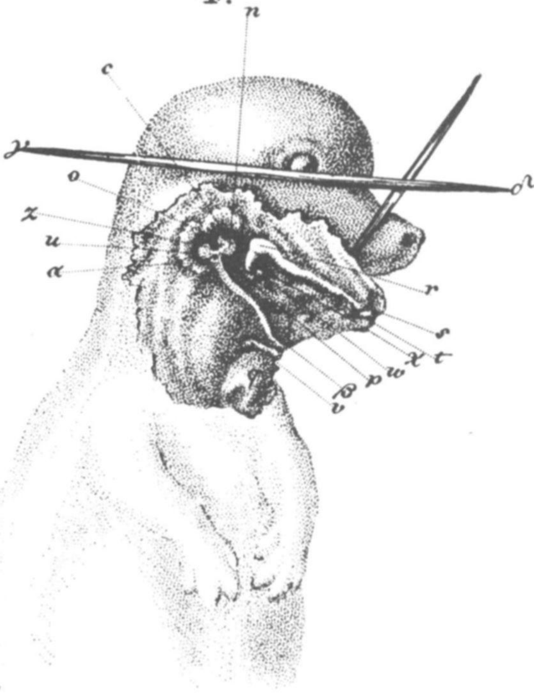
2. *The origin of mammalian middle-ear bones.* The odyssey of the stapes (stirrup) is extraordinary enough, a tale worthy of Scylla, Charybdis, and all the wiles of Circe—from gill support to a brace between jaws and braincase to a hearing bone for airborne sound. Yet the other two bones of the mammalian middle ear, named long ago by an age that knew the blacksmith's forge, have an even more curious history. The hammer and anvil (malleus and incus), as elements of the gill arch in front of the hyomandibular, became parts of the jaw in early vertebrates. In fact, they took up the central role of connecting and articulating the upper and lower jaws—as they still do in modern amphibians, reptiles, and birds. The quadrate bone of the reptilian upper jaw became the incus of mammals, while the articular bone of the lower jaw became the malleus. The transition, so improbable in bold words, is beautifully documented in the fossil record and in the embryology of all modern mammals.

The homology of reptilian jawbones to mammalian ear bones was discovered by German anatomists and embryologists well before the advent of evolutionary theory. In 1837, C. B. Reichert made the key observations and expressed the surprise that this tale has elicited ever since. With these words, Reichert introduced his section on the *Entwicklungsgeschichte der Gehdrknbchelchen* (developmental history of the little hearing bones). (German looks so god-awful for its massive words. But these tongue twisters are usually made of little words compounded, and the system becomes beautifully transparent, even charming, once you break the big items into their elements. The Germans have preferred to construct technical terms as compounds of their ordinary words, rather than from fancy and foreign Latin or Greek. A rhinoceros is a *Nashorn,* or "nose horn" as rhinoceros actually says in Greek; a square is a *Viereck,* or four-corner. Our technical literature refers to the hammer, anvil, and stirrup as "auditory ossicles"; don't you prefer the German *Gehorknochelchen,* or little hearing bones?) In any case, Reichert wrote: "Seldom have we met a case, in any part of animal organization, in which the original form of an early [embryological] condition undergoes such extensive change as in the ear bones of mammals. We would scarcely believe it. . . . Nevertheless, it happens in fact."

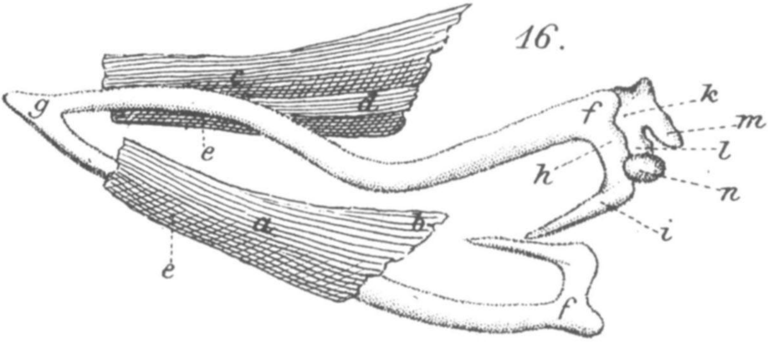
Reichert recognized all key outlines of the story: that all the ear bones derive from the first two sets of gill-arch bones, the hammer and anvil from the first arch (forming the jaw of vertebrates), and the stirrup from the second arch (forming the hyomandibular of fishes). He noted that the lower jaw first forms with a precursor called Meckel's cartilage (in honor of another great German anatomist of the generation just before, J. F. Meckel). The mandible or jawbone then ossifies on the side of Meckel's cartilage. Meanwhile, the posterior end of Meckel's cartilage, forming the back end of the jaw in the early pig embryo, ossifies and then detaches to become the malleus of the middle ear. One could hardly ask for more direct evidence, and Reichert's observations have been affirmed thousands of times since.

(As a tangential comment in my continuing campaign against textbook copying, the accompanying illustration shows Reichert's original figure of a developing lower jaw in the embryonic pig; *h* and *i* represent parts of the future malleus forming at the back end of Meckel's cartilage *(g);* the ossifying mandible *(a)* begins to surround and supplant the cartilage. Meanwhile, the incus *(k)* and the stapes *(n)* form as bones separate from the lower jaw. This figure has been copied and degraded, like xeroxes of xeroxes, ever since this 1837 original. I last saw its clone in a vertebrate anatomy textbook published in 1971. Two

4.



Two illustrations from Reichert's classic article of 1837, containing his discovery of the homologies of mammalian middle-ear bones. See text for explanation. *Courtesy of Department of Library Services, American Museum of Natural History.*



bits says that the author of this text [who undoubtedly copied the figure from a book just slightly older than his] would be shocked to learn that his picture dates from 1837. This time, everyone lucks out because Reichert was a great anatomist and his figure is basically correct; but think of the capacity for compounded error inherent in this procedure of mindless copying. I also include, to give an interesting [if gory] flavor of common styles of illustration during the early nineteenth century, one of Reichert's graphic preparations of a pig embryo, dissecting pins and all.)

Thus, every mammal records in its own embryonic growth the developmental pathway that led from jawbones to ear bones in its evolutionary history. In placental mammals, the process is complete at birth, but marsupials play history postnatally, for a tiny kangaroo or opossum enters its mother's pouch with future ear bones still attached to, and articulating, the jaws. The bones detach, move into the ear, and the new jaw joint forms—all during early life within the maternal pouch.

Paleontological and functional evidence join the embryological data to construct a firm tripod of support, giving this narrative pride of place among all transitions in the evolution of vertebrates by combining strength of documentation with fascination of content. One theme stands as the coordinating feature of this narrative (and of my entire essay): redundancy and multiple use as the handmaidens of creativity.

We might employ this theme to make an abstract prediction about the character of intermediary forms in the fossil record. Contrary to creationist claims that such a transition cannot occur in principle because hapless in-betweens would be left without a jaw hinge, the principle of redundancy suggests an obvious solution. Modern mammals hinge their jaws between squamosal (upper jaw) and dentary (lower jaw) bones; other vertebrates between quadrate (upper jaw) and articular (lower jaw) bones destined to become the incus and malleus of the mammalian ear. Suppose that mammalian ancestors developed a dentary-squamosal joint while the old quadrate-articular connection still functioned—producing an intermediary form with a double jaw joint. The old quadrate-articular joint could then be abandoned, as its elements moved to the ear, while the jaw continued to function perfectly well with the new linkage already in place.

Our woefully inadequate fossil record is not brimming with intermediary forms, for reasons often discussed in these essays. But the origin of mammals represents a happy case of abundant evidence. The abstract predictions of the last paragraph (actually advanced by paleontologists before the discoveries, so I am not just making a rhetorical point here) have been brilliantly verified in abundant fossil bone. The cynodont therapsids, our ancestral group among the so-called mammallike reptiles, show numerous trends to reduction and loosening of both quadrate and articular bones in the old reptilian jaw joint. Meanwhile, the dentary of the lower jaw enlarges and extends back to contact the upper jaw. (In mammals, the dentary forms the entire lower jaw; reptilian jaws contain several postdentary elements, all reduced and then suppressed or dispersed in mammals.) Many cynodonts develop a second articulation between the squamosal and a postdentary element of the lower jaw called the surangular. (This joint is not the later mammalian dentary-squamosal link, but its formation illustrates a multiple evolution of the intermediacy proclaimed impossible by creationists.) Finally, two or three genera of advanced cynodonts develop a second articulation of truly mammalian character between the dentary and squamosal. One such genus (although the evidence has been disputed) bears the lovely and distinctive name *Diarthrognathus,* or two-jointed jaw.

Moreover, the earliest true mammals do not yet have a fully independent malleus and incus. These bones remain affixed to the jaws and continue to participate in articulation, in both *Morganucodon* and *Kuehneotherium,* the two best known early mammals. "In this sense," wrote Edgar F. Allin in 1975, "the earliest mammals did not yet possess a 'mammalian middle ear.' " By Upper Jurassic times, still well within the early days of mammalian life in a world dominated by dinosaurs, these bones had entered the ear, and an exclusively dentary-squamosal joint had formed.

Embryology and paleontology provide adequate documentation of the "how," but we would also like more insight into the "why." In particular, why should such a transition occur—especially since the single-boned stapedial ear seems to function quite adequately (and, at least in some birds, every bit as well as the three-boned mammalian ear)? We are nowhere near the full answer to this complex question, but one hint conveys special interest and also illustrates the principle of redundancy one more time.

Pelycosaurs, those sail-backed creatures included in every set of plastic dinosaurs and every box of chocosaurus cookies, are not dinosaurs at all, but our distant ancestors—forebears of the therapsid reptiles that eventually evolved into mammals. The stapes of pelycosaurs lies in close contact with the quadrate bone of the upper jaw (forerunner of the incus that now articulates with the stapes in the mammalian middle ear). This linkage continues and sometimes intensifies in descendant therapsids—the more immediate ancestors of mammals. This anatomical connection strongly suggests that the quadrate of mammalian ancestors, while functioning primarily in jaw articulation, already played a subsidiary role in the transmission of sound. Allin argues: "From the nature of its junction with the stapes, the cynodont quadrate obviously took part in sound conduction."

Unfortunately, we cannot experiment on extinct animals and have no direct evidence for quadrate hearing in the actual ancestors of mammals. However, we do know that reptilian quadrates can transmit sound while still acting as part of a jaw joint, for several modern reptiles use an important quadrate path to their inner ear. (These creatures are not mammalian ancestors to be sure, but they do demonstrate the possibility, indeed the actuality, of this crucial multiple modality in the evolution of mammalian hearing.) Snakes, for example, have no external ear or eardrum, and many scientists had considered them entirely deaf, until recent studies illustrated sensitivity to sound over most of the body, especially around the large lung that can transmit vibrations to the inner ear. But another route offers special advantages to a creature so close to the substrate by God's direct decree: ". . . upon thy belly shalt thou go, and dust shalt thou eat all the days of thy life." Snakes hear primarily by placing their heads on the ground and passing vibrations from the lower jaw to the quadrate and finally to the stapes—thus closely following the eventual mammalian pathway. In addition, direct experiments on several lizards and on the tuatara of New Zealand show that vibrations directed at the quadrate are passed to the stapes and recorded in the brain.

May I confess an ulterior motive in closing—for complex and abstract excursions can be mere glosses upon simpler aims. In-jokes have delicious qualities because they are inaccessible to all but the initiated. But sometimes, in-jokes are so good that we long to share them, yet despair for the volume of background required. Well, this essay can be read as nothing but an extended pony for understanding one of my favorite humorous poems. My colleague John Burns, a lepidopterist now in Washington but formerly at Harvard, used to introduce our weekly seminars with his punny doggerel. We loved the poems and came more to hear his introductions than to suffer through the subsequent speeches. John finally published his verses in a volume called *Biograjfiti* (Demeter Press, 1975), with an introduction by yours truly. My favorite is a pithy epitome of mammalian ear evolution, entirely incomprehensible to 99 percent of the population, but now vouchsafed to you, my dear readers, as a small reward for your persistence and as a dessert after this ponderous dissertation:

Evolution of Auditory Ossicles

With malleus
Aforethought
Mammals
Got an earful
of their ancestors'
Jaw.

Full of Hot Air

FIORKLLO LA GUARDIA may be destined to go down in history primarily as godfather to an airport. But he was a great mayor for New York in tough years of depression and war. (My birth certificate even bears his signature—well, at least a stamped version.) He also possessed in abundance the trait that we find most welcome, but encounter all too rarely, in people of accomplishment—a willingness to acknowledge occasional and inevitable error. In his most famous quip, La Guardia once remarked, "When I make a mistake it's a beaut!"

Scientific "misconduct" is now a hot topic, both for journalists and members of Congress. In this somewhat frantic climate, we should pause to consider the essential distinction between fraud and error—for the two concepts are diametrically opposed, although self-appointed watchdogs sometimes make the tragic mistake of uniting them as graded forms of malfeasance. Fraud is a social and psychological pathology, although science must learn to police itself. Error is the inevitable byproduct of daring—or of any concentrated effort for that matter. You might as well legislate against urination after beer drinking.

No great work of science has ever been free of error, and any extensive or revolutionary work must contain a few of La Guardia's beauts. Intellectual progress is a complex network of false starts and excursions into trial and error. Darwin's *Origin of Species,* for example, sprinkles numerous errors into its ocean of reforming validity. The errors are so frequent, and so varied, that we might even try to establish categories.

Darwin, first of all, commits several errors of fact. Here I would skip the dull and quotidian misreporting of information and concentrate on the far more interesting errors based on predictions from theoretical premises that turn out to be false or exaggerated. Darwin's commitment to gradualism, for example, led him to make at least two prominent, and outstandingly wrong, conjectures: (1) He gave a time of more than 300 million years for the "denudation of the Weald" (the erosion of the region, forty miles wide, between the north and south Chalk Downs in southern England), based on his belief in the steady, grain-by-grain character of geological erosion. But alteration need not proceed so slowly, or so continuously, and the actual time is one-third to one-fifth of Darwin's generous allotment. (2) Multicellular animal life begins with geological abruptness at the "Cambrian explosion" some 550 million years ago. Darwin, who rejected biological rapidity even more zealously than the geological variety, predicted that the "explosion" must be illusory and that the pre-Cambrian history of multicellular animal life must be as long as, or longer than, the 570 million years of success ever since. We now have an excellent record of pre-Cambrian life—and no multicellular animals arise until just before the Cambrian explosion.

A second category might be labeled errors of judgment: political miscalculations really. The savvy Darwin made few mistakes in this mode, but he slipped occasionally by giving free rein to fatuous speculations in a treatise that gained its power by sinking a weighty anchor in sober fact and avoiding the fanciful conjectures of previous writing about evolution. In a passage that he would later rue, and that gave aid, comfort, rhetorical advantage, and belly laughter to the enemy, Darwin wrote:

> In North America the black bear was seen by Hearne swimming for hours with widely open mouth, thus catching, like a whale, insects in the water.... If the supply of insects were constant, and if better adapted competitors did not already exist in the country, I can see no difficulty in a race of bears being rendered, by natural selection, more and more aquatic in their structure and habits, with larger and larger mouths, till a creature was produced as monstrous as a whale.

(Later editions of the *Origin* kept the first factual sentence and expunged all the rest.) A statement like this need not be false (indeed, as a speculation, we cannot tell); the important thing, as Machiavelli would have said, is to avoid the appearance of silliness.

A third category, perhaps the most revealing, includes mistakes that most of us don't recognize because we make them ourselves. Call them errors of thoughtless convention. I include here those passive repetitions of standard cultural assumptions stated so automatically, or so deeply (and silently) embedded within the structure of an argument, that we scarcely detect their presence. Darwin may have been the greatest intellectual revolutionary of the nineteenth century, but he made a few outstanding errors in this category, most related to his ambiguity on the great bugbear of progress—a concept that had no place in the basic mechanics of natural selection, but that Darwin, as an eminent Victorian, could not abandon entirely.

Consider Darwin's treatment of the evolution of vertebrate lungs and their relationship with the swim bladders of bony fishes—an example that Darwin obviously viewed as important to his general argument because he repeats the story half a dozen times in the *Origin.* Darwin begins by noting, correctly, that the lung and swim bladder are homologous organs—different versions of the same basic structure, just as a bat's wing and a horse's foreleg share a common origin indicated by the similar arrangement of bones in body parts that now work in such different ways. But Darwin then draws a false inference from the fact of homology. He claims, with increasing confidence ending in certainty, that lungs evolved from swim bladders:

> All physiologists admit that the swim bladder is homologous . . . in position and structure with the lungs of the higher vertebrate animals; hence there seems to me to be no great difficulty in believing that natural selection has actually converted a swim bladder into a lung, or organ used exclusively for respiration. I can, indeed, hardly doubt that all vertebrate animals having true lungs have descended by ordinary generation from an ancient prototype, of which we

> know nothing, furnished with a floating apparatus or swim bladder.

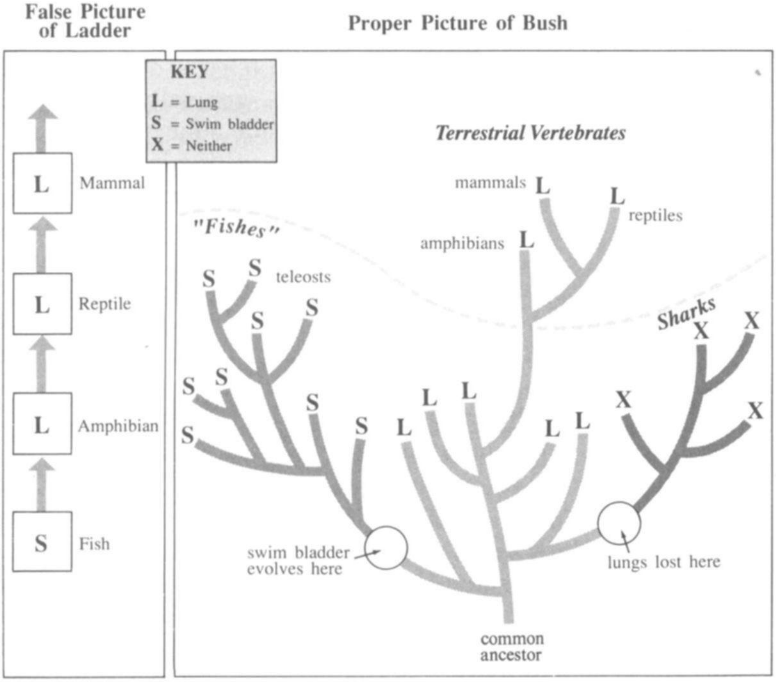
Many readers will be puzzled at this point, as I have perplexed several generations of students by presenting the argument in this form. What can be wrong with Darwin's claim? The two organs are homologous, right? Right. Terrestrial vertebrates evolved from fishes, right? Yes again. So lungs must have evolved from swim bladders, right? Wrong, dead wrong. Swim bladders evolved from lungs.

I love this example, especially as a pedagogical tool, because an outstandingly counterintuitive assertion—the evolution of swim bladders from lungs—becomes the favored hypothesis with sudden and stunning clarity as soon as we shed a common, disabling assumption and start considering the question in a different light. The problem lies with a chronic confusion—abetted by cultural prejudice in this case—between structural sequence and branching order.

The literature of experimental psychology often reports comparative data of performance on various tests for learning in, say, a planarian worm, a crab, a carp, a turtle, and a dog. These are often reported as an "evolutionary sequence" of mental advance. Such statements make evolutionary biologists howl in rage or, if our mood be better, merely with laughter. This motley crew of animals represents no evolutionary sequence at all: vertebrates did not arise from arthropods; mammals did not evolve from turtles; and carp are further from the fishes that did give rise to terrestrial descendants than aardvarks are from humans. However, although the psychologists are dead wrong in their terminology of "evolutionary order," their sequence may have some validity as a structural series—worm, bug, fish, turtle, and dog might express some increasing properly of neurological functioning.

When we turn to another common sequence—fish, amphibian, reptile, mammal, monkey, human—the problems intensify, for now we cannot even speak of a legitimate structural sequence. Frogs live in different places, but are they "higher" than swordfishes or sea horses? What odds would you put on a ground sloth going up against a *Triceratops?* Fine, you say; no necessary progress here, but surely this venerable lineage records *the* path of vertebrate evolution. And now we come to the crux of the error about lungs and swim bladders. If this sequence is *the* path of vertebrate change, then swim bladders must evolve to lungs, as Darwin said—for the canonical fish, the first member of the series, has a swim bladder, while all of us at the top have lungs.

But we wallow in a double confusion when we make this "intuitively obvious" assertion—first, the false assumption of progress, which makes the lung a "higher" organ than a swim bladder and thus unfit for creatures on the bottom; second, and more seriously, the confusion of ladders and bushes, or sequences and branching orders. Fish-amphibian-reptile-mammal is not *the* road of change among vertebrates; it represents only one path-



The correct sequence of lung evolving to swim bladder is almost inconceivable on the false evolutionary model of a ladder in vertebrate evolution. But, with the proper iconography of a bush, the sequence becomes clear. *Joe UMonmer. Courtesy of* Natural History.

way among thousands in the complexly branching bush of vertebrate evolution (the accompanying figure should make my argument clear). All the other pathways lead to creatures that we continue to call "fish" in the vernacular. In terms of variety in anatomical design, we find far more diversity among the creatures called fish than among all the terrestrial vertebrates put together. The terrestrial line is a single branch, with astounding success to be sure, but with limited diversity in underlying anatomical structure (whatever the outward variety of flying birds, slithering snakes, and thinking people). By contrast, fishes are astoundingly disparate in basic design and include lineages that separated a hundred million years before any terrestrial vertebrate arose. Consider the jawless lampreys, the boneless sharks (also lacking either lung or swim bladder), and the odd coelacanth; don't confine your image to the canonical creature impaled on a hook at the end of your rod and line.

Yes, that canonical creature—called a teleost, or member of the vast group of "higher" bony fishes—generally has a swim bladder. But teleosts; although they include almost all common fishes today, are evolutionary latecomers, arising in the sea long after mammals first evolved on land. Yes, they have swim bladders, and they are fish—but they are not ancestors to any terrestrial vertebrate. Their status, as late and derived, leaves entirely unresolved the issue of what came first: swim bladders or lungs.

A reconstruction of vertebrate branching order gives a clear answer to this question: Darwin was wrong; ancestral vertebrates had lungs. (For details of this argument, see the article by Karel F. Liem, cited in the bibliography). The first vertebrates maintained a dual system for respiration: gills for extracting gases from seawater and lungs for gulping air at the surface. A few modern fishes, including the coelacanth, the African bichir *Polypterus,* and three genera of lungfishes, retain lungs. One major group, the sharks and their allies, lost the organ entirely. In two major lineages of derived bony fishes—the chondrosteans and the teleosteans—lungs evolved to swim bladders by atrophy of vascular tissue to create a more or less empty sac and, in some cases, by loss of the connecting tube to the esophagus (called the trachea in humans and other creatures with lungs). Some fishes retain the connection of swim bladder with esophagus; they can inflate their swim bladders by gulping air at the surface. Fishes with separate swim bladders usually extract gases from blood flowing through an extremely fine and rich system of vessels surrounding the bladder and possessing one of the loveliest technical names in all biology—the *rete mirabile,* or "wondrous network."

I would not wish to issue overt praise for mistakes, but Darwin's error on the swim bladder falls into the category that we welcome as particularly instructive, for correction involves a sudden shift from the "can't be" to the completely obvious—that almost thrilling property of scales falling from eyes. The agent of correction, moreover, is not a new and pristine fact, but a change in an underlying conceptual structure.

Let us then praise Darwin's fruitful error on this basis, but also for another, and even more important, reason. Darwin may have gotten his sequence backward, but he was using the story to illustrate a vital and widely misunderstood principle of evolutionary theory—and the illustration works just as well whether swim bladders evolve to lungs or vice versa. Why, then, was Darwin so interested in this issue in the first place?

One common argument against evolution held (and still holds among the lingering opposition) that small changes within a "basic kind" might occur, producing the range from Chihuahua to Great Dane, or Shetland pony to old dobbin hauling the Budweiser truck. But transitions between types are forbidden because fundamental novelties cannot arise by evolution. The classic form of this argument holds that since "novel" structures often arise (or so evolutionists claim) from ancestral organs with strikingly different functions, transitional forms would be inviable because they would exist in the never-never land of utter unworkability, with one key function degenerated and another not quite established. To cite a classic case (with an elegant resolution as we shall see), how could reptiles evolve into mammals if bones that articulate the reptilian jaw must evolve to the malleus and incus (hammer and anvil) of the mammalian middle ear (see Essay 6)? No intermediary form could live without a jaw articulation, as the leisurely earward transition occurred. In other words, both the "before" and the "after" make sense as functional organisms, but the "in between" doesn't work.

Lung and swim bladder represent a classic example of this dilemma, whichever way the sequence proceeded. The organs are homologues, and one presumably evolved to the other. But how could the transitional form have survived, either stuck like a lead weight on the bottom as buoyancy failed, while: breathing required access to the surface; or raring to float but gasping for breath?

Darwin begins by warning us against a priori claims of impossibility in principle, for multifarious nature so often gets the last laugh over this particular form of human vanity: "We should be extremely cautious in concluding that an organ could not have been formed by transitional gradations of some kind." Darwin's ingenious solution involves a double linkage of one-for-two, with two-for-one—mysterious when stated so abstractly but beautifully simple by illustration, with lungs and swim bladders as a primary example. First, Darwin tells us, single organs often perform more than one function—one-for-two:

> Numerous cases could be given . . . of the same organ performing at the same time wholly distinct functions. . . . In such cases natural selection might easily specialize, if any advantage were thus gained, a part or organ, which had performed two functions, for one function alone, and thus wholly change its nature by insensible steps.

The primitive swim bladder, Darwin argues (and we may reverse the argument for lungs), may also have worked in a subsidiary way in gas exchange—and this latter role may have been intensified as the original use dropped out, in the evolution of the lung. But the one-for-two principle cannot resolve the problem of intermediary stages—for how could a fish breathe as the original lungs lost their primary function?

Darwin therefore calls upon his second, coupled principle of two-for-one. Many vital functions are performed by two or more organs, and one can change so long as the other continues to play the needed role. We can breathe through both our nose and mouth—and thank goodness, or we would all be dead of colds:

> Two distinct organs sometimes perform simultaneously the same function in the same individual.... In these cases, one of the two organs might with ease be modified and perfected so as to perform all the work by itself; . . . and then

> this other organ might be modified for some other and quite distinct purpose.

We can now understand why Darwin liked the example of lungs and swim bladders so much. He had made a reasonable conjecture about one-for-two in arguing for supplementary respiration in swim bladders, and he had definite evidence about two-for-one in the presence of numerous living fishes with dual systems of breathing—gills and lungs. (The official taxonomic name of the lungfishes, Dipnoi, means "two breathing.") Thus, using lungs and swim bladders as his key example in a central defense of large-scale evolution, Darwin concluded:

> For instance, a swim bladder has apparently been converted into an air-breathing lung. The same organ having performed simultaneously very different functions, and then having been specialized for one function; and two very distinct organs having performed at the same time the same function, the one having been perfected whilst aided by the other, must often have largely facilitated transitions.

Readers might fairly balk at this point. The argument coupling one-for-two and two-for-one is logically sound, but doesn't it smack of special pleading and gross improbability? How often can you expect to find such a combination? Perhaps both situations are uncommon; their conjunction would then be nearly incomprehensible. Rare times rare equals rare squared, or effectively impossible.

But we now come to the true beauty of Darwin's argument. Neither situation is rare, and the two phenomena—one-for-two and two-for-one—are not really separate at all. Both are expressions of a deeper, and profoundly important, principle—*redundancy* as the ground of creativity in any form. They are two sides of the same coin—and the coin, although priceless in intellectual value, is as common as a penny.

The notion that organs are "for" particular things, ideally suited for one and only one job, is a vestige of old-style creationism—the idea that God made each creature, fully formed and perfect in function. If each organ existed explicitly for a single role, then I suppose that one organ doing more than one thing would be rare, and that two organs doing the same thing might be even rarer. But organs were not designed for anything; they evolved—and evolution is a messy process brimming with redundancy. An organ might be molded by natural selection for advantages in one role, but anything complex has a range of other potential uses by virtue of inherited structure—as we all discover when we use a dime for a screwdriver, a credit card to force open a door, or a coat hanger to break into our locked car (not someone else's, let us hope, and surely not, let us pray, for ending unwanted pregnancies in our newly dawning era of restrictions). Any vital function narrowly restricted to one organ gives a lineage little prospect for long-term evolutionary persistence; redundancy itself should possess an enormous advantage. (Redundancy in this form solves the otherwise intractable problem of evolution in mammalian jaws, as outlined above. Intermediary forms, as shown by direct evidence of fossils, not abstract conjecture, developed a second articulation between dentary and squamosal bones [the current mammalian jaw joint], and elements of the old articulation could then lose their former function and pass into the ear.)

In fact, the swim bladder itself provides an excellent example of multiple possibilities as a norm. The swim bladder is primarily an organ of buoyancy in teleost fishes. By filling the bladder with gas, an animal that would otherwise sink becomes neutrally buoyant and can rest without expending energy in the midst of the water column. (In a related function, fishes at neutral buoyancy gain more power in forward motion because they need not divert energy into supplying lift to counteract sinking—see R. McNeill Alexander in the bibliography. Interestingly, some sharks are pelagic (floating) in habit; how can they stay up, since their entire lineage lost the organ that becomes a lung or swim bladder in other fishes? These sharks have enormous livers constructed largely of a hydrocarbon with a density considerably less than seawater—another good example of multiple use as a norm.

But the swim bladder performs at least three other important but secondary functions in many species of teleost fishes:

(1) Most curiously, perhaps, the swim bladder has reacquired a supplementary respiratory function in several lineages of fishes, all living in swampy or stagnant waters, where gulping air at the

surface might be an important alternative to breathing with gills.

(2) Many teleosts use their swim bladder as an organ of sensation. Since gas is so responsive to changes in pressure, some fishes can judge their depth in the water column with receptors embedded in the wall of their swim bladder. Many other fishes use their swim bladder as an accessory organ of hearing. Gases are more compressible than water, and sound vibrations may be recorded more sensitively in their impact upon swim bladder gases than upon any other part of the body. Supplementary hearing has evolved in at least two strikingly different ways. Some fishes have developed thin forward extensions of the swim bladder; these pass through openings of the skull and make direct contact with the ear. In another major group, the cypriniforms (including most of the world's freshwater fishes), vibrations from the swim bladder are transmitted to the ear via a chain of three separate bones located on either side of the vertebral column and called Weberian ossicles to honor the German scientist who recognized their mode of operation in 1820. (Darwin used this example of multiple function in the *Origin of Species.)*

(3) Sound production: Again, several lineages use the swim bladder either to enhance sounds made by other parts of the body or as a direct agent of production. (Some fishes are essentially silent, but many make sounds, especially in courtship or in aggressive displays.) The triggerfish *Batistes* (another lovely name) stridulates by rubbing its postclavicle bone against its cleithrum—but this otherwise minor sound is greatly amplified by resonance from the adjacent swim bladder. Another group of fishes grates its pharyngeal teeth and also turns a little rumble into a modest roar by resonance of the swim bladder. In other fishes, the swim bladder produces sounds directly by expulsion of gas bubbles. T. H. Huxley once wrote a special note to *Nature* (in 1881) to describe what can only be called herring farts. These fish expel gas in pulses from the swim bladder out an orifice adjacent to the anus. In the oh-so-proper style of scientific reporting, a British review article of 1953 described Huxley's suggestion "that the mouse-like squeaks made by captured herring might be caused by the escape of gas through the posterior opening."

If I may move, in conclusion, from minor end rumblings to a renewed assault upon the high ground, I don't know if the *Origin of Species* contains an argument more general or more important than Darwin's recognition that pervasive redundancy makes evolution possible. If animals were ideally honed, with each part doing one thing perfectly, then evolution would not occur, for nothing could change (without losing vital function in the transition), and life would quickly end as environments altered and organisms did not respond.

But rules of structure, deeper than natural selection itself, guarantee that complex features must bristle with multiple possibilities—and evolution wins its required flexibility thanks to messiness, redundancy, and lack of perfect fit. Human creativity is no different, for I think we are dealing with a statement about the very nature of organization—something so general that it must apply to any particular instance.

How sad then that we live in a culture almost dedicated to wiping out the leisure of ambiguity and the creative joy of redundancy. These days, even the most complex concepts must be reduced to photo opportunities and sound bites, and elections are decided by fifteen-second images of men surrounded by flags and alleged criminals walking through symbolic revolving doors. We may be creating a generation of sheep—and although these pleasant mammals outnumber New Zealanders by almost twenty-five to one, I rather suspect that *Homo sapiens,* properly nurtured by redundancy and ambiguity, will continue to prevail.

Redundancy, and its counterpart of ambiguity in multiple meaning, are our way, our most precious, most human way. We rail at computers because for all their awesome power, they do not grasp our essential ambiguities. They cannot adequately translate one of our languages into another, and we must speak to them in a way utterly unnatural for us—that is, without ambiguity (hence an entire industry devoted to debugging). Faced with La Guardia's or Darwin's errors, they grind to a halt. We adjust, we parry, we prevail, we transcend. It could be one hell of a partnership, so long as we keep the upper hand. I shall place my bets on the shepherds of New Zealand and hope that the analogy holds.

The Declining Empire of Apes

GOD MUST HAVE created mistakes for their wonderful value in illuminating proper pathways. In all of evolutionary biology, I find no error more starkly instructive, or more frequently repeated, than a line of stunning misreason about apes and humans. I have been confronted by this argument in a dozen guises, from the taunts of fundamentalists to the plaints of the honorably puzzled. Consider this excerpt from a letter of April 1981: "If evolution is true, and we did come from apes, then why are there still apes living. It seems if we evolved from them they should not be here."

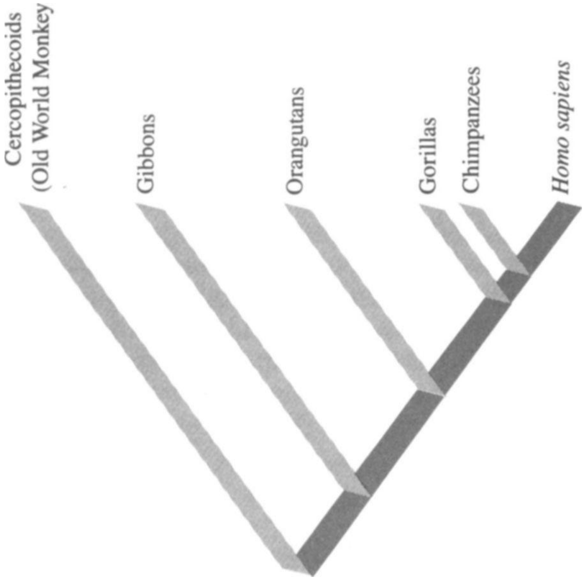
If we evolved from apes, why are apes still around? I label this error instructive because its correction is so transforming: If you accept a false notion of evolution, the statement is a deep puzzle; once you reject this fallacy, the statement is evident nonsense (in the literal sense of unintelligible, not the pejorative sense of foolish).

The argument is nonsense because its unstated premise is false. If ancestors are groups of creatures that are bodily transformed, each and every one, into descendants, then human existence would preclude the survival of apes. But, plainly, we mean no such thing in designating groups as ancestors—lest no reptiles remain because birds and mammals evolved or no fishes survive because amphibians once crawled out upon the land.

Ladders and bushes, the wrong and right metaphors respectively for the topology of evolution, resolve the persistent nonpuzzle of why representatives of ancestral groups (apes, for example) can survive alongside their descendants (humans, for example). Since evolution is a copiously branching bush, the emergence of humans from apes only means that one branch within the bush of apes split off and eventually produced a twig called *Homo sapiens,* while other branches of the same bush evolved along their own dichotomizing pathways to yield the other descendants that share most recent common ancestry with us—gibbons, orangutans, chimps, and gorillas, collectively called apes. (These modern apes are, by genealogy, no closer than we are to the common ancestor that initiated the ape-monkey split more than 20 million years ago, but human hubris demands separation—so our vernacular saddles all modern twigs but us with the ancestral name ape. The figure and its caption should make this clear.)

The proper metaphor of the bush also helps us to understand why the search for a "missing link" between advanced ape and

A Few Branches on the Bush of Apes and Old World Monkeys



The genealogical sequence of branching in the evolution of apes and humans.

incipient human—that musty but persistent hope and chimera of popular writing—is so meaningless. A continuous chain may lack a crucial connection, but a branching bush bears no single link at a crucial threshold between no and yes. Rather, each branching point successively restricts the range of closest relatives—the ancestors of all apes separate from monkeys, then gibbon lineages from ancestors of other great apes and humans, then forebears of the orangutan from the chimp-gorilla-human complex, finally precursors of chimps from the ancestors of humans. No branch point can have special status as *the* missing link—and all represent lateral relationships of diversification, not vertical sequences of transformation.

An even more powerful argument on behalf of the bush arises from the reanalysis of classical ladders in our textbooks, particularly the evolution of modern horses from little eobippus and the "ascent of man" from "the apes." A precious irony—life's little joke—pervades these warhorses of the ladder: The "best" examples must be based upon highly *unsuccessful* lineages, bushes so pruned of diversity that they survive as single twigs. (See my essay "Life's Little Joke" in *Bully for Bronlosaurus* for a fuller version of this argument.)

Successful bushes never enter our texts as classical trends, because they boast too many related survivors, and we can draw no rising ladder for the evolution of antelopes, rodents, or bats—although these are the three great success stories of mammalian evolution. But if only one twig survives, we apply a conceptual steamroller and linearize its labyrinthine path of lateral branching back to the main stem of its depleted bush. Horses, rhinos, and tapirs are not glorious culminations of ascending series within the Perissodactyla (odd-toed hoofed mammals) but three little twigs, barely hanging on, the remnants of a bush that once dominated the diversity of large mammalian herbivores. Similarly, we can specify a ladder of human ascent only because the bush of apes has dwindled to a few surviving twigs, all clearly distinct. If the bush of apes were vigorous and maintained a hundred branchlets evenly spaced at an expanding periphery, we would have many cousins and no chain of unique ancestors. Our vaunted ladder of progress is really the record of declining diversity in an unsuccessful lineage that then happened upon a quirky invention called consciousness.

This argument against human arrogance can be grasped well enough as an abstraction but becomes impressive only with its primary documentation—the record of vigorous diversity among apes in former times of greater success. The theme of previous vigor has recently received a boost from a new discovery—one that I had the great good fortune to witness last year.

The cercopithecoid, or Old World, monkeys are the closest relatives of the ape-human bush. Robert Jastrow, in his recent, popular book, *The Enchanted Loom: Mind in the Universe,* contrasts the evolutionary fate of these two sister groups:

> The monkey did not change very much from the time of his appearance, 30 million years ago, to the present day. His story was complete. But the evolution of the ape continued. He grew large and heavy, and descended from the trees.

This statement, so preciously wrong, so perfectly arse-backward, shows just how far astray the metaphor of the ladder can lead. There is no such creature, not even as a useful abstraction, as *the* monkey or *the* ape. Evolution's themes are diversity and branching. Most apes (gibbons and orangutans, and chimps and gorillas a good part of the time) are still living in trees. Old World monkeys have not stagnated; they represent the greatest success story among primates, a bush in vigorous radiation and including among its varied products baboons, colobins, rhesus and proboscis monkeys.

In fact, precisely opposite to Jastrow's claim, apes have been continuously losing and cercopithecoids gaining by the proper criteria of diversity and expansion of the bush. Let us go back to the early Miocene of Africa, some 20 million years ago, soon after the ape-monkey split, and trace the fate of these two sister groups. First of all, we would not find these Miocene ancestors as different from each other as their descendants are today—limbs of a bush usually diverge. Early Miocene apes were quite monkey-like in their modes of life. Compared with monkey forebears, early apes tended to be larger, more tree bound, more narrowly tied to fruit eating, and less likely to cope with a strongly seasonal or open environment.

Second—and the crucial point for this essay—apes were more common in two important senses during the early Miocene: more common than cercopithecoid monkeys at this early stage in their mutual evolution, and absolutely more diverse (just in Africa) than apes are today (all over the world). Taxonomic estimates vary, and this essay cannot treat such a highly technical and contentious literature, but early Miocene African apes have been placed in some three to five genera and perhaps twice as many species.

The next snapshot of time, the African middle Miocene, already records fewer species, although apes now appear for the first time in the fossil records of Europe and Asia. Old World monkeys meanwhile begin an acceleration extending right to our own time. Apes continue to decline and hang on in restricted habitats—yielding isolated groups of gibbons and orangutans in Asia, and chimps, gorillas, and the descendants of a small African group called australopithecines. If the resident zoologist of Galaxy X had visited the earth 5 million years ago while making his inventory of inhabited planets in the universe, he would surely have corrected his earlier report that apes showed more promise than Old World monkeys and noted that monkeys had overcome an original disadvantage to gain domination among primates. (He will confirm this statement after his visit next year—but also add a footnote that one species from the ape bush has enjoyed an unusual and unexpected flowering, thus demanding closer monitoring.)

We do not know why apes have declined and monkeys prevailed. We have no evidence for "superiority" of monkeys; that is, for direct struggles of Darwinian competition between apes and monkeys in the same habitat, with ape extinction and cercopithecoid prevalence as a result. Perhaps a greater flexibility in diet and environmental tolerance allowed monkeys to gain the edge, without any direct competition, in a world of changing climate and fewer stable habitats of trees and fruit. According to this interpretation, those few apes that could adapt to a more open, ground-living existence, had to develop some decidedly odd features, not in any way "prefigured" by their initial design—the knuckle walking of chimps and gorillas, and the upright gait of australopithecines and you know who.

This striking reversal of Jastrow's homily, and of all standard biases of the ladder, rests most forcefully upon the comparison of initial Miocene success with later restriction of the bush of apes.

But how great was this first flowering, and how severe, therefore, the later pruning? Unfortunately, this most crucial of all empirical questions encounters the cardinal problem of our woefully imperfect fossil record. We know the extent of later pruning; it is not likely that any living species of ape remains undiscovered on our well-explored earth. But what was the true diversity of early Miocene apes? Did they live only in Africa? What fraction of the African fauna has been preserved? What have we collected and identified of the material that has been preserved?

If our current collections contain most of what actually lived, then the pruning has been notable but modest. But suppose that we have only 10 percent or even only half the true diversity, then the story of decline and restriction among apes is far more pronounced. How can we know how much we have?

One rough indication—about the best we can do at this early stage of knowledge about Miocene primates in Africa—comes from the composition of new collections. Suppose that every time we find new early Miocene apes in Africa, they belong to species already in our collections. After several repetitions (particularly if our collections span a good range of geographies and environments), we might conclude that we have probably sampled a substantial amount of the true bush. But suppose that new sites yield new species most of the time—and that we can mark no real decline in the number of novelties. Then we might conclude that we have sampled only a small part of a much more copious bush—and that the story of decline and shortfall in the empire of apes has been more profound than we realized. Quite an effective antidote to the bias of the ladder and its attendant invitation to human arrogance!

In other words, we are seeking, as my colleague David Pilbeam, our leading student of fossil apes, said to me, "an asymptote" in the discovery of new apes. An asymptote is a limiting value approached by one variable of a curve as the other variable (often time or number of trials) increases towards infinity. When further collecting of fossils only yields more specimens of the same species, we have probably reached the asymptote in recoverable kinds of apes. We also reach asymptotes fairly quickly in training cats or cajoling children and should learn to recognize both the subtle point of diminishing returns and the actual asymptote not much further down the line.

An exciting discovery about the history of Miocene apes has recently furnished our best evidence that we have not yet come near the asymptote of the early bush of apes. This discovery provides the strongest possible evidence for an even greater intensity of life's little joke in our own evolution. The bush was bushier, the later decline in diversity more profound. We do not yet know the true extent of the initial success of apery.

In January 1986, I spent a week with Richard Leakey at his field camp on early Miocene sediments near the western shore of Lake Turkana in Africa's Great Rift Valley. Little vegetation obscures the geology of this arid region, and naked sediments stretch for miles, their eroding fossils littering the surface.

The data on genetic differences between chimps and humans suggest that our twig on the bush of apes last shared a common ancestor with chimps some 5 to 8 million years ago; in other words, the human lineage has been entirely on its own only for this short stretch of geological time. The oldest human fossils are less than 4 million years old, and we do not know which branch on the copious bush of apes budded off the twig that led to our lineage. (In fact, except for the link of Asian *Sivapithecus* to the modern orangutan, we cannot trace any fossil ape to any living species. Paleontologists have abandoned the once popular notion that *Ramapithecus* might be a source of human ancestry.) Thus, sediments between 4 and 10 million years in age are potential guardians of the Holy Grail of human evolution—the period when our lineage began its separate end run to later domination and a time for which no fossil evidence exists at all.

Richard Leakey almost surely has many square miles of good sediment from this crucial time in his field area at West Turkana. But he is not yet searching these beds. He is concentrating his efforts on older rocks of the early Miocene (15 to 20 million years ago) when the bush of apes had its great initial flowering in Africa. He is working before the time of maximal intrigue for several reasons. In part, he may be saving the best for later, perfecting his techniques and "feel" for the region before zeroing in on the potential prize. He also has the fine intuition and horse sense of any good historian—it may be best to begin at the beginning and work forward. But, most importantly, he has a professional's understanding that problems of maximal public acclaim are not always the issues of greatest scientific importance.

The public may yearn, above all, to know the status of our common ancestor with chimpanzees, but Richard Leakey recognizes that the early Miocene is also a time of mystery, promise, and conceptual importance: mystery because we know so little about the actual diversity of apes at this time of their greatest success; promise because he has sediments that can deliver many of the missing goods; conceptual importance because we have as much to learn from documenting the base of our ancestral bush as in searching for the little branchlet that led directly to us later on. The early Miocene is a good place to explore.

The ground of West Turkana glistens with crystals of quartz and calcite. The local Turkana children, passing time during long hours of tending goats under the relentless sun, collect geodes into piles and smash them to reveal the crystals inside. We are looking for duller fragments of bone.

There are no great secrets to success, no unusual basis for "Leakey's luck," beyond hard work and experience. In some areas, fossil-bearing strata are rare and must be traced through geological complexities of folding and faulting to assure that fieldworkers search only in profitable places. But here, the entire sequence is fair game (although some strata, as always, are richer than others), and all exposures of rock must be scrutinized. The key to success becomes patience and a trained workforce.

Leakey maintains a staff of trained Kenyan observers. He provides a long course in practical mammalian osteology (study of bones)—until they can distinguish the major groups of mammals from small scraps. The main ingredient of Leakey's luck is unleashing these people in the right place.

Kamoya Kimeu supervises this exploration. He has found more important fossils than any one else now alive. One night in camp, he told me his story. As a boy, he tended goats, sheep, and cattle for his father. He attended school for six years and then went to work for a farmer. His employer urged him to return to school and study to become a veterinary paramedic. Kamoya then walked for several days back to Nairobi, where his uncle told him that Louis Leakey, Richard's father, was recruiting people to "dig bones." His mother gave him only cautious approval, telling him to quit and come home if the task involved (as he then suspected) digging up human graves. But when he saw so many bones from so many kinds of creatures, he knew that nature had strewn these burial grounds. The sediments of West Turkana are, if anything, even more profuse.

When I arrived on January 16, Kamoya's team had just found a new and remarkably well-preserved ape skull (in a profession that usually works with fragments, mostly teeth, a skull more than half complete, and with a fully preserved dentition, is cause for rejoicing). The next day, we studied and mapped the geological context and then brought the specimen back to camp. I wrote in my field book: "Everyone is very excited because they have just found the finest Miocene ape skull known from Africa. It is quite new—with a long face, inflated nasal region, incisors worn flat with a diastema [gap] a finger wide to the massive canine—almost like a beaver among apes."

Research is a collectivity, and we all have our special skills.

The greatest of all fossil finders Kamoya Kimeu gathering material at West Turkana. *Photograph by Delta Willis.*

Kamoya's workers are the world's greatest spotters; Richard also has a hawk's eye, the intuition of a geologist who has lived with his land, and the organizational skills of a Washington kingpin; his wife, Meave, has an uncanny spatial sense and can beat any jigsaw champ in putting fossil fragments together; yours truly, I fear, is good for one thing only—seeing snails.

All field naturalists know and respect the phenomenon of "search image"—the best proof that observation is an interaction of mind and nature, not a fully objective and reproducible mapping of outside upon inside, done in the same way by all careful and competent people. In short, you see what you are trained to view—and observation of different sorts of objects often requires a conscious shift of focus, not a total and indiscriminate expansion in the hopes of seeing everything. The world is too crowded with wonders for simultaneous perception of all; we learn our fruitful selectivities.

I couldn't see bone fragments worth a damn—and Richard had to direct my gaze before I could even distinguish the skull from surrounding lumps of sediment. But could I ever see snails, the subject of my own field research—and no one else had ever found a single snail at that site. So I rest content with my minuscule contribution, made in character, to the collective effort. At the top right of page 143 in the November 13, 1986, issue of *Nature*— the article that describes the new skull—a few snails are included in the faunal list of the site, some added by my search image. (I also found, I believe, the first snails at the important South African hominid site of Makapansgat in 1984—where I also couldn't see a bone. I think I am destined to be known in the circle of hominid exploration as "he who only sees the twisted one.")

The traditions of nature writing demand that this personal narrative now continue at some length, with overwritten paeans to the wonder of this discovery, set in glowing cliches about the stark and fragile (two good adjectives) beauty of the countryside. But I desist. First of all, this isn't my style; it also doesn't match anything that actually happens in the field. People have varied reactions to such good fortune. Some may jump up and down, fall upon their knees to praise God, or wax eloquent about the new line wrested from nature's complex book. Most people I know, certainly including Richard, Kamoya, and myself as outsider, do not have personalities that match these romantic stereotypes. The conversation may flow more happily at dinner; some kind of glow must form within. But you still have to make sure that the trucks have gas, that the water jugs are full—and you do have to get up at dawn the next day because it's too hot to work in the afternoon. My favorite kind of excitement is quiet satisfaction.

Richard and Kamoya's team found a second, smaller ape skull that field season at West Turkana. Both are new genera, not merely variants on familiar themes of the ape's bush. Richard and Meave Leakey published two papers in the November 13, 1986, issue *of Nature* describing these new forms as *Afropitheats* (the one I witnessed) and *Turkanapitherus.* In the most interesting line of the *Afropithecus* paper, they write: *"Afropithecus* displays characters typical of a variety of Miocene hominoids combined in a single taxon." In other words, this new genus represents a unique combination of features known to vary among early apes—as if we might shuffle the known variations into many more plausible combinations as yet undiscovered. The bottom line after all this exegesis is simplicity itself: We are not at, perhaps not even near, the asymptote for true diversity of apes at their flourishing beginning. If one field season in uncharted lands could yield two new genera, how many remain undiscovered in the hundreds of square miles still open for exploration? Apes were bushier than we had ever imagined during their early days; human evolution seems even more twiggy, more contingent on the fortunes of history (not enjoined like the successive rungs of a ladder), less ordained, and more fragile. Our vaunted march to progress, the standard iconography of our evolution, is just one more expression of life's little joke.

I have consciously permitted a professional's bias to permeate this essay so far. I have been equating "success" with numbers of branches on the bush—for paleontologists tend to view large-scale evolution as the differential birth and death of species, and we slip too easily into an equation of success with exuberance of branching. But, of course, we must also consider the quality of twigs, not merely their number. *Homo sapiens* is one small twig, holding with just a few others all the heritage of a group once far more diverse in branches. Yet our twig, for better or for worse, has developed the most extraordinary new quality in all the history of multicellular life since the Cambrian explosion. We have invented consciousness with all its sequelae from Hamlet to Hiroshima. Life's little joke shows us our fragility, our smallness on the proper metaphor of the bush, but we have turned the joke upon itself with the power of one evolutionary invention.

The prophet Micah caught both sides of this tension with great understanding when he wrote that fragility and size of origin imply little about ultimate effect: "But thou, Bethlehem Ephrathah, though thou be little among the thousands of Judah, yet out of thee shall he come forth unto me that is to be ruler in Israel" (Micah 5:2). If we could merge the two themes, and if rulers could learn humility and respect from our common origins as fragile twigs on the bush of life, then we might break the equation between ability and right to dominate and might even fulfill that most famous of Biblical prophecies, which is, after all, about the proper nurturing of trees and bushes—"and they shall beat their swords into plowshares, and their spears into pruning hooks."

Defending the Heretical and the Superfluous

SAMUEL TAYLOR COLERIDGE, in a reverie laced with laudanum, presented an image of striking incongruity in describing the pleasure palace of Kubla Khan:

> It was a miracle of rare device,
> A sunny pleasure-dome with caves of ice!

This vision of tropical languor mixed with arctic sternness recalls a juxtaposition of similar disparity from my own education—Marco Polo in Chinese summer palaces and Eric the Red conning settlers by describing inhospitable arctic real estate as "Greenland." This odd matching of China with Greenland records a key episode of "white man's history," taught as universal by New York City public schools in the late 1940s.

The history of civilization, we learned, is centrifugal—a process of outward expansion from European or near Near Eastern centers. Heroes of this process were called "explorers"—and they "discovered" land after land, despite the nagging admission that all these places featured indigenous cultures often more complex and refined than the European "source" (Kubla Khan vs. the Doge of Venice).

We worked through the panoply of explorers in strict chronology. Eric the Red, a tenth-century Norseman, came first, moving northwest into bleakness and chill. Marco Polo, Kubla Khan's most famous visitor (and Coleridge's source), followed, moving southeast into exotic splendor and warmth. (Eric's son Leif might have merited a chapter in between, especially since he reached

North America several hundred years before the official date for "discovery" of our well-populated continent. But, remember, I grew up in New York, not Lake Wobegon, and the Knights of Columbus had effectively put the kibosh on any Viking claims. Leif Ericson and Vineland ranked with Odin and Thor in the category of Scandinavian mythology.)

Thus, Greenland and China—lands of nearly maximal disparity in climate and geography—have always stood together in my mind as the one-two punch of initial discovery. And now, some forty years later, my own profession of more ultimate origins has juxtaposed these incongruous places again, this time in the legitimate service of discovery about true beginnings. During the last year, fossil finds in China and Greenland have penetrated the terra incognita of animal origins with an eclat to match the deeds of any old-time explorer.

I have written many essays and an entire book on the origin of multicellular animals. Yet, from a dominant perspective in evolutionary thought, such a subject should not exist at all, at least in the sense of "first" items that an explorer might discover. We inhabit a world of graded continuity, and transformation of single-celled microscopic ancestors to multicellular animals of modern design should occur by smooth transition over such a long time that no single organism or species should qualify as an unambiguous "first."

Life is continuous in the crucial sense that all creatures form a web of unbroken genealogical linkage. But connectivity does not imply insensible transition. Nothing breaks the continuity between caterpillar and butterfly, but stages of development are tolerably discrete. Similarly, the origin of animals reminds us, in outline, of an old quip about the life of a soldier—long periods of boredom punctuated by short moments of terror. In the evolution of multicellular animals, nothing much happens for very long periods of time, while everything cascades in brief geological moments. We can talk meaningfully about "firsts," and discoveries in Greenland and China qualify for this category of ultimate importance. A quick review of basic information will set a proper context:

Life on earth is as old as it could be—a striking fact that, in itself, points to chemical inevitability in origination (given proper conditions that may be improbable in the universe). Paleontological discoveries, starting in the mid-1950s, have shattered the previous consensus—never more than a sop to our hopes for uniqueness—that life is exceedingly improbable and only arose because so much geological time provided such ample scope for the linking of unlikely events (given enough trials, you will eventually flip thirty heads in a row). Under this discredited view, life arose relatively late in the earth's history, following a long geological era called "Azoic" (or lifeless, and representing the lime needed for all those trials before the thirty fortunate successes).

But fossils of simple unicellular creatures have now been found in appropriate rocks of all ages, including the very oldest that could contain evidence of past life. The earth is 4.5 billion years old, but heat generated from two major sources—the decay of short-lived radioisotopes and bombardment by cosmic debris that pervaded the inner solar system during its early history—melted the earth's surface some 4 billion years ago. All rocks must therefore postdate this early liquefaction. The oldest known rocks on earth are a bit older than 3.8 billion years, but they have been so altered by heat and pressure that no fossils could have survived. The oldest rocks that could contain preserved organic remains are 3.5 to 3.6 billion years old from Australia and South Africa—and both deposits do feature fossils of single-celled creatures similar to modern bacteria. Hints and indications are not proofs, but I don't know what message to read in this timing but the proposition that life, arising as soon as it could, was chemically destined to be, and not the chancy result of accumulated improbabilities.

But if origination bears a signature of chemical inevitability, the pattern of later history tells a story of historical contingency dominated by portentous but unpredictable events. (I find nothing strange or unlikely in such a model of historical chanciness for subsequent pattern following a substrate of initial necessity. One might argue, for example, that the origin of speech and writing follows predictably from the evolved cognitive structure of the human mind. But the actual languages that developed, their timings and their interrelationships, would never unfold in the same way twice.)

Yet whatever attitude we adopt towards the total pattern, we must at least admit that one key event—the origin of multicellular animals—carries no prima facie signature of stately inevitability. If multicellular complexity is a predictable advance upon unicellular existence, then this salutary benefit surely took its time arising, and certainly burst upon the scene with unseemly abruptness by quirky and circuitous routes.

Nearly five-sixths of life's history is the story of single-celled creatures (with some amalgamation, towards the end to threads, sheets, and filaments of algal grade—an event entirely separate from the origin of animals in any case). Then, about 650 million years ago, the first multicellular assemblage appears in rocks throughout the world. This fauna, named Ediacara for an Australian locality, consists entirely of soft-bodied creatures with anatomical designs strikingly different from all modern animals (flattened disks, ribbons, and pancakes composed of strips quilted together). Some paleontologists have suggested that the Ediacara animals bear no relationship to modern creatures, and represent a separate, but failed, experiment in multicellular life.

Multicellular animals of modern design—and with hard parts readily preservable as fossils—first appear, also with geological alacrity, in an episode called the "Cambrian Explosion" some 550 million years ago. Trilobites, a group of fossil arthropods beloved of all collectors, provide the principal signature for this first fauna of modern design. The full flowering of this initial fauna reaches its finest expression in the exquisite, soft-bodied fossils of the Burgess Shale, subject of my recent book, *Wonderful Life.*

This basic pattern has been well publicized and is now known to most nonprofessionals with strong interests in the history of life: a long period of unicellular creatures only; followed by a rapid appearance of the Ediacara fauna, perhaps with no relationship to living animals; and the final, equally quick, origin of modern anatomical designs in the Cambrian Explosion, with maximum expression soon thereafter in the Burgess Shale.

Less well known is the fine-scale geological anatomy of the Cambrian Explosion itself. Trilobites do not appear in the earliest Cambrian strata with hard-bodied fossils; they enter the geological record in the second phase of the Cambrian, called Atdabanian. The initial phase, called Tommotian after a Russian locality, contains a fauna with an interesting balance of the familiar and the decidedly strange. The new discoveries in China and Greenland give us our first decent insight into the anatomical character of the strange component—hence the great importance of these new finds, for we cannot grasp the ordinary (so designated only because they survived to yield modern descendants) without the surrounding context of creatures that left no progeny and therefore appear to us like products of a science fiction novel.

The earth's first hard-bodied fauna of the Tommotian does include several fossils of modern design—sponges, echinoderms, brachiopods, and mollusks, for example. It also features an outstanding group of large, reef-building creatures that died out well before the end of the Cambrian. These enigmatic animals, called archaeocyathids, resemble a two-layered cone. Put one ice-cream cone within another, leave a small space between, and you have a reasonable anatomical model for an archaeocyathid. The affinities of archaeocyathids have been debated for more than a century, with uncertain results. Most paleontologists would probably vote for a position near sponges, but scientific issues are not settled at the ballot box, and other opinions enjoy strong minority support.

But by far the most enigmatic, and most mind-boggling, component of the Tommotian faunas includes a set of bits and pieces with a catch-all name that spells frustration. These tiny spines, plates, caps, and cups tell us so little about their origin and affinity that paleontologists dub them the "small, shelly fauna," or SSF for short. "Small shellies" may be a charming phrase, when issued from the mouth of a professional who usually spouts incomprehensible Latin jargon, but please remember that this name conveys ignorance and frustration rather than delight.

We may envision two obvious potential interpretations for the SSF. Perhaps they are the coverings of tiny, entire organisms, a diminutive fauna for a first try at modernity. But perhaps—and this second alternative has always seemed more likely to paleontologists—they are bits and pieces representing the disarticulated coverings of larger multicellular organisms studded with hundreds or thousands of these SSF elements. This second position certainly makes sense. We can easily imagine that the ability to secrete hard skeletons had not fully developed in these earliest days, and that many of the first skeletonized organisms did not bear a discrete, fully protective shell, but rather a set of disconnected, or poorly coordinated fragments that only later coalesced to complete skeletons. These fragments, disarticulating after death, would form the elements of the SSF.

If this second interpretation prevails, then paleontologists are in deep trouble, and well up the proverbial creek named for the droppings of these and all later creatures. For how can we possibly reconstruct a complete animal from partial fragments that didn't even form a coherent skeleton, and that clothed a creature of entirely unknown shape and form? Yet we can obtain no real insight into the full nature of this crucial, first Tommotian fauna until we can reanimate these most important components of the SSF. Jigsaw puzzles are hard enough when we have all the pieces and their ensemble forms a picture that can guide us as we assemble the parts. But the SSF fragments set a daunting and almost hopeless task, for they probably represent pieces from one hundred different jigsaw puzzles all mixed together. The pieces contain no pictures, and we probably have less than one piece in ten of the total covering for each frame. Moreover, to make matters even worse, we don't know the sizes or shapes of the frames.

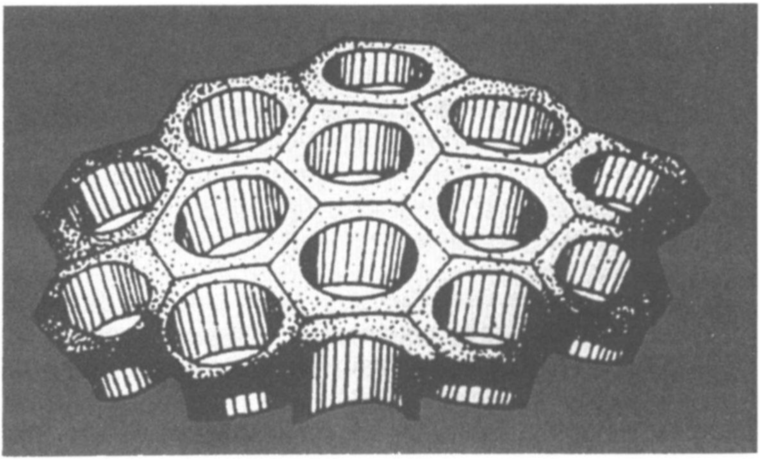
In this light, the reanimation of a complete SSF animal from preserved skeletal fragments seems truly hopeless—and so it has been, as two decades of work have produced no plausible reconstructions. We must adopt another strategy—unfortunately passive in one sense, though active in another. We must hope to discover a different kind of fossil—not the common disarticulated bits that cannot be reassembled, but a rare preservation of an entire SSF organism with all its elements in place. I call such a change in focus passive because we must wait for the discovery of a basically soft-bodied creature with its covering bits of shell still in place—and soft-bodied preservation is rare in the fossil record. But this strategy is also active because we now have good guidelines for exploration; we now know where and how to look for soft-bodied fossils.

The discoveries in Greenland and China can now be placed into proper context and excitement in a single sentence: They represent the first remains of entire SSF organisms, preserved with full coverings of their separated skeletal elements. The second interpretation of the SSF has prevailed. These cups, caps, cones, and spines are bits and pieces of incomplete skeletons upon larger organisms—and we finally have some insight into the nature of these important creatures; the dominant component of the earth's first skeletonized fauna. (The SSF elements arise in the earliest Tommotian beds, but persist into subsequent Cambrian strata. The SSF animals of China and Greenland were found in later rocks containing trilobites as well, but their SSF elements are identical with those found in earliest Tommotian sediments, so the two organisms are true representatives of this heretofore mysterious first fauna.)

Microdictyon is a classic element of the SSF. The hard parts, and previously only-known components, are round to oval, gently convex, phosphatic caps, no more than 3 mm in diameter. Each cap is a meshwork of hexagonal cells with round holes in the center of each cell (see figure). How could a paleontologist possibly move from this limited morphology to a reconstruction of the animal that secreted these partial coverings?

Since scientists, having no access to divine inspiration or the magical arts, cannot make such a move, *Microdictyon* has simply stood as a stratigraphic marker of its time and a complete mystery in anatomical terms. *Microdictyon* has been found worldwide in rocks of Tommotian to middle Cambrian age in Asia, Europe, North and Central America, and Australia.

In 1989, three Chinese colleagues from the Nanjing Institute

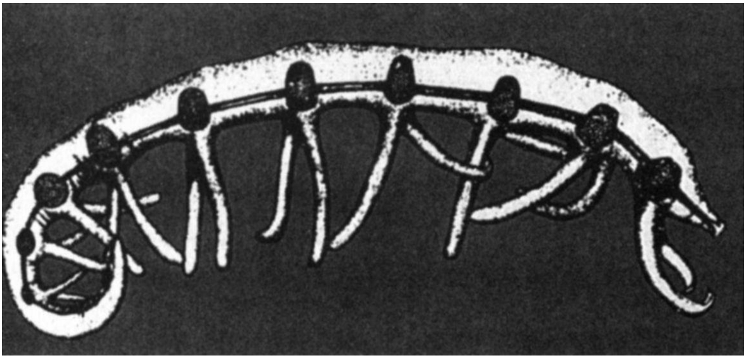


A plate of *Microdictyon* showing the characteristic meshwork. Acia Palaeontologica Sinica, *Vol. 28, No. 1, p. 5.*

of Geology and Paleontology—Chen Jun-yuan, Hou Xianguang, and Lu Hao-zhi—published a remarkable article in volume 28 of the *Acta Paleontologia Sinica.* (I remain profoundly grateful for the international character and cooperative traditions of paleontological work. Our science is global, and we would be stymied if we lost access to information from selected parts of the world. I thank both Drs. Chen and Hou for sending me reprints of their work along with letters providing further valuable data about their discoveries.)

Drs. Chen, Hou, and Lu have been working with the remarkable Chengjiang fauna of south-central China, an equivalent in age and soft-bodied preservation of the famous Burgess Shale in western Canada. Among other stunning creatures of unknown affinity, they discovered several specimens of a worm-like animal, some 8 cm in length.

This creature (see figure) bore ten thin pairs of leglike appendages, generally decreasing in strength from front to back. Traces of a simple, tubular gut can be seen on most specimens. But, most remarkable of all, this animal carried pairs of rounded phosphatic caps, inserted in pairs on the body sides, just above the joining points of the legs with the trunk. Each pair of legs, in other words, sports a corresponding pair of caps on the trunk above. These caps, *mirabile dictu,* are the elements previously



Restoration of *Microdictyon sinicum* showing the paired side plates. Acta Palaeontologica Sinica, *Vol. 28, No. 1. p.* **5.**

named *Microdictyon,* but known only from the uninterpretable hard-part dabs. Their discovery on the Chinese animal not only adds a fascinating and mysterious creature to the roster of earliest animals, but also confirms our long-held suspicions about the SSF. *Microdictyon,* at least, is just an element covering a much larger body. Moreover, the hard parts enclose only a small portion of the body and do not articulate with each other (the space between pairs of caps is about double the diameter of the caps themselves). How could we possibly have inferred the character of the animal from the caps alone?

Halkieria forms an even better known and more frustrating element of the SSF. Collected from lower Cambrian rocks throughout the world, halkieriids are preserved as sclerites (flattened blades and spines of calcification, just a millimeter or two in length). The sclerites assume several characteristic shapes, named siculate (narrow, crescentric, and asymmetrical), cultrate (elongate and more symmetrical), and palmate (wider and flattened like the palm of a hand). Although some paleontologists have tried to reconstruct halkieriids as tiny creatures, each living within or around a single sclerite, most agree that the halkieriid animal must have been substantially bigger and covered with large numbers of sclerites.

In July 1989, in a most inhospitable spot on Peary Land in northern Greenland, some twenty-one specimens of a halkieriid animal were finally unearthed from another deposit capable of preserving soft parts. (The spectacular results from the Burgess Shale have inspired paleontologists to devote attention to the discovery and exploitation of these rare and precious soft-bodied fossil faunas. Science, at its best, not only answers questions, but provokes new problems and guides fruitful research by posing issues previously unconsidered.)

In July 1990, S. Conway Morris and J. S. Peel published the first report on the halkieriid animal. Again, paleontological suspicions are confirmed, but with an amazing twist and surprise. The halkieriid is, as anticipated, a large animal (up to 7 cm), bearing many sclerites—up to 2,000 or more. The body is elongate, flattened, and wormlike, with the sclerites arranged in zones corresponding to forms previously named (see figure). Siculate sclerites surround the base of the animal (the underlying bottom surface probably carried no hard parts, as the animal crawled on a naked sole). A groove separates the zone of siculate sclerites from a lateral region of cultrates. The top surface of the creature bears more flattened, palmate sclerites.

So far, so good—and quite in line with predictions. But nature always throws us a surprise or two. Each end carries a prominent and entirely unanticipated shell. These are found in the same position on every specimen, and therefore represent no fluke of juxtaposition or odd preservation. The anterior shell is roughly rectangular, the larger posterior shell (up to 1 cm in length) more oval and flattened. With apparent growth lines and an apex near the margin, this posterior shell, if found separately, would surely have been called a brachiopod or mollusk valve. (I suspect that several named mollusks and brachiopods of the Tommotian will

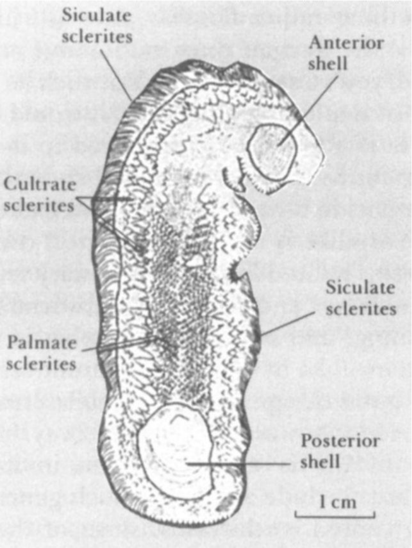


Figure of a halkieriid showing the fields of sclerites and the two end plates. *Reprinted by permission from* Nature. *June, p. SOS: Copyright © 1990 Marmillian Magazines Limited.*

turn out to be halkieriid end plates). Conway Morris and Peel wisely offer no interpretation of these elements, though others have suggested that the terminal shells might have plugged the ends of a U-shaped tube, if halkieriids burrowed as do many modern worm-shaped organisms.

We are, of course, enormously gratified to know, for the first time, some prominent animals of the SSF fauna, the earth's initial complement of modern creatures with hard parts. But should we be surprised? (I realize that the phrase "SSF fauna" is as redundant as pizza pie and AC current, but abbreviations achieve a life of their own and may then be modified, even by one of their own elements).

One misguided reply might proffer little surprise (and relative indifference to my efforts in this essay). After all, we knew that the scattered SSF elements had to represent some kind of animal or other, and now that we have found two of the creatures, they turn out to be something rather familiar after all. Just a couple of worms—and as Mr. Reagan once said about redwoods, when you've seen one, you've seen 'em all. But such an attitude would be more than just deplorably Philistine; it would be dead wrong as well. *Wormlike* is a functional term used to describe flexible, soft-bodied organisms that are basically bilaterally symmetrical, with sensory organs in a head at front, and excretory organs at the rear end. Wormlike is not a genealogical concept uniting a group of organisms related in any evolutionary sense of common parentage. *Microdictyon* and *Halkieria* are wormlike only in this functional meaning, and no anatomical plan is more common and more often evolved by radically different creatures. Wormlike bodies are good designs for any mobile creature that must move with efficiency towards food and away from enemies—and no mode of life is more common in nature. Modern wormlike creatures include animals of such genealogical disparity as truly segmented earthworms, slugs of the snail lineage, sea cucumbers of the echinoderm phylum, *Amphioxus* of our own parentage (or at least cousinship), and a host of phyla that we all once learned in high school—Platyhelminthes (including laboratory planaria and tapeworms in vertebrate intestines), Nematoda, Kinorhynchia, Pogonophora, Chaetognatha, and so forth.

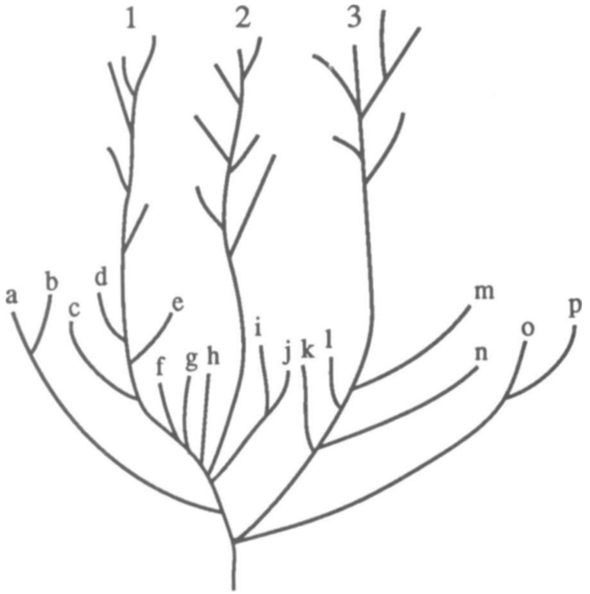
The proper evolutionary perspective is genealogical. Bats may be functionally similar to birds, but they are mammals by descent. Ichthyosaurs may look and work like fishes, but they are reptiles by ancestry. In this more fundamental context of genealogy, both *Microdictyon* and *Halkieria* are puzzling. The *Microdictyon* animal looks like an onychophoran, a small modern group considered by some as transitional between the Annelida (segmented worms) and the Arlhropoda (insects, spiders and crustaceans—see next essay). *Halkieria* has been compared with the later *Wiwaxia* from the Burgess Shale, but *Wiwaxia* itself is an enigma, and the two shells at the end of *Halkieria* are just plain odd. Perhaps better evidence will establish some homologies with known groups, but for now, *Halkieria* must be viewed as a unique creature of unknown affinity with any other animal.

Thus, we may dismiss the "seen one worm, seen 'em all" argument as simply wrong, but a more sophisticated version of "should we be surprised" does have potential merit. Consider any genealogical system that ends up with a few well-differentiated survivors, all rather distant one from the other. Modern life surely displays this cardinal feature. Our modern phyla represent designs of great distinctness, and our diverse world contains nothing in between sponges, corals, insects, snails, sea urchins, and fishes (to choose standard representatives of the most prominent phyla). A distant past must have included many linking forms, now extinct. These links would not resemble fanciful hybrids between living organisms (a cat-dog or a cow-horse), because modern lineages have been separate for so long. They would, instead, be odd animals with veiled hints of several lineages to come and many unique features of their own (as we actually find in mammals like *Hyracotherutin,* the 50-million-year-old ancestor of both horses and rhinoceroses).

Consider a figure and a nonbiological analogy (with thanks to R. T. Simmonds of Nordland, Washington, who wrote to me about this example in another context). The modern Romance languages—French, Spanish, Portuguese, Italian, and Romanian—all derive from Latin and represent clearly separate entities, despite evident similarities. But if we could—as we cannot—trace all the lineages leading from Latin, we would find a forest of village dialects linking all these end-points together. Many would be odd and unique, others smoothly transitional. We would learn that our modern descendants are just a small sample of the total richness, most now lost. We do get some hints of the full tree in survival of a few "minor phyla" (Catalan and Romansh, for example), and in historical records of a few extinct lineages (Provencal and Burgundian). But if we could go back to the beginnings of the spread, Dr. Simmonds conjectures, we would probably encounter a veritable Cambrian Explosion of lost variants.

In this sense, a phenomenon like the Cambrian Explosion must generate a majority of lineages that will seem peculiar in comparison with modern survivors—for these form the web of intermediary links that must die out if we are to emerge (as we have) with a limited set of widely separated designs (see figure). But I would raise two strong arguments against any boredom about *Microdictyon* and *Halkieria* on these grounds.

First of all, the forest of extinct lineages includes two categories of differing degrees of strangeness with respect to modern survivors. Unless modern survivors include forms at all the ancient peripheries—and this seems most unlikely, since peripheries are tenuous places—then many extinct lines will lie outside the range of all modern designs, and will feature more than an amalgam of primitive, but intermediary, characters. The point may sound abstract, but can be easily grasped in the diagram. Only lineages 1, 2, and 3 have emerged from the forest of this "Cambrian Explosion" to yield modern descendants. Now consider the lettered representatives from an early time of maximal diversity. Some of these lineages (e-1 of the diagram) do lie within the bounds of modern groups; in our retrospective view, we will regard them as unique, but not fetchingly odd. But other lineages (a-d and m-p of the diagram) lie outside the limits of modern groups, often well beyond (p, for example, lies further from lineage 3 than 3 does from any modern survivor). These creatures will be read in our parochial light (recognizing only 1, 2, and 3 for "standard" animals) as bewitchingly peculiar—and all but the most benighted dolt will take a keen interest. (The Burgess Shale excites our imagination largely because several of its "weird wonders" probably lie in this exterior domain, well outside the boundaries of modern groups).



A hypothetical genealogy of the early history of multicellular life, illustrating the likelihood that many of these early forms had anatomies that would be judged outside the range of modern survivors. *Iromie Weeramonfry. Courtesy* Natural History.

Thus, on my first argument, we cannot exclude *Microdictyon* and *Halkieria* from fascination just because we recognize that any genealogical system—like our diagram, like modern life, like the Romance languages—must include a great majority of early lineages deemed unique by modern standards. For *Microdictyon* and *Halkieria* may belong to the special group of *outsiders* (a-d and m-p), truly resident in the world of science fiction, and not to the more comfortable *insiders* (e-1) that only mix and match the cardinal features of later groups.

But suppose that *Microdictyon* and *Halkieria* do turn out to rank among the insiders? Do we then lose interest, shrug our shoulders, put down this essay, and move on to the horoscopes and gossip columns? We now come to the second, and I think more important, argument—an aesthetic or moral claim really, not an empirical proposition. What is fascination? Do we invest our interest only in unknown things beyond the boundaries of current categories? Do we not yearn for more beauty, more diversity, more examples, more wrinkles of novelty, more cases for inspiration, in the things we love and partially know? Do we not grieve for one hundred lost cantatas of Bach even though we may listen to more than two hundred? Would we not give our eye tooth (what's a canine more or less) for the unknown works of Aristotle? Would we not trade half our GNP for tapes of Socrates in conversation with his students?

Why do intellectuals feel such special pain in the destruction of the library of Alexandria—the greatest repository of ancient texts, begun by Alexander the Great, maintained by the Ptolemaic monarchs of Egypt, and finally destroyed, according to the legend you choose to follow, by the Romans, the early Christians, or the conquering Moslems? In part, we lament the loss of the utterly unknown. But we miss just as much the opportunity to relish a greatly expanded diversity among people and ideas that we already know and love. We miss the joy of making concrete, the pleasure of holding what has disappeared forever. What is history all about if not the exquisite delight of knowing the details, and not only the abstract patterns. Even if *Microdictyon* and *Halkieria* are only "inside" animals between surviving phyla, they are still prominent creatures of our earliest multicellular world. They have unique forms and peculiar features—shells on both ends, or lateral dabs in pairs. We want to know as many of these creatures as we can, for they are papyrus rolls in the great and largely lost library of our own past.

One legend of Alexandria, almost surely false, states that the library was still intact when Moslems captured the city in the seventh century. The emir Amrou Ibn el-Ass, having conquered Alexandria in 640, wrote to the caliph Omar asking (in part) what should be done with the library (and hoping against hope that the caliph would spare this great treasure). But Omar replied with the most stunning statement of "heads I win, tails you lose" in all human history. The books, he proclaimed, are either contrary to the Koran, in which case they are heretical and must be destroyed—or they are consonant with the Koran, in which case they are superfluous and must also be destroyed. The contents of the library were therefore burned to heat water in the public baths of Alexandria. The books and scrolls kept the fires going for six months.

The Omar of this legend will never win any praise from intellectuals, but I do grasp his point in an entirely reversed way. *Microdictyon* and *Halkieria* are, in a sense, either heretical (if lying outside the range of modern forms) or superfluous (if lying inside). But they are equally wonderful, and worthy of our most cherished interest and protection, in either case—and in this judgment lies the difference between most of us and the enemies of the light. In this lies the turf that we must defend at all costs.

The Reversal of *Hallucigenia*

YOU CAN GENERATE a lot of mischief just by strolling. When God asked Satan what he'd been doing, the foremost of the fallen angels responded: ". . . going to and fro in the earth and . . . walking up and down in it" (Job 1:7). But you can also do a lot of good. Aristotle preferred to teach while ambling along the covered walk, or *peripatos,* of his Lyceum in Athens. His followers were therefore called peripatetics. In Greek, *apatos* is a path, and *peri* means "about." The name for Aristotle's philosophical school therefore reflects the master's favorite activity.

The same etymology lies behind my all-time favorite technical name for an animal—the genus *Peripatus.* I just love the sound, especially when pronounced by my Scottish friends who really know how to roll their r's. I can hardly ever bring myself to write about this animal without expressing delight in its name. The only reference in my book *Wonderful Life* speaks of the "genus with the lovely name *Peripatus."*

Peripatus is an elongated invertebrate with many pairs of stout, fleshy legs—hence the chosen name for this obligate walker. The Reverend Lansdown Guilding—quite a name itself, especially given the old stereotype of English clergymen as amateur natural historians—discovered and designated *Peripatus* in 1826. He falsely placed his new creature into the mollusk phylum (with clams, snails, and squids) because he mistook the antennae of *Peripatus* for the tentacles of a slug. Since true mollusks don't have legs, Guilding named his new beast for a supposed peculiarity.

Peripatus is the most prominent member of a small group known as Onychophora. Modern onychophorans are terrestrial invertebrates of the Southern Hemisphere (with limited extension into a few regions of the Northern Hemisphere tropics)—hence little known and never observed in natural settings by residents of northern temperate zones.

About eighty species of living onychophorans have been described. They live exclusively in moist habitats, usually amid wet leaves or rotting wood. Most species are one to three inches in length, although the size champion from Trinidad, appropriately named *Macroperipatm,* reaches half a foot. They resemble caterpillars in outward appearance (although not in close evolutionary relationship). They are elongated, soft bodied, and unsegmented (the ringlike "annulations" on antennae, legs, and sometimes on the trunk are superficial and do not indicate the presence of segments, or true divisions of the body). The onychophoran head bears three paired appendages: antennae, jaws, and just adjacent to the jaws, the so-called slime papillae. Onychophorans are carnivores and can shoot a sticky substance from these papillae, thus ensnaring their prey or their enemies. Behind the head, and all along the body, onychophorans carry fourteen to forty-three pairs (depending on the species) of simple walking legs, called lobopods. The legs terminate in a claw with several spines—the source of their name, for Onychophora means "talon bearer."

The Onychophora present the primary case for a classical dilemma in taxonomy: How do we classify small groups of odd anatomy? (Oddness, remember, is largely a function of rarity. If the world contained a million species of onychophorans and only fifty of beetles, we would consider the insects as bizarre.) The chief fault **Wid** foible of classical taxonomy lies in its passion for clean order—an imposition bound to distort a messy world of continuity and complexity. A small group of distinctive anatomy sticks out like the proverbial sore thumb, and taxonomists yearn to heal the conceptual challenge by enforcing an alliance with something more familiar. Two related traditions have generally been followed in this attempt, both misleading and restrictive: the shoehorn ("cram 'em in") and the straightening rod ("push 'em between").

The shoehorn works by cramming odd groups into large and well-established categories, usually by forced and fanciful comparison of one or two features with characteristic forms of the larger group. For example, the Onychophora have sometimes been allied with the Uniramia, the dominant arthropod group that includes insects and myriapods (millipedes and centipedes), because both have single-branched legs (never mind that arthropod legs are truly segmented and that onychophoran lobopods are constructed on an entirely different patters).

The straightening rod tries to push a jutting thumb of oddness back into a linear array by designating the small and peculiar group as intermediary between two large and conventional categories. The Onychophora owe whatever small recognition they possess to this strategy—for they have most commonly been interpreted as living relicts of the evolutionary transition between two great phyla: the Annelida (segmented worms, including leeches and the common garden earthworm) and the Arthropoda (about 80 percent of animal species, including insects, spiders, and crustaceans). In this argument, *Peripatus* is a superworm for its legs and a diddly fly for building these legs without true segments.

A third possibility obviously exists and clearly bears interesting implications. This third way has been supported, often by well-respected taxonomists, but our general preference for shoehorns and straightening rods has given it short shrift. The Onychophora, under this view, might represent a separate group, endowed with sufficient anatomical uniqueness to constitute its own major division of the animal kingdom, despite the low diversity of living representatives. After all, the criterion for separate status should be degree of genealogical distinctness, not current success as measured by number of species. A lineage may need a certain minimal membership just to provide enough raw material so that evolution can craft sufficient difference for high taxonomic rank. But current diversity is no measure of available raw material through geological history. Evolution is ebb and flow, waxing and waning; once-great groups can be reduced to a fraction of their past glory. A great man once told us that the last shall be first, but just by the geometry of evolution, and not by moral law, the first can also become last. Perhaps the Onychophora were once a much more diverse group, standing wide and tall in their distinctness, while *Peripatus* and its allies now form a pitifully reduced remnant.

(By speaking of potential distinctness, I am not making an untenable claim for total separation without any relationship to other phyla. Very few taxonomists doubt that onychophorans, along with other potentially distinct groups known as tardigrades and pentastomes, have their evolutionary linkages close to annelids and arthropods. But this third view places onychophorans as a separate branch of life's tree—splitting off near the limbs of annelids and arthropods and eventually joining them to form a major trunk—whereas the shoehorn would stuff onychophorans into the Arthropoda, and the straightening rod would change life's geometry from a tree to a line and place onychophorans between primitive worms and more advanced insects.)

We can only test this third possibility by searching for onychophorans in the fossil record—a daunting task because they have no preservable hard parts and therefore do not usually fossilize. I write this essay because several striking new discoveries and interpretations, all made in the past year or two, now point to a markedly greater diversity for onychophorans right at the beginning of modern multicellular life, following the Cambrian explosion some 550 million years ago. These discoveries arise from two fortunate circumstances: First, onychophorans have been found in the rare soft-bodied faunas occasionally preserved by happy geological accidents in the fossil record; second, some ancient onychophorans possessed hard parts and can therefore appear in ordinary fossil deposits.

I fully realize that this expansion in onychophoran diversity at the beginning of multicellular animal life can scarcely rank as the hottest news item of the year. Most readers of these essays, after all, have probably never heard the word *onychophoran* and, lamentably, have no acquaintance with poor, lovely *Peripatus.* So why get excited about old onychophorans if you never knew that modern ones existed in the first place? Do hear me out if you harbor these doubts. Much more than *Peripatus* lies at stake, for validation of the third position—that onychophorans represent a separate branch of life's tree—has broad and interesting implications for our entire concept of evolution and organic order. I also think that you will marvel at the details of these early onychophorans for their own sake—and their weirdness.

We have actually known a bit about ancient onychophorans for most of this century, thanks once again to that greatest of treasure troves for soft-bodied fossils, the Burgess Shale. In 1911, two years after discovering the Burgess Shale, C. D. Walcott gave the unpronounceable name *Aysheaia* (we generally call it "a-shy-a" in the trade) to an animal that he described as an annelid worm. Many taxonomists, just viewing Walcott's illustrations, immediately saw that the creature looked much more like an onychophoran. In 1931, G. Evelyn Hutchinson, who became the world's greatest ecologist and was, perhaps, the finest person I have ever had the privilege of knowing, published a definitive account on the onychophoran affinities of *Aysheaia.* Hutchinson had studied *Peripatus* in South Africa and he knew onychophoran anatomy intimately. As an ecologist, he was powerfully intrigued by the issue of how an ordinary marine invertebrate like *Aysheaia* could evolve into a terrestrial creature like *Peripatus* with such minimal change in outward anatomy. *{Aysheaia* had fewer pairs of legs and fewer claws per leg than do modern onychophorans. It also bore a terminal mouth at the body's end, while living onychophorans have a ventral mouth on the underside. In addition, *Aysheaia* had no slime papillae and could not use such a device to shoot sticky stuff through ocean waters in any case. But, all told, the differences are astonishingly slight for more than 500 million years of time and a maximal ecological shift from ocean to land.)

One other ancient onychophoran was recognized before last year—a European form named *Xenusion,* found during the 1920s. But *Aysheaia* and *Xenusion* did not shake the shoehorn or the straightening rod. Only two fossils, both so similar to modern forms, do not make an impressive show of diversity. Onychophorans remained a tiny and uniform group, ripe for stuffing in or between larger phyla and not meriting a status of its own.

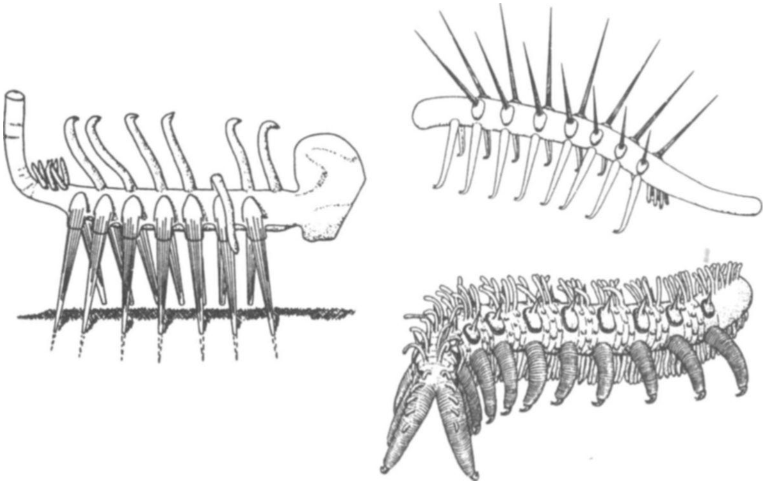
In the last essay, I described the beginning of the onychophoran coming of age (I was going to say "renaissance," but a renaissance is a rebirth, and onychophorans never had an earlier period of flowering in our consciousness). I described the discovery in China of the animal that bore the small, circular, meshwork plates known for many years from lowermost Cambrian rocks as *Microdictyon.* This fossil comes from the remarkable Chengjiang fauna of south-central China, a Burgess Shale equivalent (although slightly older), with beautiful soft-bodied preservation of many animals already known from the more famous Canadian site (and several novelties as well, including the *Microdictyon* animal). The plates called *Microdictyon* are attached in pairs to the side of the animal just above the junction of paired lobopods with the trunk of the body. The animal itself looks like an onychophoran. If this interpretation holds, then some ancient onychophorans had hard parts. The Chengjiang fauna also contains a second probable onychophoran with plates, named *Luolishania.*

Thus, the early fossil record of onychophorans had begun to expand in numbers and anatomical variety, including fully soft-bodies forms like *Aysheaia* and creatures with small pairs of plates like *Microdictyon* and *Luolishania.* But the big boost, the event that might finally push onychophorans over the border of distinct respectability, finally occurred on May 16, 1991, when the Swedish paleontologist L. Ramskold and his Chinese colleague Hou Xianguang published an article in the British journal *Nature* (science, at its best, is truly international—see bibliography).

Ramskold and Hou dropped a bombshell that makes elegant sense of a major paleontological puzzle of recent years. In 1977, Simon Conway Morris described the weirdest of all Burgess Shale organisms with the oddest of all monikers: *Hallucigenia,* named, as Simon wrote, for "the bizarre and dream-like appearance of the animal." He described *Hallucigenia* (see figure) as a tubular body supported by seven pairs of long, pointed spines—not jointed arthropod appendages or fleshy lobopods, but rigid spikes. In Conway Morris's reconstruction, a single row of seven fleshy tubes, each ending in a pair of little pincers, runs along the back, with a tuft of six smaller tubes, perhaps in three pairs, behind the larger seven. The head, not well preserved on any specimen, was depicted as a bulbous extension and the tail as a straight, upward-curving tube.

Hallucigenia was bizarre enough in appearance, but even more puzzlement attended the issue of how such a creature could function. In particular, how could a tiny animal, no more than an inch in length, be stable on seven pairs of rigid spikes for "legs"? And if stable, how could it possibly move? Some of our best functional morphologists, including Mike Labarbera of the University of Chicago, struggled with this issue and found no resolution.

The unlikely morphology, and the even more troublesome question of function, led many paleontologists to dispute Conway Morris's reconstruction (and Simon himself also began to doubt his original conclusions). In my book *Wonderful Life,* I presented Conway Morris's original version and then opted for a



LEFT: CONWAY MORRIS'S ORIGINAL RECONSTRUCTION OF HALLUCIGENIA. SIMON CONWAY MORRIS (1977): REPRINTED BY PERMISSION OF PALAEONTOLOGY. RIGHT TOP: RAMSKOLD AND HOU'S INVERSION OF HALLUCIGENIA AS AN ONYCHOPHORAN. REPRINTED BY PERMISSION FROM NATURE; COPYRIGHT © 1991 MACMILLAN MAGAZINES LIMITED. RIGHT BOTTOM: RAMSKOLD AND HOU'S RECONSTRUCTION OF THE NEW CHENGJIANG ONYCHOPHORAN WITH SIDE PLATES AND SPINES. REPRINTED BY PERMISSION FROM NATURE; COPYRIGHT © 1991, MACMILLAN MAGAZINES LIMITED.

different interpretation proposed by several colleagues before me—that *Hallucigenia* is a part broken off from a larger (and still unknown) animal. I wrote:

> *Hallucigenia* is so peculiar, so hard to imagine as an efficiently working beast that we must entertain the possibility of a very different solution. Perhaps *Hallucigenia* is not a complete animal, but a complex appendage of a larger creature, still undiscovered. The "head" end of *Hallucigenia* is no more than an incoherent blob in all known fossils. Perhaps it is no head at all, but a point of fracture, where an appendage (called *Hallucigenia)* broke off from a larger main body.

I received several dozen much appreciated letters from readers of my book, suggesting different reconstructions for some of the oddball creatures of the Burgess Shale. *Hallucigenia* received the lion's share of attention—and one suggestion cropped up again and again, in at least twenty separate letters. These correspondents, nearly all amateurs in natural history, pointed out that *Hallucigenia* would make much more sense turned upside down—for the spines, which never made any sense as organs of locomotion, could then function far more reasonably for protection!

I responded to these letters with, for me, the decisive rejoinder that a single row of tentacles (Simon's version of the upper surface) would work even more poorly than paired spines as devices of locomotion. How could an animal balance, not to mention hop around, on a single row of tentacles? Yet I couldn't deny that everything else made more sense upside down.

It doesn't happen often, but if Ramskold and Hou are correct—and I think they are—then the gut feeling of amateurs has triumphed over the weight of professional opinion. For Ramskold and Hou have, unbeknownst to them of course, followed the advice of my correspondents. They have turned *Hallucigenia* upside down, but with an added twist (intellectual, not geometric) as well—they have inverted it into an onychophoran!

Ramskold and Hou present two major arguments for their inversion of *Hallucigenia.* First, they must tackle the issue that hung me up: How can a single row of tentacles function as legs? They acknowledge the problem, of course, but suggest that Conway Morris was wrong and that two rows of paired tentacles are actually present along the surface that he called dorsal, or topmost. If Ramskold and Hou are correct, then the major objection to reversing *Hallucigenia* disappears—for two rows of flexible tentacles look like the ordinary legs of a bilaterally symmetrical creature. Moreover, when you turn *Hallucigenia* upside down on the assumption that two rows of tentacles adorn the topside of Conway Morris's version, then the inverted beast immediately says "onychophoran" to any expert, for the little paired pincers at the end of each tentacle become dead ringers for onychophoran claws. Ramskold and Hou have not yet developed enough evidence to prove the double row of tentacles conclusively, but our museum at Harvard contains the sample best suited for resolving this issue—a slab of rock with more than a dozen *Hallucigenia* specimens. I have lent this slab to Ramskold and Hou, and I suspect that an answer will soon be forthcoming.

Second, they must explain how an onychophoran could possess the several pairs of long, pointed, upward-protruding spines that an inversion of *Hallucigenia* places along the top edge of the animal—for some fossil onychophorans bear plates. (*Microdictyon* and *Luolishania* as previously discussed), but none yet described carry spines. Here, Ramskold and Hou present compelling evidence in a form much favored by natural historians—a sequence or continuum linking a strange and unexpected form to something familiar through a series of intermediates.

Start the series with *Microdictyon.* This animal, probably an onychophoran, carried pairs of flat plates along the side of its body just above the insertion of lobopods. Go next to a new and as yet unnamed "armored lobopod," again from the prolific Chengjiang fauna. This clear onychophoran also bore paired plates in the same position as in *Microdictyon.* But each plate now carries a small spine (see figure)—nothing like the elongation in *Hallucigenia,* but evidence that onychophoran plates can support spines. For a third step, go to isolated plates collected in lower Cambrian rocks of North Greenland by J. S. Peel and illustrated by Swedish paleontologist Stefan Bengtson in a commentary in *Nature* written to accompany Ramskold and Hou's paper. These Greenland plates have the same meshwork structure as those of *Microdictyon*— and onychophoran affinity seems a reasonable conjecture (although in this case, we have only found preserved plates, not the entire body). But the Greenland plates carry spines verging on the length of *Hallucigenia* spikes. We now require only a small step to a fourth term in the series—to an onychophoran bearing plates with highly elongated spines: in other words, to *Hallucigenia* turned upside down!

We are witnessing a veritable explosion of Cambrian onychophorans—*Aysheaia* and *Xenusion* with their soft bodies, *Microdictyon* and *Luolishania* with plates, the unnamed Chengjiang creature with plates and short spines, the Greenland form with longer spines, and finally, inverted *Hallucigenia* with greatly extended spines.

The reversal of *Hallucigenia* has capped and sealed the tale. The larger conclusion seems inescapable: In the great period of maximal anatomical variety and experimentation that followed right after the Cambrian explosion first populated the earth with multicellular animals of modern design, the Onychophora represented a substantial and independent group of diverse and successful marine organisms. The modern terrestrial species are a tiny and peripheral remnant, a bare clinging to life for a lineage that once ranked among the major players. The shoehorn and straightening rod have served us poorly as strategies of interpretation. Groups with few species may be highly distinct in genealogy-

Onychophorans, moreover, are not the only small cluster of straggling survivors within groups that were once major branches of life's tree. The distinct phylum of priapulid worms, for example, contains fewer than 20 species worldwide, compared with some 8,000 for marine polychaete worms, members of the dominant phylum Annelida. Yet, in the Cambrian period at the beginning of multicellular history, priapulids and polychaetes were equally common and similarly endowed (or so it seemed) with prospects for long-term success. Moreover, just as onychophorans have held on by surviving in the peripheral habitat of terrestrial life (for a formerly marine group), modern priapulids all live in harsh and marginal environments—mostly in cold or deep waters and often with low levels of oxygen.

In recognizing the Onychophora as a distinct group with an ancient legacy of much greater breadth, we may regret the loss of tidiness provided by the shoehorn and straightening rod, but we should rejoice in the interesting conceptual gains. For by our latest reckoning of life's early history, "uncomfortable" groups like the Onychophora should exist today. We once thought that the history of life moved upward and outward from simple beginnings in a few primitive, ancestral lines to ever more and ever better—the conventional notion that I have called the cone of increasing diversity. On this model, an ancient and distinctive genealogical status for several small groups (like the Onychophora) makes no sense—for life's early history, at the point of the cone, shouldn't have featured many distinct anatomies at all. The large living groups of mollusks, arthropods, annelids, vertebrates, etc.—all of which have fossil records extending back to this beginning—provide quite enough material for legacies from these early times of limited simplicity. But the reinterpretation of the Burgess Shale, and our burgeoning interest in the early history of multicellular life in general, have indicated that the cone model is not only wrong but also backward. Life may have reached a maximal spread of anatomical experimentation in these early days—and later history may be epitomized as a diminution of initial possibilities by decimation, rather than a continual expansion.

In this reversed model of a grass field, with most blades clipped off and just a few proliferating wildly thereafter, we should expect to find some blades that survived the mower but never flowered extensively again—whereas, in the cone model, the forest of blades never existed, and the early history of life provides insufficient raw material for many distinct modern groups like the Onychophora.

However much I may regret the loss of a wonderful weirdo in the reversal of *Hallucigenia,* and in its consequent change in status from oddball to onychophoran, I am more than compensated by fascinating insight into the history of ancestry for my favorite name bearer, *Peripatus.* I revel in the knowledge that these marginal and neglected animals belong to a once-mighty group that included armored members with plates and long spines. And I rejoice in the further knowledge thus provided about the strange and potent times of life's early multicellular history. (My regret, in any case, could not possibly be more irrelevant to nature's constitution, either now or 500 million years ago. *Hallucigenia* was what it was. My hopes, and those of any scientist, are only worth considering as potential biases that can block our understanding of nature's factuality.)

Peripatus may walk prouder in the pleasures of pedigree. We humans, as intellectual descendants of Aristotle, the original peripatetic, might consider a favorite motto from "the master of them that know"—well begun is half done (from the *Politics,* book 5, chapter 4). Apply it first to the onychophorans themselves—for in a tough world dominated by contingent good fortune in surviving extinction, a strong beginning of high diversity affords maximal prospect for some legacy long down the hard road. But apply it also to us, the paleontologists who strive to understand this complex history of life. By turning *Hallucigenia* upside down, we have probably taken a large step toward getting the history of life right side up.

A Dog's Life in Galton's Polyhedron

IN THE OPENING sentence of *Hereditary Genius* (1869), the founding document of eugenics, Francis Galton (Charles Darwin's brilliant and eccentric cousin—see Essay 31 for another tale of this remarkable man) proclaimed that "a man's natural abilities are derived by inheritance." He then added, making an appeal by analogy to changes induced by domestication:

> Consequently, as it is easy . . . to obtain by careful selection a permanent breed of dogs or horses gifted with peculiar powers of running, or of doing anything else, so it would be quite practicable to produce a highly-gifted race of men by judicious marriages during several consecutive generations.

Darwin had also invoked domestication as his first argument in the *Origin of Species.* Darwin began his great treatise, not with fanfare or general proclamation, but with a discussion of breeding in domestic pigeons (see Essay 25).

Darwin attributed the wondrous variety among pigeons, dogs, and other domesticated animals to the nearly limitless power of selection: "Breeders habitually speak of an animal's organization as something plastic, which they can model almost as they please." He quotes one authority on the "great power of this principle of selection": "It is the magician's wand, by means of which he may summon into life whatever form and mold he pleases."

This optimistic notion—that diligence in selection can produce almost any desired trait by artificial selection of domesticated animals or cultivated plants—has inspired the customary extrapolation into nature's larger scales, leading to a conclusion that natural selection must work even more inexorably to hone wild creatures to a state of optimal design. As Darwin wrote:

> How fleeting are the wishes and efforts of man! how short his time! and consequently how poor will his products be compared with those accumulated by nature during whole geological periods. Can we wonder, then, that nature's productions . . . should be infinitely better adapted to the most complex conditions of life, and should plainly bear the stamp of far higher workmanship. It may be said that natural selection is daily and hourly scrutinizing, throughout the world, every variation, even the slightest; rejecting that which is bad, preserving and adding up all that is good; silently and insensibly working.

This common claim for organic optimality cannot be reconciled with a theme that I regard as the primary message of history—the lesson of the panda's thumb and the flamingo's smile: The quirky hold of history lies recorded in oddities and imperfections that reveal pathways of descent. The allure of perfection speaks more to our cultural habits and instructional needs than to nature's ways (good design inspires wonder and provides excellent material for boxed illustrations in textbooks). Optimality in complex structure would probably bring evolution to a grinding halt, as flexibility disappeared on the altar of intricate adaptation (how might we change a peacock for different environments of its unknown future?).

In any case, leaving aside the abstractions of how nature ought to work, we have abundant empirical evidence that enormous effort in husbandry does not always bring its desired reward. Poultrymen have never broken the "egg-a-day barrier" (no breed of hen consistently lays more than one egg each day), and we are now trying to produce frost-resistant plants by introducing foreign DNA with techniques of genetic engineering because we have not been able to develop such traits by selection upon the natural variation of these plants. We do not know whether such failures represent our own stupidity or lack of sufficient diligence (or time) or whether they record intrinsic structural and genetic limits upon the power of selection. In any case, selection, either natural or artificial, is not the agent of organic optimality that our newspapers and textbooks so often portray. Limits are as powerful and interesting a theme as engineering triumph.

Francis Galton himself, in the same book that promised so much for human futures by controlled breeding, presented our most incisive metaphor for the other side of the coin—the limits to improvement imposed by inherited form and function. (Darwin was also intrigued by the subject of limits and devoted as much attention to this aspect of growth and development as to natural selection itself—see his longest book, the two-volume *Variation in Animals and Plants Under Domestication,* 1868.) Following the optimistic notion of unrestricted molding, we might view an organism as a billiard ball lying on a smooth table. The pool cue of natural selection pushes the ball wherever environmental pressure or human intent dictates. The speed and direction of motion (evolutionary changes) are controlled by the external force of selection. The organism, in short, does not push back. Evolution is a one-way street; outside pushes inside.

But suppose, Galton argues, organisms are not passive spheres but polyhedrons resting upon stable facets.

> The changes are not by insensible gradations; there are many, but not an infinite number of intermediate links. . . . The mechanical conception would be that of a rough stone, having, in consequence of its roughness, a vast number of natural facets, on any one of which it might rest in "stable" equilibrium. . . . If by a powerful effort the stone is compelled to overpass the limits of the facet on which it has hitherto found rest, it will tumble over into a new position of stability. . . . The stone . . . can only repose in certain widely separated positions.

Galton proposes no new force. The polyhedral stone will not move at all unless natural selection pushes hard. But the polyhedron's response to selection is restricted by its own internal structure; it can only move to a limited number of definite places. Thus, following the metaphor of Gabon's polyhedron to its conclusion, the actual directions of evolutionary change record a dynamic interaction of external push and internal constraint. The constraints are not merely negative limits to Panglossian possibilities, but active participants in the pathways of evolutionary change. St. George Mivart, whom Darwin acknowledged as his most worthy critic, adopted Gallon's polyhedron as the basis of his argument and wrote (1871):

> The existence of internal conditions in animals corresponding with such facets is denied by pure Darwinians. . . . The internal tendency of an organism to certain considerable and definite changes would correspond to the facets on the surface of the spheroid.

If Gabon's polyhedron ranks as more than mere verbiage, then we must be able to map the facets of genetic and developmental possibility. We must recast our picture of evolution as an interaction of outside (selection) and inside (constraint), not as an untrammeled trajectory toward greater adaptation. We can find no better subject for investigating facets than Darwin's own prototype for evolutionary arguments—changes induced in historical time through conscious selection by breeders upon domesticated animals. I can imagine no better object than our proverbial best friend—the dog—Gallon's own choice for comparison in the very first sentence of his manifesto for human improvement.

We should begin by asking why dogs, cows, and pigs, rather than zebras, seals, and hippos are among our domesticated animals? Are all creatures malleable to our tastes and needs, and do our selections therefore reflect the best possible beef and service? Or do some of the strongest and tastiest not enter our orbit because selection cannot overcome inherited features of form or behavior that evolved in other contexts and now resist any recruitment to human purposes?

From the first—or at least since Western traditions abandoned the idea that God had designed creatures explicitly for human use—biologists have recognized that only certain forms of behavior predispose animals to domestication and that our successes represent a subset of available species, not by any means an optimally chosen few amidst unlimited potential. In particular, we have recruited our domestic animals from social species with hierarchies of rank and domination. In the basic "trick" of domestication—what we call "taming" in our vernacular—we learn the animal's own cues and signals, thus assuming the status of a dominant creature within the animal's own species. We tame creatures by subverting their own natural behavior. If animals do not manifest a basic sociability and propensity to submit under proper cues, then we have not been able to domesticate them, whatever their potential as food or beast of burden. As Charles Lyell wrote in 1832:

> Unless some animals had manifested in a wild state an aptitude to second the efforts of man, their domestication would never have been attempted. ... It conforms itself to the will of man, because it had a chief to which in a wild state it would have yielded obedience ... it makes no sacrifice of its natural inclinations. . . . No solitary species . . . has yet afforded true domestic races. We merely develop to our own advantage propensities which propel the individuals of certain species to draw near to their fellows.

The dog is our primary pet because its ancestor, the wolf *Cants lupus,* had evolved behaviors that, by a fortunate accident of history, included a predisposition for human companionship. Thus, our story begins with a push onto a facet of Gabon's polyhedron. Domestication required a preexisting structure of behavior.

We might readily admit this prerequisite, yet marvel at the stunning diversity of domestic breeds and conclude that any shape or habit might be modeled from the basic wolf prototype. We would be wrong again.

We can usually formulate "big" questions easily enough; the key to good science lies in our ability to translate such ideas into palpable data that can help us to decide one way or the other. We can readily state the issue of limits versus optimality, but how shall we test it? In most cases, we approach such generalities best by isolating a small corner that can be defined and assessed with precision. This tactic often disappoints nonscientists, for they feel that we are being paltry or meanspirited in focusing so narrowly on one particular; yet I would rather tackle a well-defined iota, so long as I might then add further bits on the path to omega, than meet a great issue head-on in such ill-formed complexity that I could only waffle or pontificate about the grand and intangible.

A standard strategy for the study of limits lies in the field of *allometry,* or changes in shape associated with variation in size. Two sequences of size differences might be important for studying variation in form among breeds of domestic dogs: *ontogeny,* or changes in shape that occur during growth of individual dogs from fetus to adult; and *interspecific scaling,* or differences in shape among adults of varying sizes within the family Canidae, from small foxes to large wolves. We might search for regularities in the relationship between size and shape in these two sequences and then ask whether variation among dog breeds follows or transcends these patterns. If, for all their stunning diversity, dogs of different breeds end up with shapes predicted for their size by the ontogenetic or interspecific series, then inherited patterns of growth and history constrain current selection along channels of preferred form. Growth and previous evolution will act as facets of Galton's polyhedron, favored positions imposed from within upon the efforts of breeders.

The biological literature includes a large but obscure series of articles (mostly *auf Deutsch),* dating to the early years of this century, on allometry in domestic breeds. These themes have been neglected by English and American evolutionists during the past thirty years, primarily because an overconfident, strict Darwinism had so strongly emphasized the power of adaptation that the older subject of limits lost its appeal. But exciting progress in our understanding of genetic architecture and embryological development has begun to strike a proper balance between the external strength of selection and the internal channels of inherited structure. I sense a welcome reappearance of Galton's polyhedron in the primary technical literature of evolutionary biology. As one example, consider a recent study of ontogenetic and interspecific allometry in dogs by Robert K. Wayne.

Wayne asks how inherited patterns of allometry might constrain the variety of domestic breeds. He finds, for example, that all measures of skull length (face, jaws, and cranium) show little variation in three senses: First, the ontogenetic and interspecific patterns are similar (baby dogs look like small foxes in the proportions of length elements); second, we note little change of shape as size increases (baby dogs are like old dogs, and small foxes are like large wolves); third, we find little variation among breeds or species at any common size (all young dogs of the same size have roughly equal length elements).

These three observations suggest that natural variation among canids offers little raw material for fanciers to create breeds with exotic skull lengths. Wayne has confirmed this suspicion by noting that few adults of different breeds, from toy poodle to Great Dane, depart far from the tight relationship predicted by ontogeny or interspecies scaling: The length elements of a small breed may be predicted from the proportions of puppies in larger breeds or from small adult foxes.

Wayne points out that the criteria of artificial selection in domesticated races (the quirky human preferences imposed upon toy or fancy breeds, for example) must differ dramatically from the basis of natural selection in wild species—"the dog's ability to catch, dismember, or masticate live prey." If length elements are so constant in such radically different contexts, then their invariance probably reflects an intrinsic limit on variability rather than a fortuitous concurrence in different circumstances. Wayne concludes:

> Despite considerable variability in the time, place and conditions of origination of dog breeds, the scaling of skull-length measurement components is relatively invariant. All [small] dog breeds are exact allometric dwarfs with respect to measures of skull length. It is unlikely that such a specific morphological relationship has been the direct result of selection by breeders. Rather, a lack of developmental variation seems a better explanation.

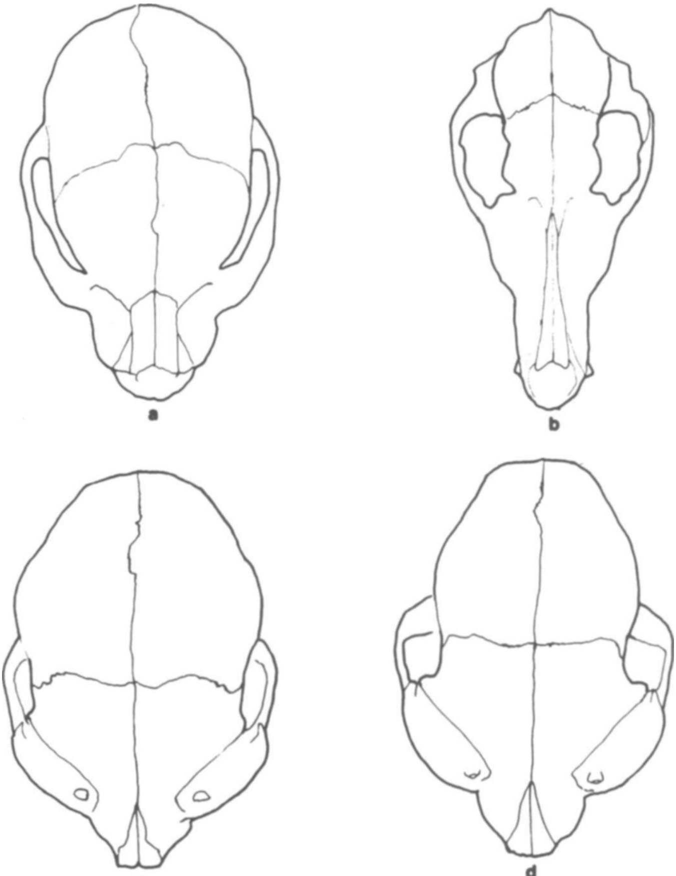
When we turn to skull widths, however, we note variation where lengths showed constancy: Puppies differ from adult foxes of the same size; puppies also turn into dogs of greatly altered shape, and small foxes are easily distinguished from large wolves by proportions of width elements. The material available to dog breeders should be extensive.

Wayne finds that dog breeds do vary greatly in width elements. (We might be tempted to say, "So what; doesn't everyone know this from a lifetime of casual inspection?" Yet our intuitions are often faulty. Wayne shows that small, snubnosed breeds have wide faces, not short skulls or jaws. Readers might be chuckling and saying, what's the difference—doesn't overwide amount to the same thing as undershort, as in the fat man's riposte that he is only too short for his weight? But the statements are not equivalent, for we are comparing lengths and widths with a common standard of body size. Small breeds are the right length, but unusually wide, for their size.) The great variation among dog breeds is not uniform among all parts, but concentrated in those features that supply raw material in growth and evolutionary history. Dog breeds form along permitted paths of available variation.

This study of internal potential helps us to predict which features will form the basis for variety among breeds (not simply what the selector wishes, but what the selectee can provide). But we can extend this insight much further to encompass the great differences in variety among domesticated species. If some features of dogs differ more among breeds because internal factors must supply the requisite variation, then perhaps, by extension, some entire species develop more diversity, not because human selectors have been more assiduous or because human needs require such variety, but because the internal facets of Galton's polyhedron are many, closely spaced, and varied.

Why do breeds of dogs differ so greatly, and those of cats relatively little? (Cats vary widely in color and character of coat but not much in shape. Nothing in the world of felines can approach the disparity in skull form between a stubby Pekingese and an elongated borzoi.) Before we speculate about diminished human effort or desire to explain Garfield versus Lassie, we should consider the more fundamental fact that available variation in the ontogeny and interspecific scaling among cats offers very little for breeders to select. Lions differ from tabbies far less than large from small dogs while, more importantly, kittens grow to adult cats with only a fraction of the change in shape that accompanies the transformation of puppy to grown dog. Consider the accompanying figure taken from Wayne's article and comparing, at the same size, neonates and adults of cats and dogs. Dogs have contributed to their own flexibility; cats, as ever, are recalcitrant.

Wayne makes a persuasive case that comparative diversity among domesticated species depends more upon available variation in the growth of wild ancestors than in the extent of human



Skulls of dogs (upper row) and cats (lower row) show the differences between neonates (left) and adult animals (right). Note the much greater range of change in dogs vs. cats.

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efforts. Horses change relatively little in shape during growth, and the heads of Shetland ponies do not differ much from those of the largest workhorses. Pigs, on the other hand, are second only to dogs in diversity of breeds. They are also unmatched among farm animals for marked change of shape during growth.

Amounts of intrinsic variation therefore set limits and supply possibilities to breeders. But even the most variable of wild species do not become putty in the hands of breeders. Pigs and dogs vary in definite ways during their growth, and only certain shapes are available for selection at definite sizes. Wayne's most persuasive case for internal limits lies in his demonstration that sets of traits in a standard "ontogenetic trajectory" (a sequence of stages from puppy to adult) tend to hang together. Dog breeds are not a hodgepodge of isolated traits, each taken at will from any stage of ontogeny. Traits of juvenility remain associated, and many breeds, particularly among small dogs, continue to look like puppies when adult—an evolutionary process called *paedomorphosis* (child-shaped) or *neoleny* (literally, "holding on to youth").

Wayne has shown that—without exception—adults of small breeds resemble the juvenile stages of large dogs more than the adults of other wild canid species (small foxes)—a convincing demonstration that inherited patterns of growth set possibilities of change. Dogs resolutely stick to their own trajectories of growth. "To some extent," Wayne concludes, "many dog breeds represent morphological snapshots between these developmental endpoints. . . . This suggests that small domestic dogs differ from foxes because puppies of small dogs cannot grow out of their distinctive neonate morphology."

We know, of course, that breeders can do many wonderful and peculiar things, from making a dachshund into a frankfurter to turning a chihuahua into a hairless rat or a sheepdog into a woolly mimic of its charges. But these peculiarities are imposed upon a basic and unaltered pattern set by constraints of inherited growth. The trajectory of ontogeny provides, as Raymond Coppinger states, a "rough first draft" for all breeds.

If ordinary variation in growth provides the main source for breeders, then a wild species' own juvenile stages are the primary storehouse of available change. Under this basic theme of limits, we may understand an old and otherwise puzzling observation about domesticated versus wild species. Over and over again, we note that domestic species develop more juvenile proportions than their wild ancestors. We cannot explain this difference by smaller size (since domestic breeds are often larger than their ancestors) or by conscious selection on the old theme of planned optimality, for what possible common adaptive advantage could have inspired breeders to produce such a similarly shortened face in Middle white pigs, the Niatu oxen of South America, and the Pekingese of the Chinese imperial court (see figure). The only sensible coordinating theme behind these similarities is retention by neoteny of juvenile traits common to most vertebrates.

If these shared neotenous traits of domesticated species are not products of direct selection by breeders, then what is the common basis of their origin? Most experts argue that these juvenile traits are spinoffs from the true object of selection—tame and playful behavior itself. Organisms may vary as much in rates of development as in form. By breeding only those animals that retain the favored juvenile traits of pliant and flexible behavior past the point of sexual maturity, humans hasten the process of domestication itself. Since traits are locked together in development, not infinitely dissociable as hopes for optimality require, selection for desired juvenile behavior brings features of juvenile morphology along for the ride. (We may, in some cases, also select juvenile morphology for its aesthetic appeal—large eyes and rounded craniums, for example—and obtain valuable spinoffs in behavior). In short, these common juvenile features are facets of Galton's polyhedron—correlated consequences of selection for something else—not direct objects of human desire.

This theme of correlated consequences brings me to a final point. We have explored the role of developmental constraint in shaping many features of dogs—their difference in diversity from other domesticated species; the disparate contributions made by various parts of their bodies to the unparalleled variety among breeds; the restricted sources of variation for construction of breeds, particularly the limits imposed by tendencies for traits to "hang together" during growth.

We might view these themes in a pessimistic light—as a brake upon the power of selection to build with all the freedom of a human sculptor. But I suggest a more positive reading. Constraints of development embody the twin and not-so-contradictory themes of limits and opportunities. Constraints do preclude certain fancies, but they also supply an enormous pool of available potential for future change. So what if the pool has borders; the water inside is deep and inviting. The pessimist might view correlated characters in growth as a sad foreclosure of certain combinations. But an optimist might emphasize the power for rapid change provided by the possibility of recruiting so many

Neotenically shortened faces of domesticated animals. From top to bottom: pig, ox, and Pekingese dog. *Courtesy of The Natural History Museum, London.*

features at once. The great variation that dogs develop during their growth builds an enormous pool all by itself. A wide range of juvenile stages becomes available for recruitment by neoteny—a potential precluded if youngsters look and act like adults.

This great pool of potential has been used over and over again by breeders of domestic dogs. We should view this restricted variation as the main source of their success, not the tragic limit to their hopes. My colleague Raymond Coppinger, of Hampshire College, has spent ten years promoting the use of guarding dogs (a great European tradition that never caught on in America) as an alternative to shooting, poisoning, and other mayhem in the protection of sheep from coyotes and other predators. He has placed more than five hundred dogs with farmers in thirty-five states. Coppinger notes the great, and usually unappreciated, difference between guarding and herding breeds. Herders control the movement of sheep by using predatory behaviors of adult dogs—stalking, chasing, biting, and barking—but inhibiting the final outcome. These breeds feature adult traits of form and behavior; they display no neotenous characteristics.

Guard dogs, on the other hand, simply move with and among the flock. They work alone and do not control the flock's motion. They afford protection primarily by their size, for few coyotes will attack a flock accompanied by a one-hundred-pound dog. They behave toward sheep as puppies do towards other dogs—licking the sheep's face as a puppy might in asking for food, chasing and biting with the playfulness of young dogs, even mounting sheep as young dogs mount each other in sexual play and rehearsal. This neotenous behavior accompanies a persistently juvenile morphology, as these dogs grow short faces, big eyes, and floppy ears.

Coppinger has raised guarding and herding dogs together from babyhood. They show little difference in behavior until puberty. Herders then develop the standard traits of adulthood—border collies begin to stalk, while retrievers and pointers live up to their names. But the guarders develop no new patterns and simply retain their youthful traits. Thus, a valuable set of features can be recruited together because they already exist as the normal form and behavior of juvenile dogs. Patterns of growth are rich reservoirs, not sterile strictures.

One tradition of argument identifies neoteny with all that is good and kind—"Except ye be converted, and become as little children, ye shall not enter into the kingdom of heaven." Yet I resist any facile transference between natural realities and human hopes if only because the dark side of social utility should teach us caution in proposing analogies.

Neoteny certainly has its dark side in social misconstruction. Konrad Lorenz, who, to put it as kindly as possible, made his life in Nazi Germany more comfortable by tailoring his views on animal behavior to the prevailing orthodoxy, often argued during the early 1940s that civilization is the analogue of domestication. Domestic animals are often neotenous; neotenous animals retain the flexibility of youth and do not develop the instinctive and healthy aversion that mature creatures feel toward deformed and unworthy members of their race. Since humans have therefore lost this instinctive power to reject the genetically harmful, Lorenz defended Nazi racial and marriage laws as a mirror of nature's mature ways.

Still, I cannot help noting, since dogs are descended from wolves, and humans really are neotenous in both form and behavior (without justifying Lorenz's fatuous and hateful reveries), that the neoteny of sheep-guarding dogs does fulfill, in a limited sense, one of the oldest and most beautiful of all prophecies: "The wolf also shall dwell with the lamb . . . and a little child shall lead them."

Betting on Chance—and No Fair Peeking

DOUBLE ENTENDRE can be delicious. Who does not delight in learning that Earnest, in Oscar Wilde's play, is a good chap, not a worthy attitude. And who has ever begrudged that tragic figure his little joke. But double meanings also have their dangers—particularly when two communities use the same term in different ways, and annoying confusion, rather than pleasant amusement or enlightenment, results.

Differences in scientific and vernacular definitions of the same word provide many examples of this frustrating phenomenon. "Significance" in statistics, for example, bears little relation to the ordinary meaning of something that matters deeply. Mouse tails may be "significantly" longer in Mississippi than in Michigan—meaning only that average lengths are not the same at some level of confidence—but the difference may be so small that no one would argue for significance in the ordinary sense. But the most serious of all misunderstandings between technical and vernacular haunts the concepts of probability and particularly the words *random* and *chance.*

In ordinary English, a random event is one without order, predictability, or pattern. The word connotes disaggregation, falling apart, formless anarchy, and fear. Yet, ironically, the scientific sense *of random* conveys a precisely opposite set of associations. A phenomenon governed by chance yields maximal simplicity, order, and predictability—at least in the long run. Suppose that we are interested in resolving the forces behind a large-scale pattern of historical change. Randomness becomes our best hope for a maximally simple and tractable model. If we flip a penny or throw a pair of dice, once a second for days on end, we achieve a rigidly predictable distribution of outcomes. We can predict the margins of departure from 50-50 in the coins or the percentage of sevens for our dice, based on the total number of throws. When the number of tosses becomes quite large, we can give precise estimates and ranges of error for the frequencies and lengths of runs—heads or sevens in a row—all based on the simplest of mathematical formulas from the theory of probability. (Of course, we cannot predict the outcome of any particular trial or know when a run will occur, as any casual gambler should—but so few do—know.)

Thus, if you wish to understand patterns of long historical sequences, pray for randomness. Ironically, nothing works so powerfully against resolution as conventional forms of determinism. If each event in a sequence has a definite cause, then, in a world of such complexity, we are lost. If *A* happened because the estuary thawed on a particular day, leading to *B* because Billy the Seal swam by and gobbled up all those fishes, followed by *C* when Sue the Polar Bear sauntered through—not to mention ice age fluctuations, impacting asteroids, and drifting continents of the truly long run—then how can we hope to predict and resolve the outcome?

The beauty (and simplicity) of randomness lies in the absence of these maximally confusing properties. Coin flipping permits no distinctive personality to any time or moment; each toss can be treated in exactly the same way, whenever it occurs. We can date geological time with precision by radioactive decay because each atom has an equal probability of decaying in each instant. If causal individuality intervened—if 10:00 A.M. on Sunday differed from 5:00 P.M. on Wednesday, or if Joe the uranium atom, by dint of moral fiber, resisted decay better than his brother Tom, then randomness would fail and the method would not work.

One of the best illustrations for this vitally important, but counterintuitive, principle of maximal long-term order in randomness comes from my own field of evolutionary biology—and from a debate that has greatly contributed to making professional life more interesting during the past twenty years. Traditional Darwinism includes an important role for randomness—but only as a source of variation, or raw material, for evolutionary change, not as an agent for the direction of change itself. For Darwin, the predominant source of evolutionary change resides in the deterministic force of natural selection. Selection works for cause and adapts organisms to changing local environments. Random variation supplies the indispensable "fuel" for natural selection but does not set the rate, timing, or pattern of change. Darwinism is a two-part theory of randomness for raw material and conventional causality for change—*Chance and Necessity,* as so well epitomized by Jacques Monod in the title of his famous book about the nature of Darwinism.

In the domain of organisms and their good designs, we have little reason to doubt the strong, probably dominant influence of deterministic forces like natural selection. The intricate, highly adapted forms of organisms—the wing of a bird or the mimicry of a dead twig by an insect—are too complex to arise as long sequences of sheer good fortune under the simplest random models. But this stricture of complexity need not apply to the nucleotide-by-nucleotide substitutions that build the smallest increments of evolutionary change at the molecular level. In this domain of basic changes in DNA, a "neutralist" theory, based on simple random models, has been challenging conventional Darwinism with marked success during the past generation.

When the great Japanese geneticist Motoo Kimura formulated his first version of neutral theory in 1968 (see bibliography), he was impressed by two discoveries that seemed difficult to interpret under the conventional view that natural selection overwhelms all other causes of evolutionary change. First, at the molecular level of substitutions in amino acids, measured rates indicated a constancy of change across molecules and organisms—the so-called molecular clock of evolution. Such a result makes no sense in Darwin's world, where molecules subject to strong selection should evolve faster than others, and where organisms exposed to different changes and challenges from the environment should vary their evolutionary rates accordingly. At most, one might claim that these deterministic differences in rate might tend to "even out" over very long stretches of geological time, yielding roughly regular rates of change. But a molecular clock surely gains an easier interpretation from random models. If deterministic selection does not regulate most molecular changes—if, on the contrary, most molecular variations are neutral, and therefore rise and fall in frequency by the luck of the draw—then mutation rate and population size will govern the tempo of change. If most populations are large, and if mutation rates are roughly the same for most genes, then simple random models predict a molecular clock.

Second, Kimura noted the recent discovery of surprisingly high levels of variation maintained by many genes among members of populations. Too much variation poses a problem for conventional Darwinism because a cost must accompany the replacement of an ancestral gene by a new and more advantageous state of the same gene—namely, the differential death, by natural selection, of the now disfavored parental forms. This cost poses no problem if only a few old genes are being pushed out of a population at any time. But if hundreds of genes are being eliminated, then any organism must carry many of the disfavored states and should be ripe for death. Thus, selection should not be able to replace many genes at once. But the data on copious variability seemed to indicate a caldron of evolutionary activity at far too many genetic sites—too many, that is, if selection governs the changes in each varying gene. Kimura, however, recognized a simple and elegant way out of this paradox. If most of the varying forms of a gene are neutral with respect to selection, then they are drifting in frequency by the luck of the draw. Invisible to natural selection because they make no difference to the organism, these variations impose no cost in replacement.

In twenty years of copious writing, Kimura has always carefully emphasized that his neutral theory does not disprove Darwinism or deny the power of natural selection to shape the adaptations of organisms. He writes, for example, at the beginning of his epochal book *The Neutral Theory of Molecular Evolution* (1983):

> The neutral theory is not antagonistic to the cherished view that evolution of form and function is guided by Darwinian selection, but it brings out another facet of the evolutionary process by emphasizing the much greater role of mutation pressure and random drift at the molecular level.

The issue, as so often in natural history (and as I emphasize so frequently in these essays), centers upon the relative importance of the two processes. Kimura has never denied adaptation and natural selection, but he has tended to view these processes as quantitatively insignificant in the total picture—a superficial and minor ripple upon the ocean of neutral molecular change, imposed every now and again when selection casts a stone upon the waters of evolution. Darwinians, on the other hand, at least before Kimura and his colleagues advanced their potent challenge and reeled in the supporting evidence, tended to argue that neutral change occupied a tiny and insignificant corner of evolution—an odd process occasionally operating in small populations at the brink of extinction anyway.

This argument about relative frequency has raged for twenty years and has been, at least in the judgment of this bystander with no particular stake in the issue, basically a draw. More influence has been measured for selection than Kimura's original words had anticipated; Darwin's process is no mere pockmark on a sea of steady tranquility. But neutral change has been established at a comfortably high relative frequency. The molecular clock is neither as consistent nor as regular as Kimura once hoped, but even an imperfect molecular timepiece makes little sense in Darwin's world. The ticking seems best interpreted as a pervasive and underlying neutralism, the considerable perturbations as a substantial input from natural selection (and other causes).

Nonetheless, if forced to award the laurels in a struggle with no clear winners, I would give the nod to Kimura. After all, when innovation fights orthodoxy to a draw, then novelty has seized a good chunk of space from convention. But I bow to Kimura for another and more important reason than the empirical adequacy of neutralism at high relative frequency, for his theory so beautifully illustrates the theme that served as an introduction to this essay: the virtue of randomness in the technical as opposed to the vernacular sense.

Kimura's neutralist theory has the great advantage of simplicity in mathematical expression and specification of outcome. Deterministic natural selection yields no firm predictions for the histories of lineages—for you would have to know the exact and particular sequences of biotic and environmental changes, and the sizes and prior genetic states of populations, in order to forecast an outcome. This knowledge is not attainable in a world of imperfect historical information. Even if obtainable, such data would only provide a prediction for a particular lineage, not a general theory. But neutralism, as a random model treating all items and times in the same manner, yields a set of simple, general equations serving as precise predictions for the results of evolutionary change. These equations give us, for the first time, a base-level criterion for assessing any kind of genetic change. If neutralism holds, then actual outcomes will fit the equations. If selection predominates, then results will depart from predictions—and in a way that permits identification of Darwinian control. Thus, Kimura's equations have been as useful for selectionists as for neutralists themselves; the formulas provide a criterion for everyone, and debate can center upon whether or not the equations fit actual outcomes. Kimura has often emphasized this point about his equations, and about random models in general. He wrote, for example, in 1982:

> The neutral theory is accompanied by a well-developed mathematical theory based on the stochastic theory of population genetics. The latter enables us to treat evolution and variation quantitatively, and therefore to check the theory by observations and experiments. .

The most important and useful of these predictions involves a paradox under older Darwinian views. If selection controls evolutionary rate, one might think that the fastest tempos of alteration would be associated with the strongest selective pressures for change. Speed of change should vary directly with intensity of selection. Neutral theory predicts precisely the opposite—for an obvious reason once you start thinking about it. The most rapid change should be associated with unconstrained randomness—following the old thermodynamic imperative that things will invariably go to hell unless you struggle actively to maintain them as they are. After all, stability is far more common than change at any moment in the history of life. In its ordinary everyday mode, natural selection must struggle to preserve working combinations against a constant input of deleterious mutations. In other words, natural selection, in our technical parlance, must usually be "purifying" or "stabilizing." Positive selection for change must be a much rarer event than watchdog selection for tossing out harmful variants and preserving what works.

Now, if mutations are neutral, then the watchdog sees nothing and evolutionary change can proceed at its maximal tempo—the neutral rate of substitution. But if a molecule is being preserved by selection, then the watchdog inhibits evolutionary change. This originally counterintuitive proposal may be regarded as the key statement of neutral theory. Kimura emphasizes the point with italics in most of his general papers, writing for example (in 1982): *"Those molecular changes that are less likely to be subjected to natural selection occur more rapidly in evolution."*

Both the greatest success, and the greatest modification, of Kimura's original theory have occurred by applying this principle that selection slows the maximal rate of neutral molecular change. For modification of the original theory, thousands of empirical studies have now shown that watchdog selection, measured by diminished tempo of change relative to predictions of randomness, operates at a far higher relative frequency than Kimura's initial version of neutralist theory had anticipated. For success, the firm establishment of the principle itself must rank as the greatest triumph of neutralism—for the tie of maximal rate to randomness (rather than to the opposite expectation of intense selection) does show that neutralism exerts a kind of base-level control over evolution as a whole.

The most impressive evidence for neutralism as a maximal rate has been provided by forms of DNA that make nothing of potential selective value (or detriment) to an organism. In all these cases, measured tempos of molecular change are maximal, thus affirming the major prediction of neutralism.

1. *Synonymous substitutions.* The genetic code is redundant in the third position. A sequence of three nucleotides in DNA codes for an amino acid. Change in either of the first two nucleotides alters the amino acid produced, but most changes in the third nucleotide—so-called synonymous substitutions—do not alter the resulting amino acid. Since natural selection works on features of organisms, in this case proteins built by DNA and not directly on the DNA itself, synonymous substitutions should be invisible to selection, and therefore neutral. Rates of change at the third position are usually five or more times as rapid as changes at the functional first and second positions—a striking confirmation of neutralism.

2. *Introns.* Genes come in pieces, with functional regions (called exons) interrupted by DNA sequences (called introns) that are

snipped out and not translated into proteins. Introns change at a much higher evolutionary rate than exons.

3. *Pseudogenes.* Certain kinds of mutations can extinguish the function of a gene—for example, by preventing its eventual translation into protein. These so-called pseudogenes begin with nearly the same DNA sequence as the functional version of the gene in closely related species. Yet, being entirely free from function, these pseudogenes should exert no resistance against the maximal accumulation of changes by random drift. Pseudogenes become a kind of ultimate test for the proposition that absence of selection promotes maximal change at the neutral rate—and the test has, so far, been passed with distinction. In pseudogenes, rates of change are equal, and maximal, at all three positions of the triplet code, not only at the third site, as in functional genes.

I was inspired to write about neutral theory by a fascinating example of the value of this framework in assessing the causes of evolutionary rates. This example neither supports nor denies neutralism but forms a case in the middle, enlightened by the more important principle that random models provide simple and explicit criteria for judgment.

While supposedly more intelligent mammals are screwing up royally above ground, Near Kastern mole rats of the species *Spalax ehrenbergi* are prospering underneath. Subterranean mammals usually evolve reduced or weakened eyes, but *Spalax* has reached an extreme state of true blindness. Rudimentary eyes are still generated in embryology, but they are covered by thick skins and hair. When exposed to powerful flashes of light, *Spalax* shows no neurological response at all, as measured by electrodes implanted in the brain. The animal is completely blind.

What then shall we make of the invisible and rudimentary eye? Is this buried eye now completely without function, a true vestige on a path of further reduction to final disappearance? Or does the eye perform some other service not related to vision? Or perhaps the eye has no direct use, but must still be generated as a prerequisite in an embryological pathway leading to other functional features. How can we decide among these and other alternatives? 'The random models of neutral theory provide our most powerful method. If the rudimentary eye is a true vestige, then its proteins should be changing at the maximal neutral rate. If selection has not been relaxed, and the eye still functions in full force (though not for vision), then rates of change should be comparable to those for other rodents with conventional eyes. If selection has been relaxed due to blindness, but the eye still functions in some less constrained way, then an intermediate rate of change might be observed.

The eye of 5. *ehrenbergi* still builds a lens (though the shape is irregular and cannot focus an image), and the lens includes a protein, called aA-crystallin. The gene for this protein has recently been sequenced and compared with the corresponding gene in nine other rodents with normal vision (see article by W. Hendriks, J. Leunissen, E. Nevo, H. Bloemendal, and W. W. de Jong in bibliography).

Hendriks and colleagues obtained the most interesting of possible results from their study. The aA-crystallin gene is changing much faster in blind *Spalax* than in other rodents with vision, as relaxation of selection due to loss of primary function would suggest. The protein coded by the *Spalax* gene, for example, has undergone nine amino acid replacements (of 173 possible changes), compared with the ancestral state for its group (the murine rodents, including rats, mice, and hamsters). All other murines in the study (rat, mouse, hamster, and gerbil) have identical sequences with no change at all from the ancestral state. The average tempo of change in aA-crystallin among vertebrates as a whole has been measured at about 3 amino acid replacements per 100 positions per 100 million years. *Spalax* is changing more than four times as fast, at about 13 percent per 100 million years. (Nine changes in 173 positions is 5.2 percent; but the *Spalax* lineage is only 40 million years old—and 5.2 percent in 40 million corresponds to 13 percent in 100 million years.) Moreover, *Spalax* has changed four amino acids at positions that are absolutely constant in all other vertebrates studied—seventy-two species ranging from dogfish sharks to humans.

"These findings," Hendriks and colleagues conclude, "all clearly indicate an increased tolerance for change in the primary structure of aA-crystallin in this blind animal." So far so good. But the increased tempo of change in *Spalax,* though marked, still reaches only about 20 percent of the characteristic rate for pseudogenes, our best standard for the maximal, truly neutral pace of evolution. Thus, *Spalax* must still be doing enough with its eyes to damp the rate of change below the maximum for neutrality. Simple models of randomness have taught us something interesting and important by setting a testable standard, approached but not met in this case, and acting as a primary criterion for judgment.

What then is aA-crystallin doing for *Spalax?* What can a rudimentary and irregular lens, buried under skin and hair, accomplish? We do not know, but the established intermediate rate of change leads us to ask the right questions in our search for resolution.

Spalax is blind, but this rodent still responds to changes in photoperiod (differing lengths of daylight and darkness)—and apparently through direct influence of light regimes themselves, not by an indirect consequence that a blind animal might easily recognize (increase in temperature due to more daylight hours, for example). A. Haim, G. Heth, H. Pratt, and E. Nevo (see bibliography) showed that *Spalax* would increase its tolerance for cold weather when exposed to a winterlike light regime of eight light followed by sixteen dark hours. These mole rats were kept at the relatively warm temperature of 22°C, and were therefore not adjusting to winter based on clues provided by temperature. Animals exposed to twelve light and twelve dark hours at the same temperature did not improve their thermoregulation as well. Interestingly, animals exposed to summerlike light regimes (sixteen light and eight dark), but at colder temperatures of 17°C, actually *decreased* their cold-weather tolerance. Thus, even though blind, *Spalax* is apparently using light, not temperature, as a guide for adjusting physiology to the cycle of seasons.

Hendriks and colleagues suggest a possible explanation, not yet tested. We know that many vertebrates respond to changes in photoperiod by secreting a hormone called melatonin in the pineal gland. The pineal responds to light on the basis of photic information transmitted via the retina. *Spalax* forms a retina in its rudimentary eye, yet how can the retina, which perceives no light in this blind mammal, act in concert with the pineal gland? But Hendriks and colleagues note that the retina can also secrete melatonin itself—and that the retina of *Spalax* includes the secreting layer. Perhaps the retina of *Spalax* is still functional as a source of melatonin or as a trigger of the pineal by some mechanism still unknown. (I leave aside the fascinating, and completely unresolved, issue of how a blind animal can respond, as *Spalax* clearly does, to seasonal changes in photoperiod.)

If we accept the possibility that *Spalax* may need and use its retina (in some nonvisual way) for adaptation to changing seasons, then a potential function for the lens, and for the aA-crystallin protein, may be sought in developmental pathways, not in direct utility. The lens cannot work in vision, and aA-crystallin focuses no image, but the retina does not form in isolation and can only be generated as part of a normal embryological pathway that includes the prior differentiation of other structures. The formation of a lens vesicle may be a prerequisite to the construction of a retina—and a functioning retina may therefore require a lens, even if the lens will be used for nothing on its own.

Evolution is strongly constrained by the conservative nature of embryological programs. Nothing in biology is more wondrously complex than the production of an adult vertebrate from a single fertilized ovum. Nothing much can be changed very radically without discombobulating the embryo. The intermediate rate of change in lens proteins of a blind rodent—a tempo so neatly between the maximal pace for neutral change and the much slower alteration of functioning parts—may point to a feature that has lost its own direct utility but must still form as a prerequisite to later, and functional, features in embryology.

Our world works on different levels, but we are conceptually chained to our own surroundings, however parochial the view. We are organisms and tend to see the world of selection and adaptation as expressed in the good design of wings, legs, and brains. But randomness may predominate in the world of genes—and we might interpret the universe very differently if our primary vantage point resided at this lower level. We might then see a world of largely independent items, drifting in and out by the luck of the draw—but with little islands dotted about here and there, where selection reins in tempo and embryology ties things together. What, then, is the different order of a world still larger than ourselves? If we missed the different world of genie neutrality because we are too big, then what are we not seeing because we are too small? We are like genes in some larger world of change among species in the vastness of geological time. What are we missing in trying to read this world by the inappropriate scale of our small bodies and minuscule lifetimes?

Bushes and Ladders in Human Evolution

MY FIRST TEACHER of paleontology was almost as old as some of the animals he discussed. He lectured from notes on yellow foolscap that he must have assembled during his own days in graduate school. The words changed not at all from year to year, but the paper got older and older. I sat in the first row, bathed in yellow dust, as the paper cracked and crumbled every time he turned a page.

It is a blessing that he never had to lecture on human evolution. New and significant prehuman fossils have been unearthed with such unrelenting frequency in recent years that the fate of any lecture notes can only be described with the watchword of a fundamentally irrational economy—planned obsolescence. Each year, when the topic comes up in my courses, I simply open my old folder and dump the contents into the nearest circular file. And here we go again.

A front-page headline in the *New York Times* for October 31, 1975, read: "Man traced 3.75 million years by fossils found in Tanzania." Dr. Mary Leakey, unsung hero of the famous clan, had discovered the jaws and teeth of at least eleven individuals in sediments located between two layers of fossil volcanic ash dated at 3.35 and 3.75 million years, respectively. (Mary Leakey, usually described only as Louis's widow, is a famous scientist with more impressive credentials than those of her flamboyant late husband. She also discovered several of the famous fossils usually attributed to Louis, including the "nutcracker man" of Olduvai, *Australopithecus boi-*

set, their first important find.) Mary Leakey classified these fragments as the remains of creatures in our genus *Homo,* presumably of the East African species *Homo habilis,* first described by Louis Leakey.[2]

So what? In 1970, Harvard paleontologist Brian Patterson dated an East African jaw at 5.5 million years. True, he attributed the fragment to the genus *Australopithecus,* not to *Homo.* But *Australopithecus* has been widely regarded as the direct ancestor of *Homo.* While taxonomic convention requires the award of different names to stages of an evolving lineage, this custom should not obscure biological reality. If *H. habilis* is the direct descendant of *A. afncanus* (and if the two species differ little in anatomical features), then the oldest "human" might as well be the oldest *Australopithecus,* not the oldest recipient of the arbitrary designation *Homo.* What, then, is so exciting about some jaws and teeth a million and a half years younger than the oldest *Australopithecus?*

I believe that Mary Leakey's find is the second most important discovery of the decade. To explain my excitement, I must provide some background in human paleontology and discuss a fundamental, but little appreciated, issue in evolutionary theory—the conflict between "ladders" and "bushes" as metaphors for evolutionary change. I want to argue that *Australopithecus,* as we know it, may not be the ancestor of *Homo;* and that, in any case, ladders do not represent the path of evolution. (By "ladders" I refer to the popular picture of evolution as a continuous sequence of ancestors and descendants.) Mary Leakey's jaws and teeth are the oldest "humans" we know.

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[2] I wrote this essay in January, 1976. True to the admonition of my last paragraph, Mary Leakey's attribution of the Laetolil jaws to the genus *Homo* has been challenged by several colleagues. They assert no alternate hypothesis, but merely argue that jaws alone offer too little for a certain diagnosis. In any case, the primary assertion of this article remains valid—from our knowledge of African fossils, the genus *Homo* may be as old as the australopithecines. Moreover, we still have no firm evidence for any progressive change within any hominid species.

The metaphor of the ladder has controlled most thinking about human evolution. We have searched for a single, progressive sequence linking some apish ancestor with modern man by gradual and continuous transformation. The "missing link" might as well have been called the "missing rung." As the British biologist J. Z. Young recently wrote (1971) in his *Introduction to the Study of Man:* "Some interbreeding but varied population gradually changed until it reached the condition we recognize as that of *Homo sapiens.* "

Ironically, the metaphor of the ladder first denied a role in human evolution to the African australopithecines. *A. afncanns* walked fully erect, but had a brain less than one-third the size of ours (see essay 22). When it was discovered in the 1920s, many evolutionists believed that all traits should change in concert within evolving lineages—the doctrine of the "harmonious transformation of the type." An erect, but small-brained ape could only represent an anomalous side branch destined for early extinction (the true intermediate, I assume, would have been a semierect, half-brained brute). But, as modern evolutionary theory developed during the 1930s, this objection to *Australopithecus* disappeared. Natural selection can work independently upon adaptive traits in evolutionary sequences, changing them at different times and rates. Frequently, a suite of characters undergoes a complete transformation before other characters change at all. Paleontologists refer to this potential independence of traits as "mosaic evolution."

Secured by mosaic evolution, *A. afncanus* attained the exalted status of direct ancestor. Orthodoxy became a three-runged ladder: *A. afncanus-H. erectus* (Java and Peking Man)-*H. sapiens.*

A small problem arose during the 1930s when another species of australopithecine was discovered—the so-called robust form, *A. robustus* (and later the more extreme "hyper-robust," *A. boisei,* found by Mary Leakey in the late 1950s). Anthropologists were forced to admit that two species of australopithecines lived contemporaneously and that the ladder contained at least one side branch. Still, the ancestral status of *A. afncanus* was not challenged; it merely acquired a second and ultimately unsuccessful descendant, the small-brained, big-jawed robust lineage.

Then, in 1964, Louis Leakey and his colleagues began a radical reassessment of human evolution by naming a new species from East Africa, *Homo habilis.* They believed that *H. habilis* was a contemporary of the two australopithecine lineages; moreover, as the name implies, they regarded it as distinctly more human than either of its contemporaries. Bad news for the ladder: three coexisting lineages of prehumans! And a potential descendant *(H. habilis)* living at the same time as its presumed ancestors. Leakey proclaimed the obvious heresy: both lineages of australopithecines are side branches with no direct role in the evolution of *Homo sapiens.*

But *H. habilis,* as Leakey defined it, was controversial for two reasons. The conventional ladder could still be defended:

1. The fossils were scrappy and came from different places and times. Many anthropologists argued that Leakey's definition had mixed two different things, neither a new species: some older material properly assigned to *A. africanus,* and some younger fossils belonging to *H. erectus.*

2. The dating was insecure. Even if *H. habilis* represented a valid species, it might be younger than most or all of the known australopithecines. Orthodoxy could become a four-runged ladder: *A. africanus-H. habilis-H. erectus-H. sapiens.*

But, as a new consensus began to coalesce about the expanded ladder, Louis and Mary Leakey's son Richard reported the find of the decade in 1973 . He had unearthed a nearly complete skull with a cranial capacity near 800 cc, almost twice that of any *A. africanus* specimen. Moreover, and this is the crucial point, he dated the skull at between 2 and 3 million years, with a preference for something near the older figure—that is, older than most australopithecine fossils, and not far from the oldest, 5.5-million-year date. *H. habilis* was no longer a chimera of Louis's imagination. (Richard Leakey's specimen is often cautiously designated only by its field number, ER-1470. But whether or not we choose to use the name *Homo habilis,* it is surely a member of our genus, and it is just as surely a contemporary of *Australopithecus.)*

Mary Leakey has now extended the range of *H. habilis* back another million years (perhaps closer to 2 million years, if 1470 is closer to 2 than to 3 million years old, as many experts now believe). *H. habilis* is not the direct descendant of known *A. africanus;* the new finds are, in fact, older than almost all specimens of *A. africanus* (and the taxonomic status of all fragmentary specimens older than Mary Leakey's *H. habilis* is in doubt). Based on the fossils as we know them, *Homo* is as old as *Australopithecus.* (One can still argue that *Homo* evolved from an older, as yet undiscovered *Australopithecus.* But no evidence supports such a claim, and I could speculate with equal justice that *Australopithecus* evolved from an unknown *Homo.)*

Chicago anthropologist Charles Oxnard has dealt *Australopithecus* another blow from a different source. He studied the shoulder, pelvis, and foot of australopithecines, modern primates (great apes and some monkeys), and *Homo* with the rigorous techniques of multivariate analysis (the simultaneous statistical consideration of large numbers of measures). He concludes—though many anthropologists disagree—that the australopithecines were "uniquely different" from either apes or humans, and argues for "the removal of the different members of this relatively small-brained, curiously unique genus *Australopithecus* into one or more parallel side lines away from a direct link with man."

What has become of our ladder if we must recognize three coexisting lineages of hominids *(A. africanus,* the robust australopithecines, and *H. habilis),* none clearly derived from another? Moreover, none of the three display any evolutionary trends during their tenure on earth: none become brainier or more erect as they approach the present day.

At this point, I confess, I cringe, knowing full well what all the creationists who deluge me with letters must be thinking. "So Gould admits that we can trace no evolutionary ladder among early African hominids; species appear and later disappear, looking no different from their great-grandfathers. Sounds like special creation to me." (Although one might ask why the Lord saw fit to make so many kinds of hominids, and why some of his later productions, *H. erectus* in particular, look so much more human than the earlier models.) I suggest that the fault is not with evolution itself, but with a false picture of its operation that most of us hold—namely the ladder; which brings me to the subject of bushes.

I want to argue that the "sudden" appearance of species in the fossil record and our failure to note subsequent evolutionary change within them is the proper prediction of evolutionary theory as we understand it. Evolution usually proceeds by "speciation"—the splitting of one lineage from a parental stock—not by the slow and steady transformation of these large parental stocks. Repeated episodes of speciation produce a bush. Evolutionary "sequences" are not rungs on a ladder, but our retrospective reconstruction of a circuitous path running like a labyrinth, branch to branch, from the base of the bush to a lineage now surviving at its top.

How does speciation occur? This is a perennial hot topic in evolutionary theory, but most biologists would subscribe to the "allopatric theory" (the debate centers on the admissibility of other modes; nearly everyone agrees that allopatric speciation is the most common mode). *Allopatric* means "in another place." In the allopatric theory, popularized by Ernst Mayr, new species arise in *very small* populations that become isolated from their parental group at the *periphery* of the ancestral range. Speciation in these small isolates is *very rapid* by evolutionary standards—hundreds or thousands of years (a geological microsecond).

Major evolutionary change may occur in these small, isolated populations. Favorable genetic variation can quickly spread through them. Moreover, natural selection tends to be intense in geographically marginal areas where the species barely maintains a foothold. In large central populations, on the other hand, favorable variations spread very slowly, and most change is steadfastly resisted by the well-adapted population. Small changes occur to meet the requirements of slowly altering climates, but major genetic reorganizations almost always take place in the small, peripherally isolated populations that form new species.

If evolution almost always occurs by rapid speciation in small, peripheral isolates—rather than by slow change in large, central populations—then what should the fossil record look like? We are not likely to detect the event of speciation itself. It happens too fast, in too small a group, isolated too far from the ancestral range. We will first meet the new species as a fossil when it reinvades the ancestral range and becomes a large central population in its own right. During its recorded history in the fossil record, we should expect no major change; for we know it only as a successful, central population. It will participate in the process of organic change only when some of its peripheral isolates speciate to become new branches on the evolutionary bush. But it, itself, will appear "suddenly" in the fossil record and become extinct later with equal speed and little perceptible change in form.

The fossil hominids of Africa fully meet these expectations. We know about three coexisting branches of the human bush. I will be surprised if twice as many more are not discovered before the end of the century. The branches do not change during their recorded history, and if we understand evolution aright, they should not—for evolution is concentrated in rapid events of speciation, the production of new branches.

Homo sapiens is not the foreordained product of a ladder that was reaching toward our exalted estate from the start. We are merely the surviving branch of a once luxuriant bush.

The Misnamed, Mistreated, and Misunderstood Irish Elk

Nature herself seems by the vast magnitude and stately horns, she has given this creature, to have singled it out as it were, and showed it such regard, with a design to distinguish it remarkably from the common herd of all other smaller quadrupeds.

THOMAS MOLYNEUX, *1697*

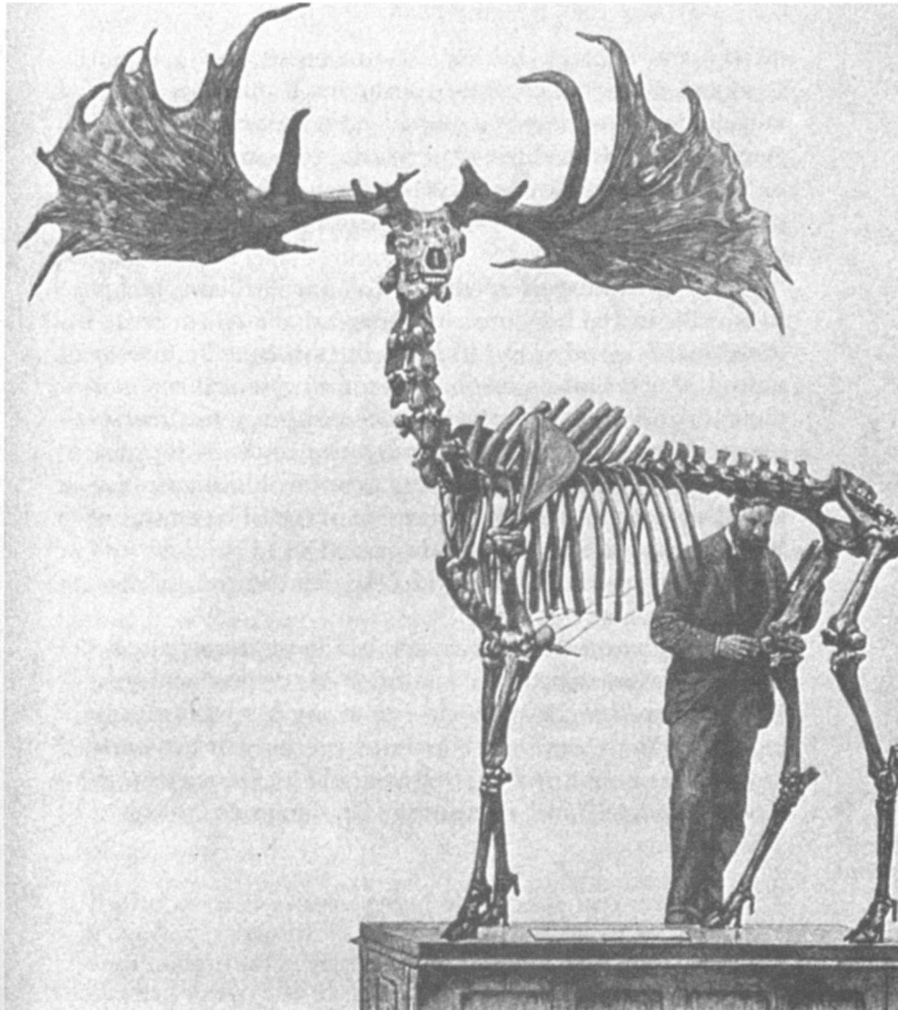
THE IRISH ELK, the Holy Roman Empire, and the English horn form a strange ensemble indeed. But they share the common distinction of their completely inappropriate names. The Holy Roman Empire, Voltaire tells us, was neither holy, nor Roman, nor an empire. The English horn is a continental oboe; the original versions were curved, hence "angular" (corrupted to English) horn. The Irish Elk was neither exclusively Irish, nor an elk. It was the largest deer that ever lived. Its enormous antlers were even more impressive. Dr. Molyneux marveled at "these spacious horns" in the first published description of 1697. In 1842, Rathke described them in a language unexcelled for the expression of enormity as *bewunderungswuerdig.* Although the Guiness book of world records ignores fossils and honors the American moose, the antlers of the Irish Elk have never been exceeded, or even approached, in the history of life. Reliable estimates of their total span range up to 12 feet. This figure seems all the more impressive when we recognize that the antlers were probably shed and regrown annually, as in all other true deer.

Fossil antlers of the giant deer have long been known in Ireland, where they occur in lake sediments underneath peat deposits. Before attracting the attention of scientists, they had been used as gateposts, and even as a temporary bridge to span a rivulet in County Tyrone. One story, probably apocryphal, tells of a huge bonfire made of their bones and antlers in County Antrim to celebrate the victory over Napoleon at Waterloo. They were called elk because the European moose (an "elk" to Englishmen) was the only familiar animal with antlers that even approached those of the giant deer in size.

The first known drawing of giant deer antlers dates from 1588. Nearly a century later, Charles II received a pair of antlers and (according to Dr. Molyneux) "valued them so highly for their prodigious largeness" that he set them up in the horn gallery of Hampton Court, where they "so vastly exceed" all others in size "that the rest appear to lose much of their curiosity."

Ireland's exclusive claim vanished in 1746 (although the name stuck) when a skull and antlers were unearthed in Yorkshire, England. The first continental discovery followed in

A drawing of the giant deer in Thomas Molyneux's 1697 article shows the antlers incorrectly rotated forward ninety degrees.



A worthy predecessor of the author measures the other end of an Irish Elk. Figure originally published by J. G. Millais in 1897.

1781 from Germany, while the first complete skeleton (still standing in the museum of Edinburgh University) was exhumed from the Isle of Man in the 1820s.

We now know that the giant deer ranged as far east as Siberia and China and as far south as northern Africa. Specimens from England and Eurasia are almost always fragmentary, and nearly all the fine specimens that adorn so many museums throughout the world come from Ireland. The giant deer evolved during the glacial period of the last few million years and may have survived to historic times in continental Europe, but it became extinct in Ireland about 11,000 years ago.

"Among the fossils of the British empire," wrote James Parkinson in 1811, "none are more calculated to excite astonishment." And so it has been throughout the history of paleontology. Putting aside both the curious anecdotes and the sheer wonder that immensity always inspires, the importance of the giant deer lies in its contribution to debates about evolutionary theory. Every great evolutionist has used the giant deer to defend his favored views. The controversy has centered around two main issues: (1) Could antlers of such bulk be of any use? and (2) Why did the giant deer become extinct?

Since debate on the Irish Elk has long centered on the reasons for its extinction, it is ironic that the primary purpose of Molyneux's original article was to argue that it must still be alive. Many seventeenth-century scientists maintained that the extinction of any species would be inconsistent with God's goodness and perfection. Dr. Molyneux's article of 1697 begins:

> That no real species of living creatures is so utterly extinct, as to be lost entirely out of the World, since it was first created, is the opinion of many naturalists; and 'tis grounded on so good a principle of Providence taking care in general of all its animal productions, that it deserves our assent.

Yet the giant deer no longer inhabited Ireland, and Molyneux was forced to search elsewhere. After reading traveler's reports of antler size in the American moose, he concluded that the Irish Elk must be the same animal; the tendency toward exaggeration in such accounts is apparently universal and timeless. Since he could find neither figure nor an accurate description of the moose, his conclusions are not as absurd as modern knowledge would indicate. Molyneux attributed the giant deer's demise in Ireland to an "epidemick distemper," caused by "a certain ill constitution of air."

For the next century arguments raged along Molyneux's line—to which modern species did the giant deer belong? Opinion was equally divided between the moose and the reindeer.

As eighteenth-century geologists unraveled the fossil record of ancient life, it became more and more difficult to argue that the odd and unknown creatures revealed by fossils were all still living in some remote portion of the globe. Perhaps God had not created just once and for all time; perhaps He had experimented continually in both creation and destruction. If so,, the world was surely older than the six thousand years that literalists allowed.

The question of extinction was the first great battleground of modern paleontology. In America, Thomas Jefferson maintained the old view, while Georges Cuvier, the great French paleontologist, was using the Irish Elk to prove that extinction did occur. By 1812 Cuvier had resolved two pressing issues: by minute anatomical description, he proved that the Irish Elk was not like any modern animal; and by placing it among many fossil mammals with no modern counterparts, he established the fact of extinction and set the basis for a geologic time scale.

Once the fact of extinction had been settled, debate moved to the time of the event: in particular, had the Irish elk survived the flood? This was no idle matter, for if the flood or some previous catastrophe had wiped out the giant deer, then its demise had natural (or supernatural) causes. Archdeacon Maunsell, a dedicated amateur, wrote in 1825: "1 apprehended they must have been destroyed by some overwhelming deluge." A certain Dr. MacCulloch even believed that the fossils were found standing erect, noses elevated—a final gesture to the rising flood, as well as a final plea: don't make waves.

If, however, they had survived the flood, then their exterminating angel could only have been the naked ape himself. Gideon Mantell, writing in 1851, blamed Celtic tribes; in

1830, Hibbert implicated the Romans and the extravagant slaughters of their public games. Lest we assume that our destructive potential was recognized only recently, Hibbert wrote in 1830: "Sir Thomas Molyneux conceived that a sort of distemper, or pestilential murrain, might have cut off the Irish Elks. . . . It is, however, questionable, if the human race has not occasionally proved as formidable as a pestilence in exterminating from various districts, whole races of wild animals."

In 1846, Britain's greatest paleontologist, Sir Richard Owen, reviewed the evidence and concluded that in Ireland at least, the giant deer had perished before man's arrival. By this time, Noah's flood as a serious geologic proposition had passed from the scene. What then had wiped out the giant deer?

Charles Darwin published the *Origin of Species* in 1859. Within ten years virtually all scientists had accepted the *fact* of evolution. But the debate about causes and mechanisms was not resolved (in Darwin's favor) until the 1940s. Darwin's theory of natural selection requires that evolutionary changes be adaptive—that is, that they be useful to the organism. Therefore, anti-Darwinians searched the fossil record for cases of evolution that could not have benefited the animals involved.

The theory of orthogenesis became a touchstone for anti-Darwinian paleontologists, for it claimed that evolution proceeded in straght lines that natural selection could not regulate. Certain trends, once started, could not be stopped even if they led to extinction. Thus certain oysters, it was said, coiled their valves upon each other until they sealed the animal permanently within; saber-toothed "tigers" could not stop growing their teeth or mammoths their tusks.

But by far the most famous example of orthogenesis was the Irish Elk itself. The giant deer had evolved from small forms with even smaller antlers. Although the antlers were useful at first, their growth could not be contained and, like the sorceror's apprentice, the giant deer discovered only too late that even good things have their limits. Bowed by the weight of their cranial excrescences, caught in the trees or mired in the ponds, they died. What wiped out the Irish Elk? They themselves or, rather, their own antlers did.

In 1925, the American paleontologist R. S. Lull invoked the giant deer to attack Darwinism: "Natural selection will not account for overspecialization, for it is manifest that, while an organ can be brought to the point of perfection by selection, it would never be carried to a condition where it is an actual menace to survival... [as in] the great branching antlers of the extinct Irish deer."

Darwinians, led byjulian Huxley, launched a counterattack in the 1930s. Huxley noted that as deer get larger—either during their own growth or in the comparison of related adults of different sizes—the antlers do not increase in the same proportion as body size; they increase faster, so that the antlers of large deer are not only absolutely larger but also relatively larger than those of small deer. For such regular and orderly change of shape with increasing size, Huxley used the term allometry.

Allometry provided a comfortable explanation for the giant deer's antlers. Since the Irish Elk had the largest body size of any deer, its relatively enormous antlers could have been a simple result of the allometric relationship present among all deer. We need only assume that increased body size was favored by natural selection; the large antlers might have been an automatic consequence. They might even have been slightly harmful in themselves, but this disadvantage was more than compensated by the benefits of larger size, and the trend continued. Of course, when problems of larger antlers outweighted the advantages of larger bodies, the trend would cease since it could no longer be favored by natural selection.

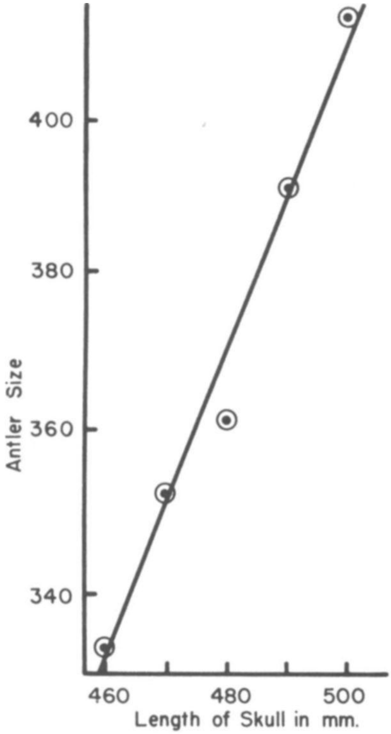
Almost every modern textbook of evolution presents the Irish Ellk in this light, citing the allometric explanation to counter orthogenetic theories. As a trusting student, I had assumed that such constant repetition must be firmly based on copious data. Later I discovered that textbook dogma is self-perpetuating; therefore, three years ago I was disappointed, but not really surprised, to discover that this widely touted explanation was based on no data whatsoever. Aside from a few desultory attempts to find the largest set of antlers, no one had ever measured an Irish Elk. Yardstick in hand, I resolved to rectify this situation.

The National Museum of Ireland in Dublin has seventeen specimens on display and many more, piled antler upon antler, in a nearby warehouse. Most large museums in western Europe and America own an Irish Elk, and the giant deer adorns many trophy rooms of English and Irish gentry. The largest antlers grace the entranceway to Adare Manor, home of the Earl of Dunraven. The sorriest skeleton sits in the cellar of Bunratty Castle, where many merry and slightly inebriated tourists repair for coffee each evening after a medieval banquet. This poor fellow, when I met him early the morning after, was smoking a cigar, missing two teeth, and carrying three coffee cups on the tines of his antlers. For those who enjoy invidious comparisons, the largest antlers in America are at Yale; the smallest in the world at Harvard.

To determine if the giant deer's antlers increased allometrically, I compared antler and body size. For antler size, I used a compounded measure of antler length, antler width, and the lengths of major tines. Body length, or the length and width of major bones, might be the most appropriate measure of body size, but I could not use it because the vast majority of specimens consist only of a skull and its attached antlers. Moreover, the few complete skeletons are invariably made up of several animals, much plaster, and an occasional ersatz (the first skeleton in Edinburgh once sported a horse's pelvis). Skull length therefore served as my measure of overall size. The skull reaches its final length at a very early age (all my specimens are older) and does not vary thereafter; it is, therefore, a good indicator of body size. My sample included seventy-nine skulls and antlers from museums and homes in Ireland, Britain, continental Europe, and the United States.

My measurements showed a strong positive correlation between antler size and body size, with the antlers increasing in size two and one-half times faster than body size from small to large males. This is not a plot of individual growth; it is a relationship among adults of different body size. Thus, the allometric hypothesis is affirmed. If natural selection favored large deer, then relatively larger antlers would appear as a correlated result of no necessary significance in itself.

Yet, even as I affirmed the allometric relationship, I began to doubt the traditional explanation—for it contained a curious remnant of the older, orthogenetic view. It assumed that



Graph showing relative increase in antler size with increasing skull length in Irish Elks. Each point is the average for all skulls in a 10 mm. interval of length; the actual data include 81 individuals. Antler size increases more than 2'A times as fast as skull length—a line with a slope of 1.0 (45 degree angle with the x-axis) would indicate equal rates of increase on these logarithmic scales. The slope here is obviously very much higher.

the antlers are not adaptive in themselves and were tolerated only because the advantages of increased body size were so great. But why must we assume that the immense antlers had no primary function? The opposite interpretation is equally possible: that selection operated primarily to increase antler size, thus yielding increased body size as a secondary consequence. The case for inadaptive antlers has never rested on more than subjective wonderment born of their immensity.

Views long abandoned often continue to exert their influence in subtle ways. The orthogenetic argument lived on in the allometric context proposed to replace it. I believe that the supposed problem of "unwieldy" or "cumbersome" antlers is an illusion rooted in a notion now abandoned by students of animal behavior.

To nineteenth-century Darwinians, the natural world was a cruel place. Evolutionary success was measured in terms of battles won and enemies destroyed. In this context, antlers were viewed as formidable weapons to be used against predators and rival males. In his *Descent of Man* (1871), Darwin toyed with another idea: that antlers might have evolved as ornaments to attract females. "If, then, the horns, like the splendid accouterments of the knights of old, add to the noble appearance of stags and antelopes, they may have been modified partly for this purpose." Yet he quickly added that he had "no evidence in favor of this belief," and went on to interpret antlers according to the "law of battle" and their advantages in "reiterated deadly contests." All early writers assumed that the Irish Elk used its antlers to kill wolves and drive off rival males in fierce battle. To my knowledge this view has been challenged only by the Russian paleontologist L. S. Davitashvili, who asserted in 1961 that the antlers functioned primarily as courtship signals to females.

Now, if antlers are weapons, the orthogenetic argument is appealing, for I must admit that ninety pounds of broad-palmed antler, regrown annually and spanning twelve feet from tip to tip, seems even more inflated than our current military budget. Therefore, to preserve a Darwinian explanation, we must invoke the allometric hypothesis in its original form.

But what if antlers do not function primarily as weapons? Modern studies of animal behavior have generated an exciting concept of great importance to evolutionary biology: many structures previously judged as actual weapons or devices for display to females are actually used for ritualized combat among males. Their function is to prevent actual battle (with consequent injuries and loss of life) by establishing hierarchies of dominance that males can easily recognize and obey.

Antlers and horns are a primary example of structures used for ritualized behavior. They serve, according to Valerius Geist, as "visual dominance-rank symbols." Large antlers confer high status and access to females. Since there can be no evolutionary advantage more potent than a guarantee of successful reproduction, selective pressures for larger antlers must often be intense. As more and more horned animals are observed in their natural environment, older ideas of deadly battle are yielding to evidence of purely ritualized display without body contact, or fighting in ways clearly designed to prevent bodily injury. This has been observed in red deer by Beninde and Darling, caribou by Kelsall, and in mountain sheep by Geist.

As devices for display among males, the enormous antlers of the Irish Elk finally make sense as structures adaptive in themselves. Moreover, as R. Coope of Birmingham University pointed out to me, the detailed morphology of the antlers can be explained, for the first time, in this context. Deer with broad-palmed antlers tend to show the full width of their antlers in display. The modern fallow deer (considered by many as the Irish Elk's nearest living relative) must rotate its head from side to side in order to show its palm. This would have created great problems for giant deer, since the torque produced by swinging ninety-pound antlers would have been immense. But the antlers of the Irish Elk were arranged to display the palm fully when the animal looked straight ahead. Both the unusual configuration and the enormous size of the antlers can be explained by postulating that they were used for display rather than for combat.

If the antlers were adaptive, why did the Irish Elk become extinct (at least in Ireland)? The probable answer to this old dilemma is, I am afraid, rather commonplace. The giant deer flourished in Ireland for only the briefest of times—during the so-called Allerod interstadial phase at the end of the last glaciation. This period, a minor warm phase between two colder epochs, lasted for about 1,000 years, from 12,000 to 11,000 years before the present. (The Irish Elk had migrated to Ireland during the previous glacial phase when lower sea levels established a connection between Ireland and continental Europe.) Although it was well adapted to the grassy, sparsely wooded, open country of Allerod times, it apparently could not adapt either to the subarctic tundra that followed in the next cold epoch or to the heavy forestation that developed after the final retreat of the ice sheet.

Extinction is the fate of most species, usually because they fail to adapt rapidly enough to changing conditions of climate or competition. Darwinian evolution decrees that no animal shall actively develop a harmful structure, but it offers no guarantee that useful structures will continue to be adaptive in changed circumstances. The Irish Elk was probably a victim of its own previous success. *Sic transit gloria mundi.*

Organic Wisdom, or Why Should a Fly Eat Its Mother from Inside

SINCE MAN CREATED God in his own image, the doctrine of special creation has never failed to explain those adaptations that we understand intuitively. How can we doubt that animals are exquisitely designed for their appointed roles when we watch a lioness hunt, a horse run, or a hippo wallow? The theory of natural selection would never have replaced the doctrine of divine creation if evident, admirable design pervaded all organisms. Charles Darwin understood this, and he focused on features that would be out of place in a world constructed by perfect wisdom. Why, for example, should a sensible designer create only on Australia a suite of marsupials to fill the same roles that placental mammals occupy on all other continents? Darwin even wrote an entire book on orchids to argue that the structures evolved to insure fertilization by insects are jerry-built of available parts used by ancestors for other purposes. Orchids are Rube Goldberg machines; a perfect engineer would certainly have come up with something better.

This principle remains true today. The best illustrations of adaptation by evolution are the ones that strike our intuition as peculiar or bizarre. Science is not "organized common sense"; at its most exciting, it reformulates our view of the world by imposing powerful theories against the ancient, anthropocentric prejudices that we call intuition.

Consider, for example, the cecidomyian gall midges. These tiny flies conduct their lives in a way that tends to evoke feelings of pain or disgust when we empathize with them by applying the inappropriate standards of our own social codes.

Cecidomyian gall midges can grow and develop along one of two pathways. In some situations, they hatch from eggs, go through a normal sequence of larval and pupal molts, and emerge as ordinary, sexually reproducing flies. But in other circumstances, females reproduce by parthenogenesis, bringing forth their young without any fertilization by males. Parthenogenesis is common enough among animals, but the cecidomyians give it an interesting twist. First of all, the parthenogenetic females stop at an early stage of development. They never become normal, adult flies, but reproduce while they are still larvae or pupae. Secondly, these females do not lay eggs. The offspring develop live within their mother's body—not supplied with nutrient and packaged away in a protected uterus but right within the mother's tissues, eventually filling her entire body. In order to grow, the offspring devour their mother from the inside. A few days later, they emerge, leaving a chitinous shell as the only remains of their only parent. And within two days, their own developing children are beginning, literally, to eat them up.

Micromalthus debilis, an unrelated beetle, has evolved an almost identical system with a macabre variation. Some parthenogenetic females give birth to a single male offspring. This larva attaches to his mother's cuticle for about four or five days, then inserts his head into her genital aperture and devours her. Greater love hath no woman.

Why has such a peculiar mode of reproduction evolved? For it is unusual even among insects, and not only by the irrelevant standards of our own perceptions. What is the adaptive significance of a mode of life that so strongly violates our intuitions about good design?

To answer these questions, we proceed by the usual mode of argument in evolutionary studies: the comparative method. (Louis Agassiz did not act capriciously when he gave to the building in which I work the name that has puzzled so many generations of visitors to Harvard—the Museum of Comparative Zoology.) We must find an object for comparison that is genetically similar, but adapted to a different mode of life. Fortunately, the complex life cycle of cecidomyians provides us with a key. We do not have to compare the asexual, larval mother with a related species of uncertain affinity and genetic resemblance; we may contrast it with the genetically identical, alternate form of the same species—the normal, sexual fly. What then is different about the ecology of parthenogenetic and normal forms?

The cecidomyians feed and dwell on fungi, usually mushrooms. The mobile, normal fly fills the role of discoverer: it finds the new mushroom. Its offspring, now living on a superabundant food resource, reproduce asexually as larvae or pupae and become the flightless, feeding form of the species (a mushroom can support hundreds of these tiny flies). We know that parthenogenetic reproduction will continue as long as food is abundant. One investigator produced 250 consecutive larval generations by supplying enough food and preventing crowding. In nature, however, the mushroom is eventually used up.

H. Ulrich and his coworkers have studied the sequence of changes in response to decreasing food in the species *Mycophila speyeri.* Wheh they have abundant food, parthenogenetic mothers generate all female broods in four to five days. As the supply of food diminishes, all male and mixed male and female broods develop. If female larvae are not fed at all, they grow into normal flies.

These correlations have a fairly unambiguous adaptive basis. The flightless, parthenogenetic female stays on the mushroom and feeds. When it exhausts its resource, it produces winged descendants to find new mushrooms. But this only scratches the surface of our dilemma, for it does not address our central question: Why reproduce so quickly as a larva or pupa, and why self-destruct by a supreme sacrifice to one's children?

I believe that the solution to this dilemma lies in the phrase "so quickly." Traditional evolutionary theory concentrated on morphology in framing adaptive explanations. What, in this case, is the advantage to mushroom feeders of a persistent juvenile morphology in reproducing females? Traditional theory never found an answer because it had posed the wrong question. During the last fifteen years, the rise of theoretical population ecology has transformed the study of adaptation. Evolutionists have learned that organisms adapt not only by altering their size and shape but also by adjusting the timing of their lives and the energy invested in different activities (feeding, growth, and reproduction, for example). These adjustments are called "life history strategies."

Organisms evolve different life history strategies to fit differnt types of environments. Among theories that correlate strategy with environment, the theory of *r*- and *K*- selection, developed by R. H. MacArthur and E. O. Wilson in the mid-1960s, has surely been the most successful.

Evolution, as usually depicted in textbooks and reported in the popular press, is a process of inexorable improvement in form: animals are delicately "fine tuned" to their environment through constant selection of better-adapted shapes. But several kinds of environments do not call forth such an evolutionary response. Suppose that a species lives in an environment that imposes irregular, catastrophic mortality upon it (ponds that dry up, for example, or shallow seas ripped up by severe storms). Or suppose that food sources are ephemeral and hard to find, but superabundant once located. Organisms cannot fine tune themselves to such environments for there is nothing sufficiently stable to adjust to. Better in such a situation to invest as much energy as possible into reproduction—make as many offspring as you can, as quickly as possible, so that some will survive the catastrophe. Reproduce like hell while you have the ephemeral resource, for it will not last long and some of your progeny must survive to find the next one.

We refer to evolutionary pressures for the maximization of reproductive effort at the expense of delicate morphological adjustment as **r**-selection; organisms so adapted are **r**-strategists (**r** is the traditional measure of "intrinsic rate of increase in population size" in a set of basic, ecological equations). Species that live in stable environments, near the maximum population size that the environment can support, will gain nothing by producing hordes of poorly adjusted progeny.

Better to raise a few, finely tuned offspring. Such species are A'-strategists *(K* is the measure of environmental "carrying capacity" in the same set of equations).

The parthenogenetic larval gall midges live in a classical r-environment. Mushrooms are few and far between, but superabundant when found by such a tiny fly. Cecidomyian gall midges therefore gain a selective advantage if they use newly discovered mushrooms for building up their population as rapidly as possible. What, then, is the most efficient way to build a population quickly? Should the midges simply lay more eggs or should they reproduce as early as possible during their lives? This general issue has inspired a large literature among mathematically inclined ecologists. In most situations, the key to rapid increase is *early* reproduction. A 10 percent decrease in age at first reproduction can often yield the same effect as a 100 percent increase in fecundity.

Finally, we can understand the peculiar reproductive biology of cecidomyian gall midges: they have simply evolved some remarkable adaptations for early reproduction and extremely short generation times. In so doing, they have become consummate **r**-strategists in their classical **r**-environment of ephemeral, superabundant resources. Thus, they reproduce while still larvae, and almost immediately after hatching, they begin to grow the next generation within themselves. In *Mycophila speyen,* for example, the parthenogenetic **r**-strategist undergoes only one molt, reproduces as a true larva, and manufactures up to 38 offspring in five days. The normal, sexual adults require two weeks to develop. The larval reproducers maintain a phenomenal capacity for increase in population size. Within five weeks after its introduction into a commercial mushroom bed, *Mycophila speyeri* can reach a density of 20,000 reproductive larvae per square foot.

We may again pursue the comparative method to convince ourselves that this explanation makes sense. The cecidomyian pattern has been followed by other insects that inhabit a similar set of environments. Aphids, for example, feed on the sap of leaves. A leaf, to these tiny insects, is much like a mushroom to a gall midge—a large, ephemeral resource to be converted quickly into as many aphids as possible. Most aphids have alternate parthenogenetic forms—wingless and winged (they also have an overwintering, sexual form, which need not concern us here). As you have probably already guessed, the wingless form is a flightless feeder. Although it is not a larva, it retains many features of juvenile morphology. It also maintains a remarkable capacity for early reproduction. Embryonic development actually begins in a mother's body before her own birth, and two subsequent generations may be telescoped within each "grandmother." (Aphids, however, are not consumed by their offspring.) Their capacity for rapid increase in population size is legendary. If all its offspring lived to reproduce, a single female of *Aphis fabae* could produce 524 billion progeny in a year. Winged aphids develop more slowly when the leaf is used up. They fly off to a new leaf, where their offspring revert to the wingless form and begin their rapid cycling of generations.

What at first seemed so peculiar now seems eminently reasonable. It may even be an optimal strategy for certain environments. This much we cannot claim, for so many aspects of cecidomyian biology are entirely unknown. But we can point to the uncanny convergence upon the same strategy by a completely unrelated organism, the beetle *Micromalthus debilis.* This beetle lives and feeds in wet, rotting wood. When the wood dries out, the beetle develops a sexual form to search for new resources. The wood-dwelling, feeding form has evolved a set of adaptations that repeats the features of cecidomyians down to the most complex and peculiar detail. It also is parthenogenetic. It also reproduces at a morphologically juvenile stage. The young also develop within the mother's body and eventually devour her. Mothers also produce three types of broods: females only when food is abundant and males only or males and females when resources diminish.

We humans with our slow development (see essay 7), extended gestation, and minimal litter size are consummate *K*-strategists and we may look askance at the strategies of other organisms, but in their r-selective world the cecidomyians are surely doing something right.

Of Bamboos, Cicadas, and the Economy of Adam Smith

NATURE USUALLY manages to outdo even the most fanciful of human legends. Sleeping Beauty waited a hundred years for her prince. Bettelheim argues that her pricked finger represents the first bleeding of menstruation, her long sleep the lethargy of adolescence awaiting the onset of full maturity. Since the original Sleeping Beauty was inseminated by a king, rather than merely kissed by a prince, we may interpret her awakening as the beginning of sexual fulfillment (see B. Bettelheim, *The Uses of Enchantment,* A. Knopf, 1976, pp. 225-36).

A bamboo bearing the formidable name *Phyllostachys bambusoides* flowered in China during the year 999. Since then, with unerring regularity, it has continued to flower and set seed roughly every 120 years. *P. bambusoides* follows this cycle wherever it lives. In the late 1960s, Japanese stocks (themselves transplanted from China centuries before) set seed simultaneously in Japan, England, Alabama, and Russia. The analogy to Sleeping Beauty is not farfetched, for sexual reproduction follows more than a century of celibacy in these bamboos. But *P. bambusoides* departs from the Brothers Grimm in two important ways. The plants are not inactive during their 120 year vigil—for they are grasses, and they propagate asexually by producing new shoots from underground rhizomes. Also, they do not live happily ever after, for they die after setting seed—a long wait for a short end.

Ecologist Daniel H. Janzen of the University of Pennsylvania recounts the curious tale of *Phyllostachys* in a recent article, "Why bamboos wait so long to flower" *(Annual Review of Ecology and Systematics,* 1976). Most species of bamboo have shorter periods of vegetative growth between flowerings, but synchroneity of seeding is the rule, and very few species wait fewer than 15 years before flowering (some may wait for more than 150 years, but historical records are too sparse to permit firm conclusions).

The flowering of any species must be set by an internal, genetic clock, not imposed from without by some environmental clue. The unerring regularity of repetition supplies our best evidence for this assertion, for we do not know any environmental factor that cycles so predictably to yield the variety of clocks followed by more than a hundred species. Secondly, as mentioned above, plants of the same species flower simultaneously, even when transplanted half a world away from their native habitat. Finally, plants of the same species flower together, even if they have grown in very different environments. Janzen recounts the tale of a Burmese bamboo only half a foot high that had been burned down repeatedly by jungle fires, but flowered at the same time as its unhurt companions standing 40 feet tall.

How can a bamboo count the passing years? Janzen argues that it cannot be measuring stored food reserves because starved dwarfs flower at the same time as healthy giants. He speculates that the calendar "must be the annual or daily accumulation or degradation of a temperature-insensitive photosensitive chemical." He finds no basis for guessing whether the cycles of light are diurnal (day-night) or yearly (seasonal). As circumstantial evidence for implicating light as a clock, Janzen points out that no accurately cycling bamboo grows within 5 degrees of latitude from the equator—for variations in both days and seasons are minimized within this zone.

The flowering of bamboo recalls a tale of striking periodicity better known to most of us—the periodical cicada, or 17-year "locust." (Cicadas are not locusts at all, but large-bodied members of the order Homoptera, a group of predominantly small insects including aphids and their relatives; locusts, along with crickets and grasshoppers, form the order Orthoptera.) The story of periodical cicadas is even more amazing than most people realize: for 17 years, the nymphs of periodical cicadas live underground, sucking juices from the roots of forest trees all over the eastern half of the United States (except for our southern states, where a very similar or identical group of species emerges every 13 years). Then, within just a few weeks, millions of mature nymphs emerge from the ground, become adults, mate, lay their eggs, and die. (The best accounts, from an evolutionary standpoint, will be found in a series of articles by M. Lloyd and H. S. Dybas, published in the journals *Evolution* in 1966 and *Ecohgical Monographs* in 1974). Most remarkable is the fact that not one, but three separate species of periodical cicadas follow precisely the same schedule, emerging together in strict synchrony. Different areas may be out of phase—populations around Chicago do not emerge in the same year as forms from New England. But the 17-year cycle (13 years in the south) is invariant for each "brood"—the three species always emerge together in the same place. Janzen recognizes that cicadas and bamboo, despite their biological and geographic distance, represent the same evolutionary problem. Recent studies, he writes, "reveal no conspicuous qualitative difference between these insects and bamboo except perhaps in the way they count years."

As evolutionists, we seek answers to the question "why." Why, in particular, should such striking synchroneity evolve, and why should the period between episodes of sexual reproduction be so long? As I argued in discussing the matricidal habits of certain flies (essay 10) the theory of natural selection receives its strongest support when we devise satisfactory explanations for phenomena that strike us intuitively as bizarre or senseless.

In this case, we are confronted with a problem beyond the apparent peculiarity of such wastefulness (for very few seeds can sprout upon such saturated ground). The synchroneity of flowering or emergence seems to reflect an ordering and harmony operating upon the species as a whole, not upon its individual members. Yet Darwinian theory advocates no higher principle beyond individuals pursuing their own self-interest—i.e. the representation of their own genes in future generations. We must ask what advantage the synchroneity of sex provides for an individual cicada or bamboo plant.

The problem is similar to that faced by Adam Smith when he advocated an unbridled policy of laissez faire as the surest path to a harmonious economy. The ideal economy, Smith argued, might appear orderly and well balanced, but it would emerge "naturally" from the interplay of individuals who follow no path beyond the pursuit of their own best interests. The apparent direction towards a higher harmony, Smith argues in his famous metaphor, only reflects the operation of an "invisible hand."

> As every individual... by directing (his) industry in such a manner as its produce may be of greatest value, intends only his own gain, he is in this as in many other cases led by an invisible hand to promote an end which was no part of his intention. ... By pursuing his own interest he frequently promotes that of society more effectively than when he really intends to promote it.

Since Darwin grafted Adam Smith upon nature to establish his theory of natural selection, we must seek an explanation for apparent harmony in the advantage that it confers upon individuals. What, then, does an individual cicada or bamboo gain by indulging in sex so rarely and at the same time as all its compatriots?

In order to appreciate the most likely explanation, we must recognize that human biology often provides a poor model for the struggles of other organisms. Humans are slowly growing animals. We invest a great deal of energy in raising very few, late maturing offspring. Our populations are not controlled by the wholesale death of nearly all juvenile members. Yet many organisms follow a different strategy in the "struggle for existence": they produce vast numbers of seeds or eggs, hoping (so to speak) that a few will survive the rigors of early life. These organisms are often controlled by their predators, and their evolutionary defense must be a strategy that minimizes the chance of being eaten. Cicadas and bamboo seeds seem to be particularly tasty to a wide variety of organisms.

Natural history, to a large extent, is a tale of different adaptations to avoid predation. Some individuals hide, others taste bad, others grow spines or thick shells, still others evolve to look conspicuously like a noxious relative; the list is nearly endless, a stunning tribute to nature's variety. Bamboo seeds and cicadas follow an uncommon strategy: they are eminently and conspicuously available, but so rarely and in such great numbers that predators cannot possibly consume the entire bounty. Among evolutionary biologists, this defense goes by the name of "predator satiation."

An effective strategy of predator satiation involves two adaptations. First, the synchrony of emergence or reproduction must be very precise, thus assuring that the market is truly flooded, and only for a short time. Secondly, this flooding cannot occur very often, lest predators simply adjust their own life cycle to predictable times of superfluity. If bamboos flowered every year, seed eaters would track the cycle and present their own abundant young with the annual bounty. But if the period between episodes of flowering far exceeds the life-span of any predator, then the cycle cannot be tracked (except by one peculiar primate that records its own history). The advantage of synchroneity to individual bamboos and cicadas is clear enough: anyone out of step is quickly gobbled up (cicada "stragglers" do occasionally emerge in off years, but they never gain a foothold).

The hypothesis of predator satiation, though unproven, meets the primary criterion of a successful explanation: it coordinates a suite of observations that would otherwise remain unconnected and, in this case, downright peculiar. We know, for example, that bamboo seeds are relished by a wide variety of animals, including many vertebrates with long life spans; the rarity of flowering cycles shorter than 15 or 20 years makes sense in this context. We also know that the synchronous setting of seed can inundate an affected area. Janzen records a mat of seeds 6 inches deep below the parental plant in one case. Two species of Malagasy bamboos produced 50 kilograms of seed per hectare over a large area of

100,000 hectares during a mass flowering.

The synchrony of three species among cicadas is particularly impressive—especially since years of emergence vary from place to place, while all three species invariably emerge together in any one area. But I am most impressed by the timing of the cycles themselves. Why do we have 13 and 17 year cicadas, but no cycles of 12, 14, 15, 16, or 18? 13 and 17 share a common property. They are large enough to exceed the life cycle of any predator, but they are also prime numbers (divisible by no integer smaller than themselves). Many potential predators have 2-5-year life cycles. Such cycles are not set by the availability of periodical cicadas (for they peak too often in years of nonemergence), but cicadas might be eagerly harvested when the cycles coincide. Consider a predator with a cycle of five years: if cicadas emerged every 15 years, each bloom would be hit by the predator. By cycling at a large prime number, cicadas minimize the number of coincidences (every 5 X 17, or 85 years, in this case). Thirteen- and 17-year cycles cannot be tracked by any smaller number.

Existence is, as Darwin stated, a struggle for most creatures. The weapons of survival need not be claws and teeth; patterns of reproduction may serve as well. Occasional superfluity is one pathway to success. It is sometimes advantageous to put all your eggs in one basket—but be sure to make enough of them, and don't do it too often.

The Problem of Perfection, or How Can a Clam Mount a Fish on Its Rear End?

IN 1802, Archdeacon Paley set out to glorify God by illustrating the exquisite adaptation of organisms to their appointed roles. The mechanical perfection of the vertebrate eye inspired a rapturous discourse on divine benevolence; the uncanny similarity of certain insects to pieces of dung also excited his admiration, for God must protect all his creatures, great and small. Evolutionary theory eventually unraveled the archdeacon's grand design, but threads of his natural theology survive.

Modern evolutionists cite the same plays and players; only the rules have changed. We are now told, with equal wonder and admiration, that natural selection is the agent of exquisite design. As an intellectual descendant of Darwin, I do not doubt this attribution. But my confidence in the power of natural selection has other roots: it is not based upon "organs of extreme perfection and complication," as Darwin called them. In fact, Darwin saw truly exquisite design as a problem for his theory. He wrote:

> To suppose that the eye with all its inimitable contrivances for adjusting the focus to different distances, for admitting different amounts of light, and for the correction of spherical and chromatic aberration, could have been formed by natural selection, seems, I confess, absurd in the highest degree.

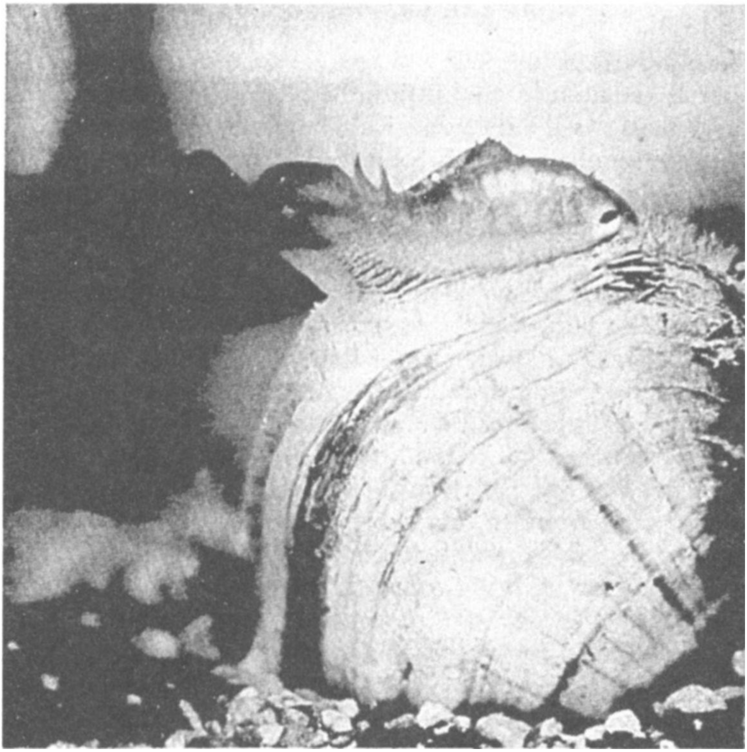
In essay 10, I invoked gall midges to illustrate the opposite problem of adaptation—structures and behaviors that seem senseless. But "organs of extreme perfection" proclaim their value unambiguously; the difficulty lies in explaining how they developed. In Darwinian theory, complex adaptations do not arise in a single step, for natural selection would then be confined to the purely destructive task of eliminating the unfit whenever a better-adapted creature suddenly appeared. Natural selection has a constructive role in Darwin's system: it builds adaptation gradually, through a sequence of intermediate stages, by bringing together in sequential fashion elements that seem to have meaning only as parts of a final product. But how can a series of reasonable intermediate forms be constructed? Of what value could the first tiny step toward an eye be to its possessor? The dung-mimicking insect is well protected, but can there be any edge in looking only **5** percent like a turd? Darwin's critics referred to this dilemma as the problem of assigning adaptive value to "incipient stages of useful structures." And Darwin rebutted by trying to find the intermediate stages and by specifying their utility.

> Reason tells me, that if numerous gradations from a simple and imperfect eye to one complex and perfect can be shown to exist, each grade being useful to its possessor . . . then the difficulty of believing that a perfect and complex eye could be formed by natural selection, though insuperable by our imagination, should not be considered as subversive of the theory.

The argument still rages, and organs of extreme perfection rank high in the arsenal of modern creationists.

Every naturalist has his favorite example of an awe-inspiring adaptation. Mine is the "fish" found in several species of the freshwater mussel *Lampsilis.* Like most clams, *Lampsilis* lives partly buried in bottom sediments, with its posterior end protruding. Riding atop the protruding end is a structure that looks for all the world like a little fish. It has a streamlined body, well-designed side flaps complete with a tail and even an eyespot. And, believe it or not, the flaps undulate with a rhythmic motion that imitates swimming.

Most clams release their eggs directly into the surrounding

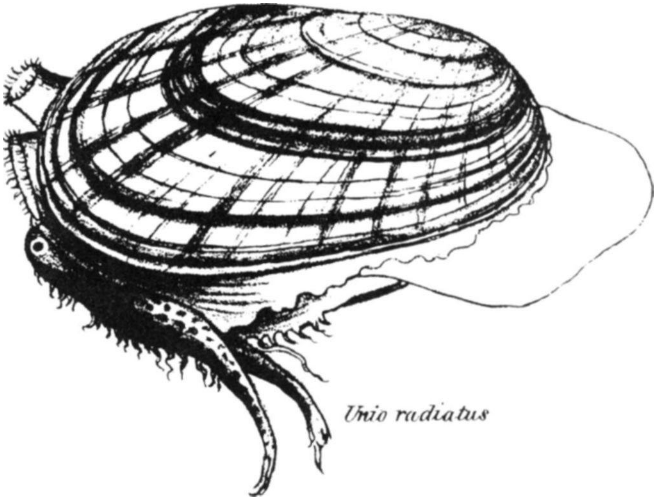


"Fish "with eyespot and tail rides atop Lampsilis ventricosa. *When a fish nears, the clam discharges larvae; some will be ingested by the fish and find their way to its gills, where they will mature.* (John H. Welsh)

water, where they are fertilized and undergo their embryonic development. But female unionids (the technical name for freshwater mussels) retain their eggs within their bodies, where they are fertilized by sperm released into the water by nearby males. The fertilized eggs develop in tubes within the gills, forming a brood pouch, or marsupium.

In *Lampsilis,* the inflated marsupium of gravid females forms the "body" of its ersatz fish. Surrounding the fish, symmetrically on both sides, are extensions of the mantle, the "skin" that encloses the soft parts of all clams and usually ends at the shell margin. These extensions are elaborately shaped and colored to resemble a fish, with a definite, often flaring "tail" at one end and an "eyespot" at the other. A special ganglion located inside the mantle edge innervates these flaps. As the flaps move rhythmically, a pulse, beginning at the tail, moves slowly forward to propel a bulge in the flaps along the entire body. This intricate apparatus, formed by the marsupium and mantle flaps, not only looks like a fish but also moves like one.

Why would a clam mount a fish on its rear end? The unusual reproductive biology of *Lampsilis* supplies an answer. The larvae of unionids cannot develop without a free ride upon fishes during their early growth. Most unionid larvae possess two little hooks. When released from their mother's marsupium, they fall to the bottom of the stream and await a passing fish. But the larvae *of Lampsilis* lack these hooks and cannot actively attach themselves. In order to survive, they must enter a fish's mouth and move to favored sites on the gills. The ersatz fish of *Lampsilis* is an animated decoy, simulating both the form and movement of the animal it must attract. When a fish approaches, *Lampsilis* discharges larvae



Isaac Lea published this figure of the decoy "fish" in 1838. I thank John H. Welsh for sending this figure to me.

from the marsupium; some of them will be swallowed by the fish and find their way to its gills.

The strategem of *Cyprogenia,* a related genus, emphasizes the importance of attracting a host. These mussels "go fishing" in a manner subsequently reinvented by disciples of Izaak Walton. The larvae attach themselves to a bright red "worm" formed by a protein manufactured within the mother's body. The "worms" are extruded through the exhalant siphon. Several observers report that fish seek out and eat these "worms," often pulling them, when only partly extruded, from the female's siphon.

We can scarcely doubt the adaptive significance of the decoy "fish," but how could it ever evolve? How did the marsupium and mantle flap come together to effect their ruse? Lucky accident or preordained direction may appeal more to our intuition than gradual construction by natural selection through some intermediate forms that, at least in their initial stages, could not have looked much like a fish. The intricate fish of *Lampsilu* is a classic illustration of a deep dilemma in Darwinism. Can we possibly devise an adaptive significance for the incipient stages of this useful structure?

The general principle advanced by modern evolutionists to solve this dilemma calls upon a concept with the unfortunate name of "preadaptation." (I say unfortunate because the term implies that species adapt in advance to impending events in their evolutionary history, when exactly the opposite meaning is intended.) The success of a scientific hypothesis often involves an element of surprise. Solutions often arise from a subtle reformulation of the question, not from the diligent collection of new information in an old framework. With preadaptation, we cut through the dilemma of a function for incipient stages by accepting the standard objection and admitting that intermediate forms did not work in the same way as their perfected descendants. We avoid the excellent question, What good is 5 percent of an eye? by arguing that the possessor of such an incipient structure did not use it for sight.

To invoke a standard example, the first fishes did not have jaws. How could such an intricate device, consisting of several interlocking bones, ever evolve from scratch? "From scratch" turns out to be a red herring. The bones were present in ancestors, but they were doing something else—they were supporting a gill arch located just behind the mouth. They were well designed for their respiratory role; they had been selected for this alone and "knew" nothing of any future function. In hindsight, the bones were admirably preadapted to become jaws. The intricate device was already assembled, but it was being used for breathing, not eating.

Similarly, how could a fish's fin ever become a terrestrial limb? Most fishes build their fins from slender parallel rays that could not support an animal's weight on land. But one peculiar group of freshwater, bottom-dwelling fishes—our ancestors—evolved a fin with a strong central axis and only a few radiating projections. It was admirably preadapted to become a terrestrial leg, but it had evolved purely for its own purposes in water—presumably for scuttling along the bottom by sharp rotation of the central axis against the substrate.

In short, the principle of preadaptation simply asserts that a structure can change its function radically without altering its form as much. We can bridge the limbo of intermediate stages by arguing for a retention of old functions while new ones are developing.

Will preadaptation help us to understand how *Lampsilis* got its fish? It might if we can meet two conditions: (1) We must find an intermediate form using at least some elements of the fish for different purposes; (2) We must specify functions other than visual decoy that the proto-fish could fulfill while it gradually acquired its uncanny resemblance.

Ligumia nasuta, a "cousin" of *Lampsilis,* seems to satisfy the first condition. Gravid females of this species do not have mantle flaps, but they do possess darkly pigmented, ribbon-like membranes that bridge the gap between partly opened shells. *Ligumia* uses these membranes to produce an unusual, rhythmic motion. The opposing edges of the ribbons part to form a gap several millimeters in length at the mid-part of the shell. Through this gap, the white color of the interior soft parts stands out against the dark pigment of the ribbon. This white spot appears to move toward the back of the shell, as a wave of separation propagates itself along the membranes. These waves may repeat about once every two seconds. J.H. Welsh wrote in the May 1969 issue of *Natural History:*

> The regularity of the rhythm is remarkably constant. To a human observer, and perhaps to a fish, the eye-catching feature here is the white spot that appears to move against the dark background of the mussel and the substrate in which it is half buried. Certainly this could be a lure to host fish and may represent a specialized adaptation from which the more elaborate, fishlike lure evolved.

We are still dealing with a device to attract fish, but the mechanism is abstract, regular motion, not visual mimicry. If this device operated while the Haps were evolving and slowly building their resemblance to a fish, then we have no problem of incipient stages. Motion of the mantle attracted fish from the start; the slow development of an "alternate technology" only enhanced the process.

Lampsilis itself fulfills the second condition. Although no one has denied the significance of visual resemblance as a lure, our leading student of *Lampsilis,* L.R. Kraemer, questions the common assumption that "flapping" of the body serves only to simulate the movements of a fish. She believes that flapping may have evolved either to aerate the larvae within the marsupium or to keep them suspended in the water after their release. Again, if flapping provided these other advantages from the start, then the fortuitous resemblance of flaps to fish might be a preadaptation. The initial, imperfect mimicry could be improved by natural selection while the flaps performed other important functions.

Common sense is a very poor guide to scientific insight for it represents cultural prejudice more often than it reflects the native honesty of a small boy before the naked emperor. Common sense dictated to Darwin's critics that a gradual change in form must indicate a progressive building of function. Since they could assign no adaptive value to early and imperfect stages of a function, they assumed either that early stages had never existed (and that perfect forms had been created all at once) or that they had not arisen by natural selection. The principle of preadaptation—functional change in structural continuity—can resolve this dilemma. Darwin ended his paragraph on the eye with this perceptive evaluation of "common sense":

> When it was first said that the sun stood still and the world turned round, the common sense of mankind declared the doctrine false; but the old saying of *Vox populi, vox Dei* [the voice of the people is the voice of God], as every philosopher knows, cannot be trusted in science.

The Validation of Continental Drift

AS THE NEW Darwinian orthodoxy swept through Europe, its most brilliant opponent, the aging embryologist Karl Ernst von Baer, remarked with bitter irony that every triumphant theory passes through three stages: first it is dismissed as untrue; then it is rejected as contrary to religion; finally, it is accepted as dogma and each scientist claims that he had long appreciated its truth.

I first met the theory of continental drift when it labored under the inquisition of stage two. Kenneth Caster, the only major American paleontologist who dared to support it openly, came to lecture at my alma mater, Antioch College. We were scarcely known as a bastion of entrenched conservatism, but most of us dismissed his thoughts as just this side of sane. (Since I am now in von Baer's third stage, I have the distinct memory that Caster sowed substantial seeds of doubt in my own mind.) A few years later, as a graduate student at Columbia University, I remember the a priori derision of my distinguished stratigraphy professor toward a visiting Australian drifter. He nearly orchestrated the chorus of Bronx cheers from a sycophantic crowd of loyal students. (Again, from my vantage point in the third stage, I recall this episode as amusing, but distasteful.) As a tribute to my professor, I must record that he experienced a rapid conversion just two years later and spent his remaining years joyously redoing his life's work.

Today, just ten years later, my own students would dismiss with even more derision anyone who denied the evident truth of continental drift—a prophetic madman is at least amusing; a superannuated fuddy-duddy is merely pitiful. Why has such a profound change occurred in the short space of a decade?

Most scientists maintain—or at least argue for public consumption—that their profession marches toward truth by accumulating more and more data, under the guidance of an infallible procedure called "the scientific method." If this were true, my question would have an easy answer. The facts, as known ten years ago, spoke against continental drift; since then, we have learned more and revised our opinions accordingly. I will argue, however, that this scenario is both inapplicable in general and utterly inaccurate in this case.

During the period of nearly universal rejection, direct evidence for continental drift—that is, the data gathered from rocks exposed on our continents—was every bit as good as it is today. It was dismissed because no one had devised a physical mechanism that would permit continents to plow through an apparently solid oceanic floor. In the absence of a plausible mechanism, the idea of continental drift was rejected as absurd. The data that seemed to support it could always be explained away. If these explanations sounded contrived or forced, they were not half so improbable as the alternative—accepting continental drift. During the past ten years, we have collected a new set of data, this time from the ocean basins. With these data, a heavy dose of creative imagination, and a better understanding of the earth's interior, we have fashioned a new theory of planetary dynamics. Under this theory of plate tectonics, continental drift is an inescapable consequence. The old data from continental rocks, once soundly rejected, have been exhumed and exalted as conclusive proof of drift. In short, we now accept continental drift because it is the expectation of a new orthodoxy.

I regard this tale as typical of scientific progress. New facts, collected in old ways under the guidance of old theories, rarely lead to any substantial revision of thought. Facts do not "speak for themselves"; they are read in the light of theory. Creative thought, in science as much as in the arts, is the motor of changing opinion. Science is a quintessentially human activity, not a mechanized, robotlike accumulation of objective information, leading by laws of logic to inescapable interpretation. I will try to illustrate this thesis with two examples drawn from the "classical" data for continental drift. Both are old tales that had to be undermined while drift remained unpopular.

I. The late Paleozoic glaciation. About 240 million years ago, glaciers covered parts of what is now South America, Antarctica, India, Africa, and Australia. If continents are stable, this distribution presents some apparently insuperable difficulties:

> A. The orientation of striae in eastern South America indicates that glaciers moved onto the continent from what is now the Atlantic Ocean (striae are scratches on bedrock made by rocks frozen into glacier bottoms as they pass over a surface). The world's oceans form a single system, and transport of heat from tropical areas guarantees that no major part of the open ocean can freeze.
>
> B. African glaciers covered what are now tropical areas.
>
> C. Indian glaciers must have grown in semitropical regions of the Northern hemisphere; moreover, their striae indicate a source in tropical waters of the Indian Ocean.
>
> D. There were no glaciers on any of the northern continents. If the earth got cold enough to freeze tropical Africa, why were there no glaciers in northern Canada or Siberia?

All these difficulties evaporate if the southern continents (including India) were joined together during this glacial period, and located farther south, covering the South Pole; the South American glaciers moved from Africa, not an open ocean; "tropical" Africa and "semitropical" India were near the South Pole; the North Pole lay in the middle of a major ocean, and glaciers could not develop in the Northern Hemisphere. Sounds good for drift; indeed, no one doubts it today.

II. The distribution of Cambrian trilobites (fossil arthropods living 500 to 600 million years ago). The Cambrian trilobites of Europe and North America divided themselves into two rather different faunas with the following peculiar distribution on modern maps. "Atlantic" province trilobites lived all over Europe and in a few very local areas on the far eastern border of North America—eastern (but not western) Newfoundland and southeastern Massachusetts, for example. "Pacific" province trilobites lived all over America and in a few local areas on the extreme western coast of Europe —northern Scotland and northwestern Norway, for example. It is devilishly difficult to make any sense of this distribution if the two continents always stood 3,000 miles apart.

But continental drift suggests a striking resolution. In Cambrian times, Europe and North America were separated: Atlantic trilobites lived in waters around Europe; Pacific trilobites in waters around America. The continents (now including sediments with entombed trilobites) then drifted toward each other and finally joined together. Later, they split again, but not precisely along the line of their previous junction. Scattered bits of ancient Europe, carrying Atlantic trilobites, remained at the easternmost border of North America, while a few pieces of old North America stuck to the westernmost edge of Europe.

Both examples are widely cited as "proofs" of drift today, but they were soundly rejected in previous years, not because their data were any less complete but only because no one had devised an adequate mechanism to move continents. All the original drifters imagined that continents plow their way through a static ocean floor. Alfred Wegener, the father of continental drift, argued early in our century that gravity alone could put continents in motion. Continents drift slowly westward, for example, because attractive forces of the sun and moon hold them up as the earth rotates underneath them. Physicists responded with derision and showed mathematically that gravitational forces are far too weak to power such a monumental peregrination. So Alexis du Toil, Wegener's South African champion, tried a different tack. He argued for a local, radioactive melting of oceanic floor at continental borders, permitting the continents to glide through. This *ad hoc* hypothesis added no increment of plausibility to Wegener's speculation.

Since drift seemed absurd in the absence of a mechanism, orthodox geologists set out to render the impressive evidence for it as a series of unconnected coincidences.

In 1932, the famous American geologist Bailey Willis strove to make the evidence of glaciation compatible with static continents. He invoked the deus ex machina of "isthmian links"—narrow land bridges flung with daring abandon across 3,000 miles of ocean. He placed one between eastern Brazil and western Africa, another from Africa all the way to India via the Malagasy Republic, and a third from Vietnam through Borneo and New Guinea to Australia. His colleague, Yale professor Charles Schuchert, added one from Australia to Antarctica and another from Antarctica to South America, thus completing the isolation of a southern ocean from the rest of the world's waters. Such an isolated ocean might freeze along its southern margin, permitting glaciers to flow across into eastern South America. Its cold waters would also nourish the glaciers of southern Africa. The Indian glaciers, located above the equator 3,000 miles north of any southern ice, demanded a separate explanation. Willis wrote: "No direct connection between the occurrences can reasonably be assumed. The case must be considered on the basis of a general cause and the local geographic and topographic conditions." Willis's inventive mind was equal to the task: he simply postulated a topography so elevated that warm, wet southern waters precipitated their product as snow. For the absence of ice in temperate and arctic zones of the Northern Hemisphere, Willis reconstructed a system of ocean currents that permitted him to postulate "a warm, subsurface current flowing northward beneath cooler surface waters and rising in the Artctic as a warm-water heating system." Schuchert was delighted with the resolution provided by isthmian links:

> Grant the biogeographer Holarctis, a land bridge from northern Africa to Brazil, another from South America to Antarctis (it almost exists today), still another from this polar land to Australia and from the latter across the Arafura Sea to Borneo and Sumatra and so on to Asia, plus the accepted means of dispersal along shelf seas and by wind and water currents and migratory birds, and he has all the possibilities needed to explain the life disper-

> sion and the land and ocean realms throughout geological time on the basis of the present arrangement of the continents.

The only common property shared by all these land bridges was their utterly hypothetical status; not an iota of direct evidence supported any one of them. Yet, lest the saga of isthmian links be read as a warped fairy tale invented by dogmatists to support an untenable orthodoxy, I point out that to Willis, Schuchert, and any right-thinking geologist of the 1930s, one thing legitimately seemed ten times as absurd as imaginary land bridges thousands of miles long—continental drift itself.

In the light of such highly fertile imaginations, the Cambrian trilobites could present no insuperable problem. The Atlantic and Pacific provinces were interpreted as different environments, rather than different places—shallow water for the Pacific, deeper for the Atlantic. With a freedom to invent nearly any hypothetical geometry for Cambrian ocean basins, geologists drew their maps and hewed to their orthodoxy.

When continental drift came into fashion during the late 1960s, the classical data from continental rocks played no role at all: drift rode in on the coattails of a new theory, supported by new types of evidence. The physical absurdities of Wegener's theory rested on his conviction that continents cut their way through the ocean floor. But how else could drift occur? The ocean floor, the crust of the earth, must be stable. After all, where could it go, if it moved in pieces, without leaving gaping holes in the earth? Nothing could be clearer. Or could it?

"Impossible" is usually defined by our theories, not given by nature. Revolutionary theories trade in the unexpected. If continents must plow through oceans, then drift will not occur; suppose, however, that continents are frozen into the oceanic crust and move passively as pieces of crust shift about. But we just stated that the crust cannot move without leaving holes. Here, we reach an impasse that must be bridged by creative imagination, not just by another field season in the folded Appalachians—we must model the earth in a fundamentally different way.

We can avoid the problem of holes with a daring postulate that seems to be valid. If two pieces of ocean floor move away from each other, they will leave no hole if material rises from the earth's interior to fill the gap. We can go further by reversing the causal implications of this statement: the rise of new material from the earth's interior may be the driving force that moves old sea floor away. But since the earth is not expanding, we must also have regions where old sea floor founders into the earth's interior, thus preserving a balance between creation and destruction.

Indeed, the earth's surface seems to be broken into fewer than ten major "plates," bounded on all sides by narrow zones of creation (oceanic ridges) and destruction (trenches). Continents are frozen into these plates, moving with them as the sea floor spreads away from zones of creation at oceanic ridges. Continental drift is no longer a proud theory in its own right; it has become a passive consequence of our new orthodoxy—plate tectonics.

We now have a new, mobilist orthodoxy, as definite and uncompromising as the staticism it replaced. In its light, the classical data for drift have been exhumed and proclaimed as proof positive. Yet these data played no role in validating the notion of wandering continents; drift triumphed only when it became the necessary consequence of a new theory.

The new orthodoxy colors our vision of all data; there are no "pure facts" in our complex world. About five years ago, paleontologists found on Antarctica a fossil reptile named *Lystrosaurus.* It also lived in South Africa, and probably in South America as well (rocks of the appropriate age have not been found in South America). If anyone had floated such an argument for drift in the presence of Willis and Schuchert, he would have been howled down—and quite correctly. For Antarctica and South America are almost joined today by a string of islands, and they were certainly connected by a land bridge at various times in the past (a minor lowering of sea level would produce such a land bridge today). *Lystrosaurus* may well have walked in comfort, on a rather short journey at that. Yet the *New York Times* wrote an editorial proclaiming, on this basis alone, that continental drift had been proved.

Many readers may be disturbed by my argument for the primacy of theory. Does it not lead to dogmatism and disrespect for fact? It can, of course, but it need not. The lesson of history holds that theories are overthrown by rival theories, not that orthodoxies are unshakable. In the meantime, I am not distressed by the crusading zeal of plate tectonics, for two reasons. My intuition, culturally bound to be sure, tells me that it is basically true. My guts tell me that it's damned exciting—more than enough to show that conventional science can be twice as interesting as anything invented by all the von Danikens and in all the Bermuda triangles of this and previous ages of human gullibility.

Size and Shape

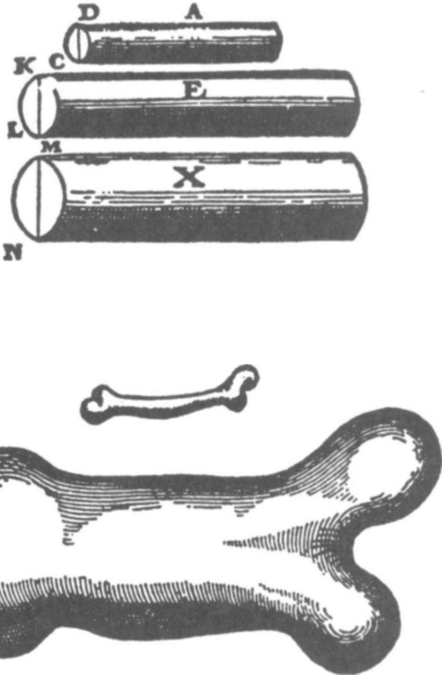
Who could believe an ant in theory?
A giraffe in blueprint?
Ten thousand doctors of what's possible
Could reason half the jungle out of being.

JOHN CIARDI'S lines reflect a belief that the exuberant diversity of life will forever frustrate our arrogant claims to omniscience. Yet, however much we celebrate diversity and revel in the peculiarities of animals, we must also acknowledge a striking "lawfulness" in the basic design of organisms. This regularity is most strongly evident in the correlation of size and shape.

Animals are physical objects. They are shaped to their advantage by natural selection. Consequently, they must assume forms best adapted to their size. The relative strength of many fundamental forces (gravity, for example) varies with size in a regular way, and animals respond by systematically altering their shapes.

The geometry of space itself is the major reason for correlations between size and shape. *Simply by growing larger,* any object will suffer continual decrease in relative surface area when its shape remains unchanged. This decrease occurs because volume increases as the cube of length (length X length X length), while surface increases only as the square (length X length): in other words, volume grows more rapidly than surface.

Why is this important to animals? Many functions that depend upon surfaces must serve the entire volume of the body. Digested food passes to the body through surfaces; oxygen is absorbed through surfaces in respiration; the strength of a leg bone depends upon the area of its cross section, but the legs must hold up a body increasing in weight by the cube of its length. Galileo first recognized this principle in his *Discorsi* of 1638, the masterpiece he wrote while



Galileo's original illustration of the relationship between size and shape. To maintain the same strength, large cylinders must be relatively thicker than small ones. For exactly the same reason, large animals have relatively thick leg bones.

under house arrest by the Inquisition. He argued that the bone of a large animal must thicken disproportionately to provide the same relative strength as the slender bone of a small creature.

One solution to decreasing surface has been particularly important in the progressive evolution of large and complex organisms: the development of internal organs. The lung is, essentially, a richly convoluted bag of surface area for the exchange of gases; the circulatory system distributes material to an internal space that cannot be reached by direct diffusion from the external surface of large organisms; the villi of our small intestine increase the surface area available for absorption of food (small mammals neither have nor need them).

Some simpler animals have never evolved internal organs; if they become large, they must alter their entire shape in ways so drastic that plasticity for further evolutionary change is sacrificed to extreme specialization. Thus, a tapeworm may be 20 feet long, but its thickness cannot exceed a fraction of an inch because food and oxygen must penetrate directly from the external surface to all parts of the body.

Other animals are constrained to remain small. Insects breathe through invaginations of their external surface. Oxygen must pass through these surfaces to reach the entire volume of the body. Since these invaginations must be more numerous and convoluted in larger bodies, they impose a limit upon insect size: at the size of even a small mammal, an insect would be "all invagination" and have no room for internal parts.

We are prisoners of the perceptions of our size, and rarely recognize how different the world must appear to small animals. Since our relative surface area is so small at our large size, we are ruled by gravitational forces acting upon our weight. But gravity is negligible to very small animals with high surface to volume ratios; they live in a world dominated by surface forces and judge the pleasures and dangers of their surroundings in ways foreign to our experience.

An insect performs no miracle in walking up a wall or upon the surface of a pond; the small gravitational force pulling it down or under is easily counteracted by surface adhesion.

Throw an insect off the roof and it floats gently down as frictional forces acting upon its surface overcome the weak influence of gravity.

The relative weakness of gravitational forces also permits a mode of growth that large animals could not maintain. Insects have an external skeleton and can only grow by discarding it and secreting a new one to accommodate the enlarged body. For a period between shedding and regrowth, the body must remain soft. A large mammal without any supporting structures would collapse to a formless mass under the influence of gravitational forces; a small insect can maintain its cohesion (related lobsters and crabs can grow much larger because they pass their "soft" stage in the nearly weightless buoyancy of water). We have here another reason for the small size of insects.

The creators of horror and science-fiction movies seem to have no inkling of the relationship between size and shape. These "expanders of the possible" cannot break free from the prejudices of their perceptions. The small people of *Dr. Cyclops, The Bride of Frankenstein, The Incredible Shrinking Man,* and *Fantastic Voyage* behave just like their counterparts of normal dimensions. They fall off cliffs or down stairs with resounding thuds; they wield weapons and swim with **Olym**pic agility. The large insects of films too numerous to name continue to walk up walls or fly even at dinosaurian dimensions. When the kindly entomologist of *Them* discovered that the giant queen ants had left for their nuptial flight, he quickly calculated this simple ratio: a normal ant is a fraction of an inch long and can fly hundreds of feet; these ants are many feet long and must be able to fly as much as 1,000 miles. Why, they could be as far away as Los Angeles! (Where, indeed, they were, lurking in the sewers.) But the ability to fly depends upon the surface area of wings, while the weight that must be borne aloft increases as the cube of length. We may be sure that even if the giant ants had somehow circumvented the problems of breathing and growth by molting, their sheer bulk would have grounded them permanently.

Other essential features of organisms change even more rapidly with increasing size than the ratio of surface to volume. Kinetic energy, in some situations, increases as length raised to the fifth power. If a child half your height falls down, its head will hit with not half, but only 1/32 the energy of yours in a similar fall. A child is protected more by its size than by a "soft" head. In return, we are protected from the physical force of its tantrums, for the child can strike with, not half, but only 1/32 of the energy we can muster. I have long had a special sympathy for the poor dwarfs who suffer under the whip of cruel Alberich in Wagner's *Das Rheingold.* At their diminutive size, they haven't a chance of extracting, with mining picks, the precious minerals that Alberich demands, despite the industrious and incessant leitmotif of their futile attempt.[4]

This simple principle of differential scaling with increasing size may well be the most important determinant of organic shape. J. B. S. Haldane once wrote that "comparative anatomy is largely the story of the struggle to increase surface in proportion to volume." Yet its generality extends beyond life, for the geometry of space constrains ships, buildings, and machines, as well as animals.

Medieval churches present a good testing ground for the effects of size and shape, for they were built in an enormous range of sizes before the invention of steel girders, internal lighting, and air conditioning permitted modern architects to challenge the laws of size. The small, twelfth-century parish church of Little Tey, Essex, England, is a broad, simple rectangular building with a semicircular apse. Light reaches the interior through windows in the outer walls. If we were to build a cathedral simply by enlarging this design, then the area of outer walls and windows would increase as length squared, while the volume that light must reach would increase as length cubed. In other words, the area of the windows would increase far more slowly than the volume that

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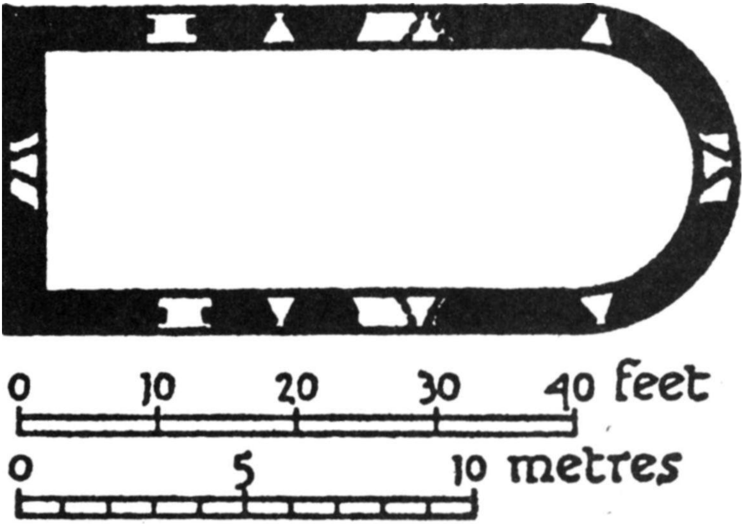
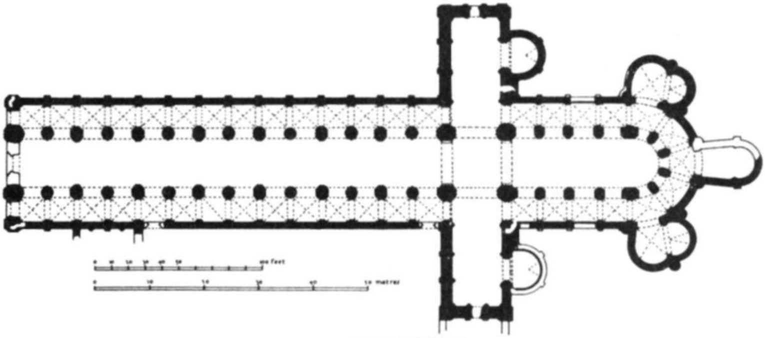
4 | A friend has since pointed out that Alberich, a rather small man himself, would only wield the whip with a fraction of the force we could exert—so things might not have been quite so bad for his underlings.




NORWICH CATHEDRAL.

7"/ii? *great range of designs among medieval churches can be attributed partly to size. The twelfth-century parish church of Little Tey, Essex, England, was only 57 feet long and had a simple floor plan, top, while the floor plan for Norwich Cathedral, also twelfth century, shows adaptations—transept, chapels—required for the 450-foot-long building. The need for light and support dictated complex cathedral layouts.*

(A. W. Clapham, *English Romanesque Architecture: After the Conquest,* Clarendon Press Oxford, 1934. Reprinted with the permission of Oxford University Press) requires illumination. Candles have limitations; the inside of such a cathedral would have been darker than the deed of Judas. Medieval churches, like tapeworms, lack internal systems and must alter their shape to produce more external surface as they are made larger. In addition, large churches had to be relatively narrow because ceilings were vaulted in stone and large widths could not be spanned without intermediate supports. The chapter house at Batalha, Portugal—one of the widest stone vaults in medieval architecture—collapsed twice during construction and was finally built by prisoners condemned to death.

Consider the large cathedral of Norwich, as it appeared in the twelfth century. In comparison with Little Tey, the rectangle of the nave has become much narrower; chapels have been added to the apse, and a transept runs perpendicular to the main axis. All these "adaptations" increase the ratio of external wall and window to internal volume. It is often stated that transepts were added to produce the form of a Latin cross. Theological motives may have dictated the position of such "outpouchings," but the laws of size required their presence. Very few small churches have transepts. Medieval architects had their rules of thumb, but they had, so far as we know, no explicit knowledge of the laws of size.

Large organisms, like large churches, have very few options open to them. Above a certain size, large terrestrial animals look basically alike—they have thick legs and relatively short, stout bodies. Large medieval churches are relatively long and have abundant outpouchings. The "invention" of internal organs allowed animals to retain the highly successful shape of a simple exterior enclosing a large internal volume; the invention of internal lighting and structural steel has permitted modern architects to design large buildings of essentially cubic form. The limits are expanded, but the laws still operate. No large Gothic church is wider than long; no large animal has a sagging middle like a dachshund.

I once overheard a children's conversation in a New York playground. Two young girls were discussing the size of dogs. One asked: "Can a dog be as large as an elephant?" Her friend responded: "No if it were as big as an elephant, it would look like an elephant." How truly she spoke.

Big Fish, Little Fish

ALFRED, LORD TENNYSON, never known for egalitarian perspectives, had this to say about the relative merit of the sexes:

> Woman is the lesser man, and all
> thy passions, matched with mine,
> Are as moonlight unto sunlight, and
> as water unto wine.

The couplet may not represent Tennyson's considered view, since the protagonist of "Locksley Hall" had lost his love to another and speaks these words during a grand poetic fit of sour grapes. Still, the literal reading—that women are smaller than men—would be accepted by most of us as a general fact of nature, not as a sexist trap. And most of us would therefore be wrong.

Human males are, of course, generally larger than human females, and most familiar mammals follow the same pattern (but see essay 11). Yet females are larger than males in a majority of animal species—and probably a large majority at that. For starters, most animal species are insects and female insects usually exceed their males in size. Why are males generally smaller?

One amusing suggestion was proposed in all seriousness just 100 years ago (as I discovered in the "50 and 100 Years Ago" column in *Scientific American* for January, 1982). A certain M. G. Delaunay argued that human races might be ranked by the relative social position of females. Inferior races suffered under female supremacy, males dominated in superior races, while equality of sexes marked races of middle rank. As collateral support for his peculiar thesis, Delaunay argued that females are larger than males in "lower" animals and smaller in "higher" creatures. Thus, the greater number of species with larger females posed no threat to a general notion of male superiority. After all, many serve and few rule.

Delaunay's argument is almost too precious to disturb with refutation, but it's probably worth mentioning that the paradigm case of a "higher" group with larger males—the mammals—is shakier than most people think (see Katherine Ralls in the bibliography). Males are larger in a majority of mammalian species, of course, but Ralls found a surprising number of species with larger females, spread widely throughout the range of mammalian diversity. Twelve of 20 orders and 20 of 122 families contain species with larger females. In some important groups, larger females are the rule: rabbits and hares, a family of bats, three families of baleen whales, a major group of seals, and two tribes of antelopes. Ralls further reminds us that since blue whales are the largest animals that have ever lived, and since females surpass males in baleen whales, the largest individual animal of all time is undoubtedly a female. The biggest reliably measured whale was 93.5 feet long and a female.

The sporadic distribution of larger females within the taxonomic range of mammals illustrates the most important general conclusion we can reach about the relative size of sexes: the observed pattern does not suggest any general or overarching trend associating predominance of either sex with anatomical complexity, geological age, or supposed evolutionary stage. Rather, the relative size of sexes seems to reflect an evolved strategy for each particular circumstance—an affirmation of Darwin's vision that evolution is primarily the story of adaptation to local environments. In this perspective, we must anticipate the usual pattern of larger females. Females, as producers of eggs, are usually more active than males in brooding their young. (Such male tenders as sea horses and various mouth-brooding fishes must receive eggs directly from a female or actively pick up eggs after a female discharges them.) Even in species that furnish no parental care, eggs must be provided with nutriment, while sperm is little more than naked DNA with a delivery system. Larger eggs require more room and a bigger body to produce them.

If females provide the essential nutriment for embryonic or larval growth, we might ask why males exist at all. Why bother with sex if one parent can supply the essential provisioning? The answer to this old dilemma seems to lie in the nature of Darwin's world. If natural selection propels evolution by preserving favored variants from a spectrum randomly distributed about an average value, then an absence of variation derails the process—for natural selection makes nothing directly and can only choose among alternatives presented. If all offspring were the xeroxed copies of a single parent, they would present no genetic variation (except for rare new mutations) and selection could not operate effectively. Sex generates an enormous array of variation by mixing the genetic material of two creatures in each offspring. If only for this reason, we shall have males to kick around for some time.

But if the biological function of males does not extend beyond the contribution of some essentially naked DNA, why bother to put so much effort into making them? Why should they, in most cases, be almost as big as females, endowed with complex organs, and quite capable of an independent life? Why should industrious bees continue to make the large and largely useless male creatures appropriately known as drones?

These questions would be difficult to answer if evolution worked for the good of species or larger groups. But Darwin's theory of natural selection holds that evolution is fundamentally a struggle among individual organisms to pass more of their genes into future generations. Since males are essential (as argued above), they become evolutionary agents in their own right; they are not designed for the benefit of their species. As independent agents, they join the struggle in their own ways—and these ways sometimes favor a larger size. In many groups, males fight (literally) for access to females, and heavyweights often have an edge. In more complex creatures, social life may emerge and become ever more elaborate. Such complexity may require the presence and active involvement of more than one parent in the rearing of offspring—and males gain a biological role transcending mere stud service.

But what of ecological situations that neither favor battle nor require parental care? After all, Tennyson's most famous biological line—his description of life's ecology as "Nature, red in tooth and claw"—does not apply in all, or most, cases. Darwin's "struggle for existence" is a metaphor and need not imply active combat. The struggle for genetic representation in the next generation can be pursued in a variety of ways. One common strategy mimics the motto of rigged elections: vote early and vote often (but substitute "fornicate" for "vote"). Males who follow this tactic have no evolutionary rationale for large size and complexity beyond what they need to locate a female as quickly as possible and to stick around. In such cases, we might expect to find males in their minimal state, a status that might have become quite general if evolution worked for the good of species—a small device dedicated to the delivery of sperm. Nature, ever obliging, has provided us with some examples of what, but for the grace of natural selection, might have been my fate.

Consider a species so thinly spread over such a broad area that males will rarely meet at the site of a female. Suppose also that females, as adults, move very little if at all: they may be attached to the substrate (barnacles, for example); they may live parasitically, within another creature; or they may feed by waiting and luring rather than by pursuit. And suppose finally that the surrounding medium can easily move small creatures about—as in the sea, with its currents and high density (see M. Ghiselin's book, *The Economy of Nature and the Evolution of Sex,* for a discussion of this phenomenon). Since males have little impetus for literal battle, since they must find a stationary female, and since the medium in which they live can provide (or substantially aid) their transport, why be large? Why not find a female fast when still quite small and young and then hang on as a simple source of sperm? Why work and feed, and grow large and complex? Why not exploit the feeding female? All her offspring will still be 50 percent you.

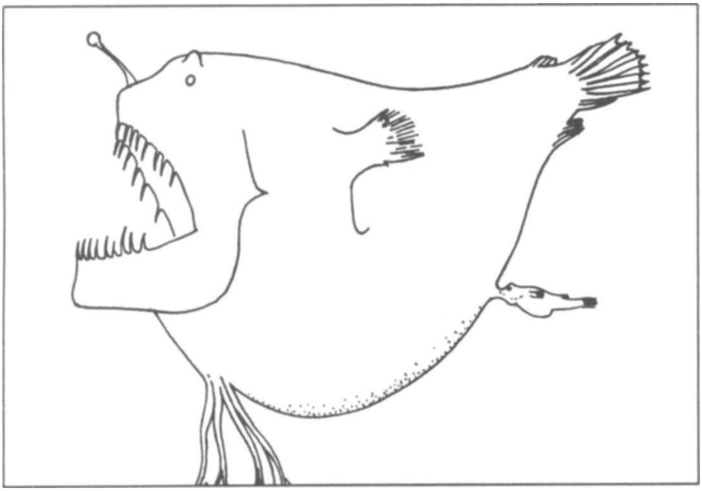
Indeed, this strategy is quite common, although little appreciated by sentient mammals of different status, among marine invertebrates that either live at great depth (where food is scarce and populations very thinly spread), or place themselves in widely dispersed spots that are hard to locate (as in many parasites). Here we often encounter that ultimate in the expression of nature's more common tendency —females larger than males. The males become dwarfs, often less than one-tenth the length of females, and evolve a body suited primarily for finding females—a sperm delivery system of sorts.

A species of *Enteroxenos,* for example, a molluscan parasite that lives inside the gut of sea cucumbers (echinoderms related to sea urchins and starfishes), was originally described as a hermaphrodite, with both male and female organs. But J. Lutzen of the University of Copenhagen recently discovered that the male "organ" is actually the degenerated product of a separate dwarf male organism that found the parasitic female and attached permanently to her. The female *Enteroxenos* fastens herself to the sea cucumber's esophagus by a small ciliated tube. The dwarf male finds the tube, enters the female's body, attaches to it in a particular place, and then loses virtually all its organs except, of course, for the testes. After a male enters, the female breaks its tubular connection with the sea cucumber's esophagus, thereby obliterating the pathway of entrance for any future males. (A strict Darwinian—I am not one—would predict that the male has evolved some device to break or cause the female to break this tubular connection, thereby excluding all subsequent males and assuring its own paternity for all the female's offspring. But no evidence yet exists for or against this hypothesis.)

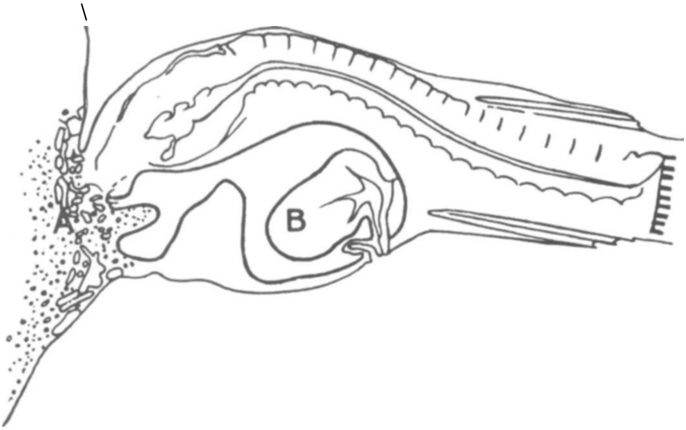
As long as such an uncomfortable phenomenon resides with unfamiliar and "lowly" invertebrates, male supremacists who seek pseudosupport from nature may not be greatly disturbed. But I am delighted to tell a similar story about one group of eminently suited vertebrates—deep-sea anglerfishes of the Ceratioidei (a large group with 11 families and nearly 100 species).

Ceratioid anglerfishes have all the prerequisites for evolving dwarf males as sperm delivery systems. They live at depth in the open ocean, mostly from 3,000 to 10,000 feel below the surface, where food is scarce and populations sparse. Females have detached the first dorsal fin ray and moved it forward over their capacious mouth. They dangle a lure at the tip of this spine and literally fish with it. They jiggle and wave the lure while floating, otherwise immobile, in the midst of the sea. The related shallower-water and bottom-dwelling anglerfishes often evolve elaborate mimetic structures for their lures—bits of tissue that resemble worms or even a decoy fish (see essay 3 in *The Panda's Thumb).* Ceratioids live well below the depth that light can penetrate sea water. Their world is one of total ambient darkness, and they must therefore provide the light of attraction themselves. Their lures glow with a luminescence supplied by light glands—a death trap for prey and, perhaps, a beacon for dwarf males.

In 1922, B. Saemundsson, an Icelandic fisheries biologist, dredged a female *Ceratias holbolli,* 26.16 inches in length. To his surprise, he found two small anglerfish, only 2.03 and 2.10 inches long, attached to the female's skin. He assumed, naturally, that they were juveniles, but he was puzzled by their degenerate form: "At first sight," he wrote, "I thought these young ones were pieces of skin torn off and loose." Another oddity puzzled him even more: these small fish were so firmly attached that their lips had grown together about a wad of female tissue projecting well into their mouths and down their throats. Saemundsson could find no other language for his description but an obviously inappropriate mammalian analogy: "The lips are grown together and are attached to a soft papilla or 'teat' protruding.



A male anglerfish (lower right), about one-and-a-half inches long, embeds itself into a ten-inch female of the same species, REPRINTED FROM NATURAL HISTORY.



A simplified cross section shows a male anglerfish attached to a female. The two fish share tissue (A), and the male's testis (B), has become enlarged, REPRINTED FROM NATURAL HISTORY.

so far as I can see, from the belly of the mother."

Three years later, the great British ichthyologist C. Tate Regan, then keeper of fishes and later boss of the British Museum (Natural History), solved Saemundsson's dilemma. The "young ones" were not juveniles, but permanently attached, sexually mature dwarf males. As Regan studied the details of attachment between male and female, he discovered the astounding fact that has ever since been celebrated as one of the greatest oddities in natural history: "At the junction of the male and the female fish there is a complete blending ... their vascular systems are continuous." In other words, the male has ceased to function as an independent organism. It no longer feeds, for its mouth is fused with the female's outer skin. The vascular systems of male and female have united, and the tiny male is entirely dependent upon the female's blood for nutrition. Of a second species with similar habits, Regan writes: "It is impossible to say where one fish begins and the other ends." The male has become a sexual appendage of the female, a kind of incorporated penis. (Both popular and technical literature often refer to the fused male as a "parasite." But I demur. Parasites live at the expense of their host. Fused males depend upon females for nutrition, but they supply in return that most precious of biological gifts—access to the next generation and a chance for evolutionary continuity.)

The extent of male submergence has been exaggerated in most popular accounts. Although attached males surrender their vascular independence and lose or reduce a set of organs no longer needed (eyes, for example), they remain more than a simple penis. Their own hearts must still pump the blood now supplied by females, and they continue to breathe with their gills and remove wastes with their kidneys. Of one firmly attached male, Regan writes:

> The male fish, although to a great extent merely an appendage of the female, and entirely dependent on her for nutrition, yet retains a certain autonomy. He is probably capable, by movements of the tail and fins, of changing his position to some extent. He breathes, he

> may have functional kidneys, and he removes from the blood certain products of his own metabolism and keeps them as pigment.... But so perfect and complete is the union of husband and wife that one may almost be sure that their genital glands ripen simultaneously, and it is perhaps not too fanciful to think that the female may possibly be able to control the seminal discharge of the male and to ensure that it takes place at the right time for the fertilization of her eggs.

Nonetheless, however autonomous, the males have not honed themselves to Darwinian optimality, for they have evolved no mechanism for excluding other males from subsequent attachment. Several males are often embedded into a single female.

(While criticizing the exaggeration of some popular accounts, allow me a tangential excursion to express a pet peeve. I relied upon primary, technical literature for all my descriptions, but I began by reading several popular renditions. All versions written for nonscientists speak of fused males as the curious tale of *the* anglerfish—-just as we so often hear about *the* monkey swinging through trees, or *the* worm burrowing through soil. But if nature teaches any lesson, it loudly proclaims life's diversity. There ain't no such abstraction as *the* clam, *the* fly, or *the* anglerfish. Ceratioid anglerfishes come in nearly 100 species, and each has its own peculiarity. Fused males have not evolved in all species. In some, males attach temporarily, presumably at times of spawning, but never fuse. In others, some males fuse and others become sexually mature while retaining their bodily independence. In still others, fusion is obligatory. In one species of obligate fusers, no sexually mature female has ever been found without an attached male—and the stimulus provided by male hormones may be a prerequisite for maturation.

These obligate fusers have become the paradigm for popular descriptions of *the* anglerfish, but they do not represent the majority of ceratioid species. I grouse because these meaningless abstractions convey seriously false impressions about nature. They greatly exaggerate nature's discontinuities by focusing on extreme forms as false paradigms for an entire group, and rarely mentioning the structurally intermediate species that often live happily and abundantly. If all fishes either had totally independent or completely fused males, then how could we even imagine an evolutionary transition to the peculiar sexual system of *the* anglerfish? But the abundance of structurally intermediate stages—temporary attachment or fusion of some males only—conveys an evolutionary message. These modern structural intermediates are not, of course, actual ancestors of fully fused species, but they do sketch an evolutionary pathway —-just as Darwin studied the simple eyes of worms and scallops to learn how a structure so complex and apparently perfect as the vertebrate eye might evolve through a chain of intermediate forms. In any case, bursting diversity is nature's watchword; it should never be submerged by careless abstraction.)

Ceratioid males embark upon their peculiar course early in life. As larvae, they feed normally and live independently. After a period of rapid change, or metamorphosis, males in species destined for fusion do not develop their alimentary canals any further, and never feed again. Their ordinary teeth disappear, and they retain and exaggerate only a few fused teeth at the tips of their mouth—useless in feeding, but well adapted for piercing and holding tight to a female. They become sleek and more streamlined, with a pointed head, compressed body, and strong, propulsive tail fin—in short, a sort of sexual torpedo.

But how do they find females, those tiny dots of connubial matter in the midst of an endless ocean? Most species must use olfactory cues, a system often exquisitely developed in fishes, as in homing salmon that smell out their natal stream. These ceratioid males develop gigantic nostrils after metamorphosis; relative to body size, some ceratioids have larger nasal organs than any other vertebrate. Another family of ceratioids fails to develop large nostrils, but these males have enormously enlarged eyes, and they must search for the ghostly light of fishing females (each species has a different pattern of illumination, and males probably recognize their proper females). The system is not entirely fail-safe, as ichthyologist Ted Pietsch recently found a male of one species attached to a female of a different species—a fatal mistake in evolutionary terms (although the two fish had not fused and might later have separated had not zealous science found and preserved them *in flagrante delicto).*

As I sit here wiggling my toes and flexing my fingers in glorious independence (and with a full one-inch advantage over my wife), I am tempted (but must resist) to apply the standards of my own cherished independence and to pity the poor fused male. It may not be much of a life in our terms, but it keeps several species of anglerfishes going in a strange and difficult environment. And who can judge anyway? In some ultimate Freudian sense, what male could resist the fantasy of life as a penis with a heart, deeply and permanently embedded within a caring and providing female? These anglerfishes represent, in any case, only the extreme expression of nature's more common pattern—smaller males pursuing an evolutionary role as sources of sperm. Do they not, therefore, teach us a generality by their very exaggeration of it? We human males are the oddballs.

I therefore take my leave of fused anglerfishes with a certain sense of awe. Have they not discovered and irrevocably established for themselves what, according to Shakespeare, "every wise man's son doth know"—"journeys end in lovers meeting"?

Nonmoral Nature

WHEN THE Right Honorable and Reverend Francis Henry, earl of Bridgewater, died in February, 1829, he left £8,000 to support a series of books "on the power, wisdom and goodness of God, as manifested in the creation." William Buckland, England's first official academic geologist and later dean of Westminster, was invited to compose one of the nine Bridgewater Treatises. In it he discussed the most pressing problem of natural theology: if God is benevolent and the Creation displays his "power, wisdom and goodness," then why are we surrounded with pain, suffering, and apparently senseless cruelty in the animal world?

Buckland considered the depredation of "carnivorous races" as the primary challenge to an idealized world where the lion might dwell with the lamb. He resolved the issue to his satisfaction by arguing that carnivores actually increase "the aggregate of animal enjoyment" and "diminish that of pain." Death, after all, is swift and relatively painless, victims are spared the ravages of decrepitude and senility, and populations do not outrun their food supply to the greater sorrow of all. God knew what he was doing when he made lions. Buckland concluded in hardly concealed rapture:

> The appointment of death by the agency of carnivora, as the ordinary termination of animal existence, ap-

> pears therefore in its main results to be a dispensation of benevolence; it deducts much from the aggregate amount of the pain of universal death; it abridges, and almost annihilates, throughout the brute creation, the misery of disease, and accidental injuries, and lingering decay; and imposes such salutary restraint upon excessive increase of numbers, that the supply of food maintains perpetually a due ratio to the demand. The result is, that the surface of the land and depths of the waters are ever crowded with myriads of animated beings, the pleasures of whose life are coextensive with its duration; and which throughout the little day of existence that is allotted to them, fulfill with joy the functions for which they were created.

We may find a certain amusing charm in Buckland's vision today, but such arguments did begin to address "the problem of evil" for many of Buckland's contemporaries—how could a benevolent God create such a world of carnage and bloodshed? Yet this argument could not abolish the problem of evil entirely, for nature includes many phenomena far more horrible in our eyes than simple predation. I suspect that nothing evokes greater disgust in most of us than slow destruction of a host by an internal parasite—gradual ingestion, bit by bit, from the inside. In no other way can I explain why ***Alien,*** an uninspired, grade-C, formula horror film, should have won such a following. That single scene of Mr. Alien, popping forth as a baby parasite from the body of a human host, was both sickening and stunning. Our nineteenth-century forebears maintained similar feelings. The greatest challenge to their concept of a benevolent deity was not simple predation—but slow death by parasitic ingestion. The classic case, treated at length by all great naturalists, invoked the so-called ichneumon fly. Buckland had sidestepped the major issue.

The "ichneumon fly," which provoked such concern among natural theologians, was actually a composite creature representing the habits of an enormous tribe. The Ichneumonoidea are a group of wasps, not flies, that in-elude more species than all the vertebrates combined (wasps, with ants and bees, constitute the order Hymenoptera; flies, with their two wings—wasps have four—form the order Diptera). In addition, many non-ichneumonid wasps of similar habits were often cited for the same grisly details. Thus, the famous story did not merely implicate a single aberrant species (perhaps a perverse leakage from Satan's realm), but hundreds of thousands—a large chunk of what could only be God's creation.

The ichneumons, like most wasps, generally live freely as adults but pass their larval life as parasites feeding on the bodies of other animals, almost invariably members of their own phylum, the Arthropoda. The most common victims are caterpillars (butterfly and moth larvae), but some ichneumons prefer aphids and others attack spiders. Most hosts are parasitized as larvae, but some adults are attacked, and many tiny ichneumons inject their brood directly into the egg of their host.

The free-flying females locate an appropriate host and then convert it to a food factory for their own young. Parasitologists speak of ectoparasitism when the uninvited guest lives on the surface of its host, and endoparasitism when the parasite dwells within. Among endoparasitic ichneumons, adult females pierce the host with their ovipositor and deposit eggs within. (The ovipositor, a thin tube extending backward from the wasp's rear end, may be many times as long as the body itself.) Usually, the host is not otherwise inconvenienced for the moment, at least until the eggs hatch and the ichneumon larvae begin their grim work of interior excavation.

Among ectoparasites, however, many females lay their eggs directly upon the host's body. Since an active host would easily dislodge the egg, the ichneumon mother often simultaneously injects a toxin that paralyzes the caterpillar or other victim. The paralysis may be permanent, and the caterpillar lies, alive but immobile, with the agent of its future destruction secure on its belly. The egg hatches, the helpless caterpillar twitches, the wasp larva pierces and begins its grisly feast.

Since a dead and decaying caterpillar will do the wasp larva no good, it eats in a pattern that cannot help but recall, in our inappropriate, anthropocentric interpretation, the ancient English penalty for treason—drawing and quartering, with its explicit object of extracting as much torment as possible by keeping the victim alive and sentient. As the king's executioner drew out and burned his client's entrails, so does the ichneumon larva eat fat bodies and digestive organs first, keeping the caterpillar alive by preserving intact the essential heart and central nervous system. Finally, the larva completes its work and kills its victim, leaving behind the caterpillar's empty shell. Is it any wonder that ichneumons, not snakes or lions, stood as the paramount challenge to God's benevolence during the heyday of natural theology?

As I read through the nineteenth- and twentieth-century literature on ichneumons, nothing amused me more than the tension between an intellectual knowledge that wasps should not be described in human terms and a literary or emotional inability to avoid the familiar categories of epic and narrative, pain and destruction, victim and vanquisher. We seem to be caught in the mythic structures of our own cultural sagas, quite unable, even in our basic descriptions, to use any other language than the metaphors of battle and conquest. We cannot render this corner of natural history as anything but story, combining the themes of grim horror and fascination and usually ending not so much with pity for the caterpillar as with admiration for the efficiency of the ichneumon.

I detect two basic themes in most epic descriptions: the struggles of prey and the ruthless efficiency of parasites. Although we acknowledge that we may be witnessing little more than automatic instinct or physiological reaction, still we describe the defenses of hosts as though they represented conscious struggles. Thus, aphids kick and caterpillars may wriggle violently as wasps attempt to insert their ovipositors. The pupa of the tortoiseshell butterfly (usually considered an inert creature silently awaiting its conversion from duckling to swan) may contort its abdominal region so sharply that attacking wasps are thrown into the air. The caterpillars of *Hapalia,* when attacked by the wasp *Apanteles machaeralis,* drop suddenly from their leaves and suspend themselves in air by a silken thread. But the wasp may run down the thread and insert its eggs nonetheless. Some hosts can encapsulate the injected egg with blood cells that aggregate and harden, thus suffocating the parasite.

J. H. Fabre, the great nineteenth-century French entomologist, who remains to this day the preeminently literate natural historian of insects, made a special study of parasitic wasps and wrote with an unabashed anthropocentrism about the struggles of paralyzed victims (see his books *Insect Life* and *The Wonders of Instinct).* He describes some imperfectly paralyzed caterpillars that struggle so violently every time a parasite approaches that the wasp larvae must feed with unusual caution. They attach themselves to a silken strand from the roof of their burrow and descend upon a safe and exposed part of the caterpillar:

> The grub is at dinner: head downwards, it is digging into the limp belly of one of the caterpillars. ... At the least sign of danger in the heap of caterpillars, the larva retreats . . . and climbs back to the ceiling, where the swarming rabble cannot reach it. When peace is restored, it slides down [its silken cord] and returns to table, with its head over the viands and its rear upturned and ready to withdraw in case of need.

In another chapter, he describes the fate of a paralyzed cricket:

> One may see the cricket, bitten to the quick, vainly move its antennae and abdominal styles, open and close its emptyjaws, and even move a foot, but the larva is safe and searches its vitals with impunity. What an awful nightmare for the paralyzed cricket!

Fabre even learned to feed paralyzed victims by placing a syrup of sugar and water on their mouthparts—thus showing that they remained alive, sentient, and (by implication) grateful for any palliation of their inevitable fate. If Jesus, immobile and thirsting on the cross, received only vinegar from his tormentors, Fabre at least could make an ending bittersweet.

The second theme, ruthless efficiency of the parasites, leads to the opposite conclusion—grudging admiration for the victors. We learn of their skill in capturing dangerous hosts often many times larger than themselves. Caterpillars may be easy game, but psammocharid wasps prefer spiders. They must insert their ovipositors in a safe and precise spot. Some leave a paralyzed spider in its own burrow. *Planiceps hirsutus,* for example, parasitizes a California trapdoor spider. It searches for spider tubes on sand dunes, then digs into nearby sand to disturb the spider's home and drive it out. When the spider emerges, the wasp attacks, paralyzes its victim, drags it back into its own tube, shuts and fastens the trapdoor, and deposits a single egg upon the spider's abdomen. Other psammocharids will drag a heavy spider back to a previously prepared cluster of clay or mud cells. Some amputate a spider's legs to make the passage easier. Others fly back over water, skimming a buoyant spider along the surface.

Some wasps must battle with other parasites over a host's body. *Rhyssella curvipes* can detect the larvae of wood wasps deep within alder wood and drill down to a potential victim with its sharply ridged ovipositor. *Pseudorhyssa alpestris,* a related parasite, cannot drill directly into wood since its slender ovipositor bears only rudimentary cutting ridges. It locates the holes made by *Rhyssella,* inserts its ovipositor, and lays an egg on the host (already conveniently paralyzed by *Rhyssella),* right next to the egg deposited by its relative. The two eggs hatch at about the same time, but the larva of *Pseudorhyssa* has a bigger head bearing much larger mandibles. *Pseudorhyssa* seizes the smaller *Rhyssella* larva, destroys it, and proceeds to feast upon a banquet already well prepared.

Other praises for the efficiency of mothers invoke the themes of early, quick, and often. Many ichneumons don't even wait for their hosts to develop into larvae, but parasitize the egg directly (larval wasps may then either drain the egg itself or enter the developing host larva). Others simply move fast. *Apanteles militaris* can deposit up to seventy-two eggs in a single second. Still others are doggedly persistent. *Aphidius gomezi* females produce up to 1,500 eggs and can parasitize as many as 600 aphids in a single working day. In a bizarre twist upon "often," some wasps indulge in polyembryony, a kind of iterated supertwining. A single egg divides into cells that aggregate into as many as 500 individuals. Since some polyembryonic wasps parasitize caterpillars much larger than themselves and may lay up to six eggs in each, as many as 3,000 larvae may develop within, and feed upon a single host. These wasps are endoparasites and do not paralyze their victims. The caterpillars writhe back and forth, not (one suspects) from pain, but merely in response to the commotion induced by thousands of wasp larvae feeding within.

Maternal efficiency is often matched by larval aptitude. I have already mentioned the pattern of eating less essential parts first, thus keeping the host alive and fresh to its final and merciful dispatch. After the larva digests every edible morsel of its victim (if only to prevent later fouling of its abode by decaying tissue), it may still use the outer shell of its host. One aphid parasite cuts a hole in the bottom of its victim's shell, glues the skeleton to a leaf by sticky secretions from its salivary gland, and then spins a cocoon to pupate within the aphid's shell.

In using inappropriate anthropocentric language for this romp through the natural history of ichneumons, I have tried to emphasize just why these wasps became a preeminent challenge to natural theology—the antiquated doctrine that attempted to infer God's essence from the products of his creation. I have used twentieth-century examples for the most part, but all themes were known and stressed by the great nineteenth-century natural theologians. How then did they square the habits of these wasps with the goodness of God? How did they extract themselves from this dilemma of their own making?

The strategies were as varied as the practitioners; they shared only the theme of special pleading for an a priori doctrine—our naturalists *knew* that God's benevolence was lurking somewhere behind all these tales of apparent horror. Charles Lyell, for example, in the first edition of his epochal *Principles of Geology* (1830-1833), decided that caterpillars posed such a threat to vegetation that any natural checks upon them could only reflect well upon a creating deity, for caterpillars would destroy human agriculture "did not Providence put causes in operation to keep them in due bounds."

The Reverend William Kirby, rector of Barham, and Britain's foremost entomologist, chose to ignore the plight of caterpillars and focused instead upon the virtue of mother love displayed by wasps in provisioning their young with such care.

> The great object of the female is to discover a proper nidus for her eggs. In search of this she is in constant motion. Is the caterpillar of a butterfly or moth the appropriate food for her young? You see her alight upon the plants where they are most usually to be met with, run quickly over them, carefully examining every leaf, and, having found the unfortunate object of her search, insert her sting into its flesh, and there deposit an egg. . . . The active Ichneumon braves every danger, and does not desist until her courage and address have insured subsistence for one of her future progeny.

Kirby found this solicitude all the more remarkable because the female wasp will never see her child and enjoy the pleasures of parenthood. Yet love compels her to danger nonetheless:

> A very large proportion of them are doomed to die before their young come into existence. But in these the passion is not extinguished. . . . When you witness

> the solicitude with which they provide for the security and sustenance of their future young, you can scarcely deny to them love for a progeny they are never destined to behold.

Kirby also put in a good word for the marauding larvae, praising them for their forbearance in eating selectively to keep their caterpillar alive. Would we all husband our resources with such care!

> In this strange and apparently cruel operation one circumstance is truly remarkable. The larva of the Ichneumon, though every day, perhaps for months, it gnaws the inside of the caterpillar, and though at last it has devoured almost every part of it except the skin and intestines, carefully all this time it avoids injuring the vital organs, as if aware that its own existence depends on that of the insect upon which it preys! . . . What would be the impression which a similar instance amongst the race of quadrupeds would make upon us? If, for example, an animal . . . should be found to feed upon the inside of a dog, devouring only those parts not essential to life, while it cautiously left uninjured the heart, arteries, lungs, and intestines,—should we not regard such an instance as a perfect prodigy, as an example of instinctive forbearance almost miraculous? [The last three quotes come from the 1856, and last pre-Darwinian, edition of Kirby and Spence's *Introduction to Entomology.*]

This tradition of attempting to read moral meaning from nature did not cease with the triumph of evolutionary theory in 1859—for evolution could be read as God's chosen method of peopling our planet, and ethical messages might still populate nature. Thus, St. George Mivart, one of Darwin's most effective evolutionary critics and a devout Catholic, argued that "many amiable and excellent people" had been misled by the apparent suffering of animals for two reasons. First, whatever the pain, "physical suffering and moral evil are simply incommensurable." Since beasts are not moral agents, their feelings cannot bear any ethical message. But secondly, lest our visceral sensitivities still be aroused, Mivart assures us that animals must feel little, if any, pain. Using a favorite racist argument of the time—that "primitive" people suffer far less than advanced and cultured folk—Mivart extrapolated further down the ladder of life into a realm of very limited pain indeed: Physical suffering, he argued,

> depends greatly upon the mental condition of the sufferer. Only during consciousness does it exist, and only in the most highly organized men does it reach its acme. The author has been assured that lower races of men appear less keenly sensitive to physical suffering than do more cultivated and refined human beings. Thus only in man can there really be any intense degree of suffering, because only in him is there that intellectual recollection of past moments and that anticipation of future ones, which constitute in great part the bitterness of suffering. The momentary pang, the present pain, which beasts endure, though real enough, is yet, doubtless, not to be compared as to its intensity with the suffering which is produced in man through his high prerogative of self-consciousness [from *Genesis of Species,* 1871].

It took Darwin himself to derail this ancient tradition—and he proceeded in the gentle way so characteristic of his radical intellectual approach to nearly everything. The ichneumons also troubled Darwin greatly and he wrote of them to Asa Gray in 1860:

> I own that I cannot see as plainly as others do, and as I should wish to do, evidence of design and beneficence on all sides of us. There seems to me too much misery in the world. I cannot persuade myself that a beneficent

> and omnipotent God would have designedly created the Ichneumonidae with the express intention of their feeding within the living bodies of Caterpillars, or that a cat should play with mice.

Indeed, he had written with more passion to Joseph Hooker in 1856: "What a book a devil's chaplain might write on the clumsy, wasteful, blundering, low, and horribly cruel works of nature!"

This honest admission—that nature is often (by our standards) cruel and that all previous attempts to find a lurking goodness behind everything represent just so much special pleading—can lead in two directions. One might retain the principle that nature holds moral messages, but reverse the usual perspective and claim that morality consists in understanding the ways of nature and doing the opposite. Thomas Henry Huxley advanced this argument in his famous essay on *Evolution and Ethics* (1893):

> The practice of that which is ethically best—what we call goodness or virtue—involves a course of conduct which, in all respects, is opposed to that which leads to success in the cosmic struggle for existence. In place of ruthless self-assertion it demands self-restraint; in place of thrusting aside, or treading down, all competitors, it requires that the individual shall not merely respect, but shall help his fellows. ... It repudiates the gladiatorial theory of existence. . . . Laws and moral precepts are directed to the end of curbing the cosmic process.

The other argument, radical in Darwin's day but more familiar now, holds that nature simply is as we find it. Our failure to discern a universal good does not record any lack of insight or ingenuity, but merely demonstrates that nature contains no moral messages framed in human terms. Morality is a subject for philosophers, theologians, students of the humanities, indeed for all thinking people. The answers will not be read passively from nature; they do not, and cannot, arise from the data of science. The factual state of the world does not teach us how we, with our powers for good and evil, should alter or preserve it in the most ethical manner.

Darwin himself tended toward this view, although he could not, as a man of his time, thoroughly abandon the idea that laws of nature might reflect some higher purpose. He clearly recognized that specific manifestations of those laws—cats playing with mice, and ichneumon larvae eating caterpillars'—could not embody ethical messages, but he somehow hoped that unknown higher laws might exist "with the details, whether good or bad, left to the working out of what we may call chance."

Since ichneumons are a detail, and since natural selection is a law regulating details, the answer to the ancient dilemma of why such cruelty (in our terms) exists in nature can only be that there isn't any answer—and that framing the question "in our terms" is thoroughly inappropriate in a natural world neither made for us nor ruled by us. It just plain happens. It is a strategy that works for ichneumons and that natural selection has programmed into their behavioral repertoire. Caterpillars are not suffering to teach us something; they have simply been outmaneuvered, for now, in the evolutionary game. Perhaps they will evolve a set of adequate defenses sometime in the future, thus sealing the fate of ichneumons. And perhaps, indeed probably, they will not.

Another Huxley, Thomas's grandson Julian, spoke for this position, using as an example—yes, you guessed it—the ubiquitous ichneumons:

> Natural selection, in fact, though like the mills of God in grinding slowly and grinding small, has few other attributes that a civilized religion would call divine. . . . Its products are just as likely to be aesthetically, morally, or intellectually repulsive to us as they are to be attractive. We need only think of the ugliness of *Saaulina* or a bladder-worm, the stupidity of a rhinoceros or a stego-

> saur, the horror of a female mantis devouring its mate or a brood of ichneumon flies slowly eating out a caterpillar.

If nature is nonmoral, then evolution cannot teach any ethical theory at all. The assumption that it can has abetted a panoply of social evils that ideologues falsely read into nature from their beliefs—eugenics and (misnamed) social Darwinism prominently among them. Not only did Darwin eschew any attempt to discover an antireligious ethic in nature, he also expressly stated his personal bewilderment about such deep issues as the problem of evil. Just a few sentences after invoking the ichneumons, and in words that express both the modesty of this splendid man and the compatibility, through lack of contact, between science and true religion, Darwin wrote to Asa Gray,

> I feel most deeply that the whole subject is too profound for the human intellect. A dog might as well speculate on the mind of Newton. Let each man hope and believe what he can.

Postscript

Michele Aldrich sent an even better literary reference than any I had found. Mark Twain, in a biting bit of satire called "Little Bessie Would Assist Providence," chronicles a conversation of mother and daughter—daughter insisting that a benevolent God would not have given her little friend "Billy Norris the typhus" and visited other unjust disasters upon decent people, mother assuring her that there must be a good reason for it all. Bessie's last rejoinder, which summarily ends the essay as you shall see, invokes our old friends, the ichneumons:

> Mr. Hollister says the wasps catch spiders and cram them down into their nests in the ground—alive, mama!—and there they live and suffer days and days

> and days, and the hungry little wasps chewing their legs and gnawing into their bellies all the time, to make them good and religious and praise God for His infinite mercies. I think Mr. Hollister is just lovely, and ever so kind; for when I asked him if he would treat a spider like that he said he hoped to be damned if he would; and then he—Dear mama, have you fainted!

James W. Tuttleton, chairman of the English department at New York University, sent me a stunning poem by Robert Frost that seems designed as a commentary upon Darwin's last statement that chance may regulate in the small, even if purpose might be found in the large. Or do we even see true purpose in the large? The poem is called, simply, "Design":

I found a dimpled spider, fat and white,
On a white heal-all, holding up a moth
Like a white piece of rigid satin cloth—
Assorted characters of death and blight
Mixed ready to begin the morning right,
Like the ingredients of a witches' broth—
A snow-drop spider, a flower like a froth,
And dead wings carried like a paper kite.

What had that flower to do with being white,
The wayside blue and innocent heal-all?
What brought the kindred spider to that height,
Then steered the white moth thither in the night?
What but design of darkness to appall?—
If design govern in a thing so small.

I was so struck by the image of the spider as a drop, the flower as a froth, the moth as a pair of two-dimensional wings. Forms so unlike, yet all white and all brought together in one spot for destruction. Why? Or, as we read the last two lines, may we even ask such a question? I think that we cannot, and I regard this insight as the most liberating theme of Darwin's revolution.

Quick Lives and Quirky Changes

POSTHUMOUS TRIUMPH IS HOLLOW, however abstractly rewarding. Nanki-Poo refused Ko-Ko's inducement to undergo a ceremonious public beheading rather than a private suicide: "There'll be a procession—bands—dead march—bells tolling . . . then, when it's all over, general rejoicings, and a display of fireworks in the evening. You won't see them, but they'll be there all the same." And I never could figure out why America's premier nineteenth-century anthropologists J. W. Powell and WJ McGee made a bet about who had the larger brain—to be settled by autopsy when the joy of victory could no longer be savored.

Nonetheless, I just made a dumb bet with a female jogging enthusiast: that no woman would win the Boston marathon in my lifetime. I'd rather lose, but expect I won't. Still, if superior average speed of running males is among the few insignificant but genuinely biological differences between human sexes, I can only respond to charges of gloating (for the abstraction I represent, but not, alas, for me and my huffing eight-minute miles) with a statement of genuine regret; how gladly would I trade this useless advantage for the most precious benefit of being female—several extra years of average life.

I do not know whether shorter male life is a generality in nature—and whether we should therefore add to smaller average size (see essay 1) another biological strike against machismo—but I just learned (with thanks to Martin L. Adamson) about an instructive extreme case.

In 1962, James H. Oliver Jr. traced the life cycle of a mite that parasitizes the cocoons of earthworms. Both males and females of *Histiostoma murchiei* pass through an egg and three juvenile stages before molting into an adult. In addition, the female intercalates one additional stage—euphoniously named the hypopus—between the second and third pre-adult phases. Females develop at a leisurely pace for such a small creature. Discounting the hypopus, the passage from egg to adult, through stages held in common with males, takes one to three weeks. The additional hypopus may extend female life greatly—for these mites find and infest other cocoons only during the hypopal stage (males always stay at home). The hypopus may, first of all, remain dormant for long periods within the skin of the previous juvenile stage, awaiting (so to speak) favorable conditions for emergence and movement to another cocoon. When the hypopus does emerge, it may then live for a long time, moving about in its own cocoon (and sometimes becoming dormant again) or moving out in search of a new home.

Males, by contrast, race through the same stages (minus the hypopus) with a celerity that should inspire Bill Rodgcrs as he trudges up Heartbreak Hill next Patriot's Day. "Adult males," Oliver writes, "have been observed copulating with their mother within 3 to 4 days after being laid as eggs"—and they die soon after this bout of incestuous joy. Why this outstanding difference in life-span between the sexes? And what has it to do with the Oedipal habits of these mites? A further look at the unusual reproductive biology of these parasites seems to provide the answer.

When a hypopus finds a new cocoon, it lays two to nine eggs within two days after molting into an adult—and without benefit of fertilization. All these eggs develop into males—the only source of potential husbands as well. What better evolutionary rationale for rapid male development could we hope to find? The females of most species must seek their husbands. These mites make them from scratch and then wait. Males of *Histiostoma murchiei* are little more than sources of sperm; the sooner they can perform, the better.

Two days after its incestuous mating, the female begins to lay eggs again and may continue for two to five days, producing as many as 500 offspring—all female this time.

In solving one problem—the differential speed of development between sexes—we have only encountered a more curious question: how can this system work in the first place; how can an unmated female, alone in a new cocoon, produce a generation of husbands, and why are the offspring of her next reproductive bout all female?

The answer to this broader question lies in the unfamiliar style of sex determination in these mites. In most animals, both males and females have paired chromosomes, and the status of one pair determines the sex of its bearer. Human females, for example, have two large sex chromosomes (designated XX), while males have one large (X) and one small (Y) chromosome in their determining pair. All unfertilized egg cells carry a single X, while sperm carry either an X or a Y. We each owe our sex to the good fortune of one sperm among the millions per ejaculate. Animals with paired chromosomes in both sexes are called diploid.

Some animals use a different system of sex determination. Females are diploid, but males have only one chromosome for each female pair and are called haploid (for half the diploid number). Males, in other words—and ironic as this may seem—develop from unfertilized eggs and have no fathers. Fertilized eggs produce diploid females. Animals using this system are called haplodiploid (because males are haploid and females diploid).

Histiostoma murchiei is haplodiploid. Hence, the unmated female in a new cocoon raises a generation of males from unfertilized eggs, and a subsequent generation of females from the resulting incest.

Haplodiploidy, a fascinating phenomenon rich in implication, has circulated through these essays in various contexts for years. It helped to explain the origin of social systems in ants and bees (see essay 33 in *Ever Since Darwin),* and it underlay the habits of a male mite who fertilizes several sisters within his mother's body, and dies before "birth" (essay 6 in *The Panda's Thumb).* It also circulates widely through the animal kingdom. Haplodiploid species have been found in rotifers, nematodes, mites, and in four separate orders of insects—the Thysanoptera (thrips), the Homoptera (aphids, cicadas, and their allies), the Coleoptera (beetles), and the Hymenoptera (ants, bees, and wasps). These groups are not closely related and their presumed common ancestors are diploid. Thus, haplodiploidy has arisen independently—and often many times—within each group. Although most of these groups contain only a few haplodiploid species amidst a host of ordinary diploids, the Hymenoptera, with more than 100,000 named species, are exclusively haplodiploid. Since vertebrates only include some 50,000 species, as Oliver reminds us, our chauvinistic impression that haplodiploidy is curious or rare should also be revised. At least 10 percent of all named animal species are haplodiploid.

Within the last decade, haplodiploidy has figured most prominently in the news (both general and scientific) for its role in an ingenious Darwinian explanation of an old biological mystery—the origin of sociality in Hymenoptera, particularly the existence of sterile "worker" castes, invariably female, in ants and bees. Since sociality evolved several times within the Hymenoptera, the invariant system of sterile female castes demands a general explanation. The larger problem is even more puzzling: why, in a presumably Darwinian world filled with organisms acting only for their personal reproductive success, should large numbers of females "forego" their own reproduction to help their mother (the queen) raise more sisters?

The ingenious explanation relies upon the peculiar asymmetries of genetic relationship between sexes in haplodiploid animals. In both diploids and haplodiploids, mothers pass half their genetic material (one set of chromosomes in each egg cell) to each offspring. They are therefore equally related (by half of their genetic selves) to both sons and daughters. A female in diploid species also shares approximately half her genes with both brothers and sisters. But a female in haplodiploid species shares three-quarters of her genes with sisters and only one-quarter with brothers for the following reason: Consider any gene (one copy on a single chromosome) in sisters. What is the probability that a brother will share it? If the gene is on a paternal chromosome, then the brother has zero probability of sharing it, for he has no paternal chromosomes. If the gene is on a maternal chromosome, then he has a 50 percent chance of sharing it with his sister—because he either received the same chromosome from his mother, or the other member of the pair. Thus, summing over all genes, the relationship between brother and sister is the average between zero (for paternal genes of sisters, necessarily absent in brothers) and 50 percent (for maternal genes)—or 25 percent.

What then is the probability that a sister will share the same gene? If it is a paternal gene, the sister must share it since fathers have only one set of chromosomes and they pass their entire genetic program to each daughter. If it is a maternal gene, the chance is 50 percent by the same argument advanced for brothers. The total relationship between sisters is therefore the average between 100 percent (for paternal genes) and 50 percent (for maternal genes)—or 75 percent.

Females are therefore more closely related to their sisters (by three-quarters) than either to their mothers (by one-half) or to their own potential offspring (also by one-half). If the Darwinian imperative leads organisms to maximize the numbers of their own genes in future generations, then females will do better by helping their mother raise sisters (as sterile workers do) than by producing their own offspring. Thus, the asymmetry of genetic relationship in haplodiploids may explain both why worker castes of social Hymenoptera are invariably female, and why sociality in this style has evolved many times among the Hymenoptera, but not among the much larger array of diploid organisms. (As always, our complex world provides an exception—the diploid termites, relatives of cockroaches, who at least include both males and females in their worker castes.)

This explanation of an old mystery has so intrigued biologists that a subtle reversal of causality has crept into some accounts. The very existence of haplodiploidy is linked with force and elegance to the evolution of sociality, and we are almost led to believe that this mode of sex determination arose "for," or at least in the context of, the marvelous social organization of ants and bees. Yet a moment's explicit reflection assures us that this cannot be so, for two reasons.

First, *all* hymenopterans are haplodiploid, but only a few lineages within the group have developed complex social systems (most hymenopterans are asocial or minimally social wasps). The common ancestor of living hymenopterans must have been haplodiploid, but it was certainly not fully social, since the complex society of highly derived bees and ants has evolved as a phyletic afterthought in several independent lineages. Causality must run in the other direction. Haplodiploidy does not exist "for" sociality unless the future can control the past. Rather, haplodiploidy arose for other reasons and then permitted, by good and unplanned fortune, the later evolution of this wonderfully complex and successful mode of sociality. But what other reasons?—which brings me, finally, to the point of this essay, to the main reason for my fascination with *Histiostoma murchiei,* and, more immediately, to the second item.

Second, when we consider the usual ecological context of haplodiploidy in a broad range of animals that may have evolved it directly (and not merely co-opted it for another use), an interesting pattern emerges. *Histiostoma murchiei* shares a mode of life with the mites that die before birth, and with many other haplodiploid animals in distantly related groups: all are "colonizers," species that survive by seeking rare but rich resources and then reproducing as fast as they can when uncommon fortune rewards their search (the vast majority of *Histiostoma*'s hypopi die before finding a fresh earthworm cocoon). Haplodiploidy provides several advantages in this chancy approach to survival. Successful colonization does not require two separate migrations of a male and a female, or even that a single migrating female be fertilized before her search for a new resource begins. Any unmated female, even a juvenile, becomes a potential source of new colonies, since she can make a generation of males all by herself and then mate with them to begin a generation of females—the strategy evolved by *Histiostoma.*

When colonizers find a rich but ephemeral resource, haplodiploidy may enhance the speed of raising new generations by permitting fertilized females to control the sex ratio of their offspring. As I argued in my essay on "death before birth" (see *The Panda's Thumb),* when brothers mate with sisters, more offspring will populate the next generation if mothers can put most of their limited reproductive energy into making females and produce only a minimal number of males (one will often do). One male may fertilize many females, and the available number of eggs, not sperm, limits the reproductive rate of a population—so why make vast numbers of superfluous males. The principle is fine in theory, but most animals cannot easily control the sex ratio of their offspring. Despite prayers and entreaties for boys in many sexist human societies, girls continue to assert their birthright (and birth rate) of nearly 50 percent.

But many haplodiploids can control the sex ratio of their offspring. If females store sperm within their bodies after mating, any eggs that bypass the storage area become males, while those that contact it become females. Haplodiploid mites with highly unequal sex ratios often produce a brood of female eggs and then shut off the sperm supply to add a male or two right at the end.

This complex of associated features—a colonizing life style, rare and ephemeral resources, rapid reproduction, and ease of rearing new generations in strange places—seems to define the original context of advantage for haplodiploidy. If we assume, as a hypothesis only, that haplodiploidy usually arises as an adaptation for life in this uncertain world, then it must be interpreted as a lucky accident with respect to its later utility in the evolution of sociality in ants and bees.

Now what could be more different, in our usual biological thinking, than the chancy life of a solitary female colonizer (whose offspring can hardly become social on a resource that doesn't last more than a generation or two), and the complexity, stability, and organization of ant and bee societies. Is it not peculiar in the extreme that haplodiploidy, a virtual prerequisite for the evolution of hymenopteran societies, probably first evolved as an adaptation for a life style almost diametrically opposed (at least in its metaphorical implications)? If I can convince you that it is not peculiar at all, but an example of a basic principle that distinguishes evolutionary biology from a common stereotype about science in general, then this essay has succeeded.

It is a clear, though lamentably common, error to assume that the current utility of a feature-permits an inference about the reasons for its evolutionary origin. Current utility and historical origin are different subjects. Any feature, regardless of how or why it first evolved, becomes available for co-optation to other roles, often strikingly different. Complex features are bursting with potentialities; their conceivable use is not confined to their original function (I confess that I have used a credit card to force a door). And these evolutionary shifts in function can be as quirky and unpredictable as the potentials of complexity are vast. It happens all the time; it virtually defines the wondrous indefiniteness of evolution.

The balancing fins of fish became the propulsive limbs of terrestrial vertebrates, while the propulsive tail became an organ that often aids in balance. The bone that suspended an ancestral fish's upper jaw to its cranium became the bone that transmits sound to the ears of reptiles. Two bones that articulated the jaws of that reptile then became the other two sound-transmitting bones of the mammalian middle ear. When we see how beautifully our hammer, anvil, and stirrup function in hearing, who would imagine that one bone once suspended jaw to cranium, while two others articulated the jaws. (By the way, before jaws even evolved, all these bones supported the gill arches of an ancestral jawless fish.) And a mode of sex determination that may first have aided a lonely female colonizer apparently became the basis of social systems rivaled only by our own in complexity.

As we probe deeper and further back, the unpredictabilities mount. I discussed the quirkiness of a functional shift toward support of sociality by a sexual system which probably evolved as an aid to colonization. But what about the larger reason for our imperfect and unpredictable world: structural limits imposed by features evolved for other reasons? Social systems, like those of ants and bees, might be of enormous advantage to hosts of other creatures. But they do not evolve largely because it is so difficult to get them started in diploid organisms (only termites have succeeded), while haplodiploid hymenopterans develop them again and again. And going one step further back (I promise to stop here), what about constraints on the evolution of haplodiploidy itself. Haplodiploidy might be a wonderful adaptation to a host of ecologies, but it cannot always be easily evolved.

Assuming that haplodiploids generally arise from diploids, what does it take to turn a haploid creature into a male- Under some systems of diploid sex determination, male haploids cannot easily evolve. A haploid human would not be male, for a single X chromosome induces the development of a sterile female. But other diploids have a so-called XX-XO system of sex determination, where females have two X chromosomes and males have a single X with no accompanying Y (but all other chromosomes in pairs). In such systems, a haploid organism might develop easily and directly into a male. (The XX-XO system is not a prerequisite for haplodiploidy, since more complex modifications can produce male haploids from other modes of diploid sex determination.)

In short, modes of sex determination limit haplodiploidy, haplodiploidy limits sociality, and sociality requires a quirky shift in the adaptive significance of haplodiploidy. What order can we find in evolution amidst such a crazy-quilt of limits to a sensibly perfect and predictable world?

Some might be tempted to read an almost mystical message into this theme—that evolution imposes an ineffable unknowability upon nature. I would strongly reject such an implication: knowledge and prediction are different phenomena. Others might try to read a sad or pessimistic message—that evolution isn't a very advanced science, or isn't even a science at all, if it can't predict the course of an imperfect world. Again, I would reject any such reading of my words about constraint and quirky functional shift.

The problem lies with our simplistic and stereotyped view of science as a monolithic phenomenon based on regularity, repetition, and ability to predict the future. Sciences that deal with objects less complex and less historically bound than life may follow this formula. Hydrogen and oxygen, mixed in a certain way, make water today, made water billions of years ago, and presumably will make water for a long time to come. Same water, same chemical composition. No indication of time, no constraints imposed by a history of previous change.

Organisms, on the other hand, are directed and limited by their past. They must remain imperfect in their form and function, and to that extent unpredictable since they are not optimal machines. We cannot know their future with certainty, if only because a myriad of quirky functional shifts lie within the capacity of any feature, however well adapted to a present role.

The science of complex historical objects is a different, not a lesser, enterprise. It seeks to explain the past, not predict the future. It searches for principles and regularities underlying the uniqueness of each species and interaction, while treasuring that irreducible uniqueness and describing all its glory. Notions of science must bend (and expand) to accommodate life. The art of the soluble, Peter Medawar's definition of science, must not become shortsighted, for life is long.

Worm for a Century, and All Seasons

IN THE PREFACE to his last book, an elderly Charles Darwin wrote: "The subject may appear an insignificant one, but we shall see that it possesses some interest; and the maxim 'de minimis lex non curat' [the law is not concerned with trifles] does not apply to science."

Trifles may matter in nature, but they are unconventional subjects for last books. Most eminent graybeards sum up their life's thought and offer a few pompous suggestions for reconstituting the future. Charles Darwin wrote about worms—*The Formation of Vegetable Mould, Through the Action of Worms, With Observations on Their Habits* (1881).

This month* marks the one-hundredth anniversary of Darwin's death—and celebrations are under way throughout the world. Most symposiums and books are taking the usual high road of broad implication—Darwin and modern life, or Darwin and evolutionary thought. For my personal tribute, I shall take an ostensibly minimalist stance and discuss Darwin's "worm book." But I do this to argue that Darwin justly reversed the venerable maxim of his legal colleagues.

Darwin was a crafty man. He liked worms well enough, but his last book, although superficially about nothing else, is (in many ways) a covert summation of the principles of

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* Darwin died on April 19, 1882 and this column first appeared in *Xalural History* in April 1982.

reasoning that he had labored a lifetime to identify and use in the greatest transformation of nature ever wrought by a single man. In analyzing his concern with worms, we may grasp the sources of Darwin's general success.

The book has usually been interpreted as a curiosity, a harmless work of little importance by a great naturalist in his dotage. Some authors have even used it to support a common myth about Darwin that recent scholarship has extinguished. Darwin, his detractors argued, was a man of mediocre ability who became famous by the good fortune of his situation in place and time. His revolution was "in the air" anyway, and Darwin simply had the patience and pertinacity to develop the evident implications. He was, Jacques Barzun once wrote (in perhaps the most inaccurate epitome I have ever read), "a great assembler of facts and a poor joiner of ideas ... a man who does not belong with the great thinkers."

To argue that Darwin was merely a competent naturalist mired in trivial detail, these detractors pointed out that most of his books are about minutiae or funny little problems—the habits of climbing plants, why flowers of different form are sometimes found on the same plant, how orchids are fertilized by insects, four volumes on the taxonomy of barnacles, and finally, how worms churn the soil. Yet all these books have both a manifest and a deeper or implicit theme—and detractors missed the second (probably because they didn't read the books and drew conclusions from the titles alone). In each case, the deeper subject is evolution itself or a larger research program for analyzing history in a scientific way.

Why is it, we may ask at this centenary of his passing, that Darwin is still so central a figure in scientific thought? Why must we continue to read his books and grasp his vision if we are to be competent natural historians? Why do scientists, despite their notorious unconcern with history, continue to ponder and debate his works? Three arguments might be offered for Darwin's continuing relevance to scientists.

We might honor him first as the man who "discovered" evolution. Although popular opinion may grant Darwin this status, such an accolade is surely misplaced, for several illustrious predecessors shared his conviction that organisms are linked by ties of physical descent. In nineteenth-century biology, evolution was a common enough heresy.

As a second attempt, we might locate Darwin's primary claim upon continued scientific attention in the extraordinarily broad and radical implications of his proffered evolutionary mechanism—natural selection. Indeed, I have pushed this theme relentlessly in my two previous books, focusing upon three arguments: natural selection as a theory of local adaptation, not inexorable progress; the claim that order in nature arises as a coincidental by-product of struggle among individuals; and the materialistic character of Darwin's theory, particularly his denial of any causal role to spiritual forces, energies, or powers. I do not now abjure this theme, but I have come to realize that it cannot represent the major reason for Darwin's continued *scientific* relevance, though it does account for his impact upon the world at large. For it is too grandiose, and working scientists rarely traffic in such abstract generality.

Everyone appreciates a nifty idea or an abstraction that makes a person sit up, blink hard several times to clear the intellectual cobwebs, and reverse a cherished opinion. But science deals in the workable and soluble, the idea that can be fruitfully embodied in concrete objects suitable for poking, squeezing, manipulating, and extracting. The idea that counts in science must lead to fruitful work, not only to speculation that does not engender empirical test, no matter how much it stretches the mind.

I therefore wish to emphasize a third argument for Darwin's continued importance, and to claim that his greatest achievement lay in establishing principles of *useful* reason for sciences (like evolution) that attempt to reconstruct history. The special problems of historical science (as contrasted, for example, with experimental physics) are many, but one stands out most prominently: Science must identify processes that yield observed results. The results of history lie strewn around us, but we cannot, in principle, directly observe the processes that produced them. How then can we be scientific about the past?

As a general answer, we must develop criteria for inferring the processes we cannot see from results that have been preserved. This is the quintessential problem of evolutionary theory: How do we use the anatomy, physiology, behavior, variation, and geographic distribution of modern organisms, and the fossil remains in our geological record, to infer the pathways of history?

Thus, we come to the covert theme of Darwin's worm book, for it is both a treatise on the habits of earthworms and an exploration of how we can approach history in a scientific way.

Darwin's mentor, the great geologist Charles Lyell, had been obsessed with the same problem. He argued, though not with full justice, that his predecessors had failed to construct a science of geology because they had not developed procedures for inferring an unobservable past from a surrounding present and had therefore indulged in unprovable reverie and speculation. "We see," he wrote in his incomparable prose, "the ancient spirit of speculation revived and a desire manifestly shown to cut, rather than patiently to untie, the Gordian Knot." His solution, an aspect of the complex world view later called uniformitarianism, was to observe the work of present processes and to extrapolate their rates and effects into the past. Here Lyell faced a problem. Many results of the past—the Grand Canyon for example—are extensive and spectacular, but most of what goes on about us every day doesn't amount to much —a bit of erosion here or deposition there. Even a Stromboli or a Vesuvius will cause only local devastation. If modern forces do too little, then we must invoke more cataclysmic processes, now expired or dormant, to explain the past. And we are in catch-22: if past processes were effective and different from present processes, we might explain the past in principle, but we could not be scientific about it because we have no modern analogue in what we can observe. If we rely only upon present processes, we lack sufficient oomph to render the past.

Lyell sought salvation in the great theme of geology: time. He argued that the vast age of our earth provides ample time to render all observed results, however spectacular, by the simple summing of small changes over immense periods. Our failure lay, not with the earth, but with our habits of mind: we had been previously unwilling to recognize how much work the most insignificant processes can accomplish with enough time.

Darwin approached evolution in the same way. The present becomes relevant, and the past therefore becomes scientific, only if we can sum the small effects of present processes to produce observed results. Creationists did not use this principle and therefore failed to understand the relevance of small-scale variation that pervades the biological world (from breeds of dogs to geographical variation in butterflies). Minor variations are the stuff of evolution (not merely a set of accidental excursions around a created ideal type), but we recognize this only when we are prepared to sum small effects through long periods of time.

Darwin recognized that this principle, as a basic mode of reasoning in historical science, must extend beyond evolution. Thus, late in his life, he decided to abstract and exemplify his historical method by applying it to a problem apparently quite different from evolution—a project broad enough to cap an illustrious career. He chose earthworms and the soil. Darwin's refutation of the legal maxim "de minimis lex non curat" was a conscious double-entendre. Worms are both humble and interesting, and a worm's work, when summed over all worms and long periods of time, can shape our landscape and form our soils.

Thus, Darwin wrote at the close of his preface, refuting the opinions of a certain Mr. Fish who denied that worms could account for much "considering their weakness and their size":

> Here we have an instance of that inability to sum up the effects of a continually recurrent cause, which has often retarded the progress of science, as formerly in the case

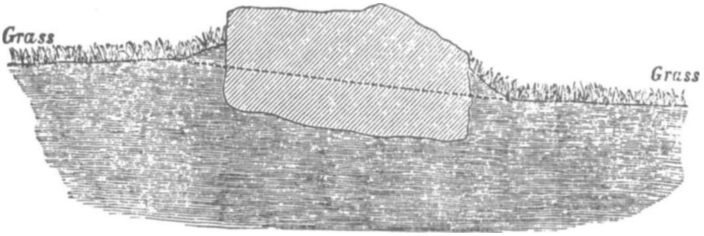
> of geology, and more recently in that of the principle of evolution.

Darwin had chosen well to illustrate his generality. What better than worms: the most ordinary, commonplace, and humble objects of our daily observation and dismissal. If they, working constantly beneath our notice, can form much of our soil and shape our landscape, then what event of magnitude cannot arise from the summation of small effects. Darwin had not abandoned evolution for earthworms; rather, he was using worms to illustrate the general method that had validated evolution as well. Nature's mills, like God's, grind both slowly and exceedingly small.

Darwin made two major claims for worms. First, in shaping the land, their effects are directional. They triturate particles of rock into ever smaller fragments (in passing them through their gut while churning the soil), and they denude the land by loosening and disaggregating the soil as they churn it; gravity and erosive agents then move the soil more easily from high to low ground, thus leveling the landscape. The low, rolling character of topography in areas inhabited by worms is, in large part, a testimony to their slow but persistent work.

Second, in forming and churning the soil, they maintain a steady state amidst constant change. As the primary theme of his book (and the source of its title), Darwin set out to prove that worms form the soil's upper layer, the so-called vegetable mold. He describes it in the opening paragraph:

> The share which worms have taken in the formation of the layer of vegetable mould, which covers the whole surface of the land in every moderately humid country, is the subject of the present volume. This mould is generally of a blackish color and a few inches in thickness. In different districts it differs but little in appearance, although it may rest on various subsoils. The uniform fineness of the particles of which it is composed is one of its chief characteristic features.



Section through one of the fallen Druidical stones at Stonehenge, showing how much it had sunk into the ground. Scale £ inch to 1 foot.

An original illustration from Darwin's worm book showing the foundering of large stones by the action of worms.

> larger ones after a time; so that after thirty years (1871) a horse could gallop over the compact turf from one end of the field to the other, and not strike a single stone with his shoes. To anyone who remembered the appearance of the field in 1842, the transformation was wonderful. This was certainly the work of the worms.

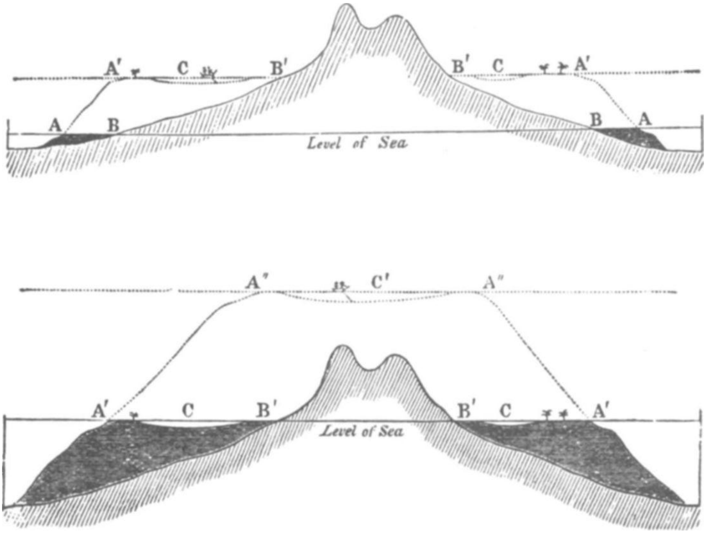
In 1871, he cut a trench in his field and found 2.5 inches of vegetable mold, entirely free from flints: "Beneath this lay coarse clayey earth full of flints, like that in any of the neighboring ploughed fields. . . . The average rate of accumulation of the mould during the whole thirty years was only .083 inch per year (i.e., nearly one inch in twelve years)."

In various attempts to collect and weigh castings directly, Darwin estimated from 7.6 to 18.1 tons per acre per year. Spread out evenly upon the surface, he calculated that from 0.8 to 2.2 inches of mold would form anew every ten years. In gathering these figures, Darwin relied upon that great, unsung, and so characteristically British institution—the corps of zealous amateurs in natural history, ready to endure any privation for a precious fact. I was particularly impressed by one anonymous contributor: "A lady," Darwin tells us, "on whose accuracy I can implicitly rely, offered to collect during a year all the castings thrown up on two separate square yards, near Leith Hill Place, in Surrey." Was she the analogue of a modern Park Avenue woman of means, carefully scraping up after her dog: one bag for a cleaner New York, the other for Science with a capital S?

The pleasure of reading Darwin's worm book lies not only in recognizing its larger point but also in the charm of detail that Darwin provides about worms themselves. I would rather peruse 300 pages of Darwin on worms than slog through 30 pages of eternal verities explicitly preached by many writers. The worm book is a labor of love and intimate, meticulous detail. In the book's other major section, Darwin spends 100 pages describing experiments to determine which ends of leaves (and triangular paper cutouts, or abstract "leaves") worms pull into their burrows first. Here we also find an overt and an underlying theme, in this case leaves and burrows versus the evolution of instinct and intelligence, Darwin's concern with establishing a usable definition of intelligence, and his discovery (under that definition) that intelligence pervades "lower" animals as well. All great science is a fruitful marriage of detail and generality, exultation and explanation. Both Darwin and his beloved worms left no stone unturned.

I have argued that Darwin's last book is a work on two levels—an explicit treatise on worms and the soil and a covert discussion of how to learn about the past by studying the present. But was Darwin consciously concerned with establishing a methodology for historical science, as I have argued, or did he merely stumble into such generality in his last book? I believe that his worm book follows the pattern of all his other works, from first to last: every compendium on minutiae is also a treatise on historical reasoning—and each book elucidates a different principle.

Consider his first book on a specific subject, *The Structure and Distribution of Coral-Reefs* (1842). In it, he proposed a theory for the formation of atolls, "those singular rings of coral-land which rise abruptly out of the unfathomable ocean," that won universal acceptance after a century of



Darwin's original illustration for his theory of coral reefs. Top figure: lower solid line, stage 1, a fringing reef (AB) abuts the shore line. Island sinks (level of sea rises) to upper dotted line, stage 2, barrier reef (A^1) separated from sinking island by a lagoon (C).

Bottom figure: lower solid line, stage 2, barrier reef (copied from upper dotted line of top figure). Island sinks further (below level of sea) to upper dotted line, stage 3, an atoll (A"), enlarged lagoon (C) marks previous location of sunken island.

subsequent debate. He argued that coral reefs should be classified into three categories—fringing reefs that abut an island or continent, barrier reefs separated from island or continent by a lagoon, and atolls, or rings of reefs, with no platform in sight. He linked all three categories with his "subsidence theory," rendering them as three stages of a single process: the subsidence of an island or continental platform beneath the waves as living coral continues to grow upward. Initially, reefs grow right next to the platform (fringing reefs). As the platform sinks, reefs grow up and outward, leaving a separation between sinking platform and living coral (a barrier reef). Finally the platform sinks entirely, and a ring of coral expresses its former shape (an atoll). Darwin found the forms of modern reefs "inexplicable, excepting on the theory that their rocky bases slowly and successively sank beneath the level of the sea, whilst the corals continued to grow upwards."

This book is about coral, but it is also about historical reasoning. Vegetable mold formed fast enough to measure its rate directly; we capture the past by summing effects of small and observable present causes. But what if rates are too slow, or scales too large, to render history by direct observation of present processes? For such cases, we must develop a different method. Since large-scale processes begin at different times and proceed at diverse rates, the varied stages of different examples should exist simultaneously in the present. To establish history in such cases, we must construct a theory that will explain a series of present phenomena as stages of a single historical process. The method is quite general. Darwin used it to explain the formation of coral reefs. We invoke it today to infer the history of stars. Darwin also employed it to establish organic evolution itself. Some species are just beginning to split from their ancestors, others are midway through the process, still others are on the verge of completing it.

But what if evidence is limited to the static object itself? What if we can neither watch part of its formation nor find several stages of the process that produced it? How can we infer history from a lion? Darwin treated this problem in his treatise on the fertilization of orchids by insects (1862); the book that directly followed the *Origin of Species.* I have discussed his solution in several essays (1, 4, 11 and *The Panda's Thumb)* and will not dwell on it here: we infer history from imperfections that record constraints of descent. The "various contrivances" that orchids use to attract insects and attach pollen to them are the highly altered parts of ordinary flowers, evolved in ancestors for other purposes. Orchids work well enough, but they are jury-rigged to succeed because flowers are not optimally constructed for modification to these altered roles. If God wanted to make insect attractors and pollen stickers from scratch, he would certainly have built differently.

Thus, we have three principles for increasing adequacy of data: if you must work with a single object, look for imperfections that record historical descent; if several objects are available, try to render them as stages of a single historical process; if processes can be directly observed, sum up their effects through time. One may discuss these principles directly or recognize the "little problems" that Darwin used to exemplify them: orchids, coral reefs, and worms—the middle book, the first, and the last.

Darwin was not a conscious philosopher. He did not, like Huxley and Lyell, write explicit treatises on methodology. Yet I do not think he was unaware of what he was doing, as he cleverly composed a series of books at two levels, thus expressing his love for nature in the small and his ardent desire to establish both evolution and the principles of historical science. I was musing on this issue as I completed the worm book two weeks ago. Was Darwin really conscious of what he had done as he wrote his last professional lines, or did he proceed intuitively, as men of his genius sometimes do? Then I came to the very last paragraph, and I shook with the joy of insight. Clever old man; he knew full well. In his last words, he looked back to his beginning, compared those worms with his first corals, and completed his life's work in both the large and the small:

> The plough is one of the most ancient and most valuable of man's inventions; but long before he existed the land was in fact regularly ploughed, and still continues to be thus ploughed by earthworms. It may be doubted whether there are many other animals which have played so important a part in the history of the world, as have these lowly organized creatures. Some other animals, however, still more lowly organized, namely corals, have done more conspicuous work in having constructed innumerable reefs and islands in the great

> oceans; but these are almost confined to the tropical zones.

At the risk of unwarranted ghoulishness, I cannot suppress a final irony. A year after publishing his worm book, Darwin died on April 19, 1882. He wished to be buried in the soil of his adopted village, where he would have made a final and corporeal gift to his beloved worms. But the sentiments (and politicking) of fellow scientists and men of learning secured a guarded place for his body within the well-mortared floor of Westminster Abbey. Ultimately the worms will not be cheated, for there is no permanence in history, even for cathedrals. But ideas and methods have all the immortality of reason itself. Darwin has been gone for a century, yet he is with us whenever we choose to think about time.

Hyena Myths and Realities

I FREELY ADMIT that the spotted, or laughing, hyena is not the loveliest animal to behold. Still, it scarcely deserved the poor reputation imposed upon it by our illustrious forebears. Three myths about hyenas helped to inspire the loathing commentary of ancient texts.

Hyenas, first of all, were regarded as scavengers and consumers of carrion. In his *Natural History,* Pliny the Elder (A.D. 23-79) spoke of them as the only animals that dig up graves in search of corpses *(ab uno animali sepulchra erui inquisitione corporum).* Conrad Gesner, the great sixteenth-century cataloger of natural history, reported that they gorge themselves so gluttonously after finding a corpse that their bellies swell to become taut as a drum. They then seek a narrow place between two trees or stones, force themselves through it, and extrude the remains of their meal simultaneously at both ends.

Hans Kruuk, who spent years studying spotted hyenas on their home turf (the plains of East Africa), has labored to dispel these ancient myths (see his book *The Spotted Hyena,* University of Chicago Press, 1972). He reports that hyenas will scavenge when they get the opportunity. (Almost all carnivores, including the noble lion, will happily feast upon the dead product of another animal's labor.) But spotted hyenas live in hunting clans of up to eighty animals. Each clan controls a territory and kills most of its own food—

mainly zebra and wildebeest—in communal, nocturnal pursuit.

As a second insult, hyenas were widely regarded as hybrids. Sir Walter Raleigh excluded them from Noah's ark since he believed that God had only saved thoroughbreds. Hyenas were reconstituted after the flood through the unnatural union of a dog and cat. In fact, the three living species of hyena form a family of their own within the order Carnivora. They are most closely related to the mustelids (weasels and their allies).

As a final, phony blot on their escutcheon, and in the unkindest cut of all, many ancient writers charged that hyenas were hermaphrodites, bearing both male and female organs. Medieval bestiaries, always trying to draw a moral lesson from the depravity of beasts, focused on this supposed sexual ambivalence. A twelfth-century document, translated by T. H. White, declared:

> Since they are neither male nor female, they are neither faithful nor pagan, but are obviously the people concerning whom Solomon said: "A man of double mind is inconstant in all his ways." About whom also the Lord said: "Thou canst not serve God and Mammon."

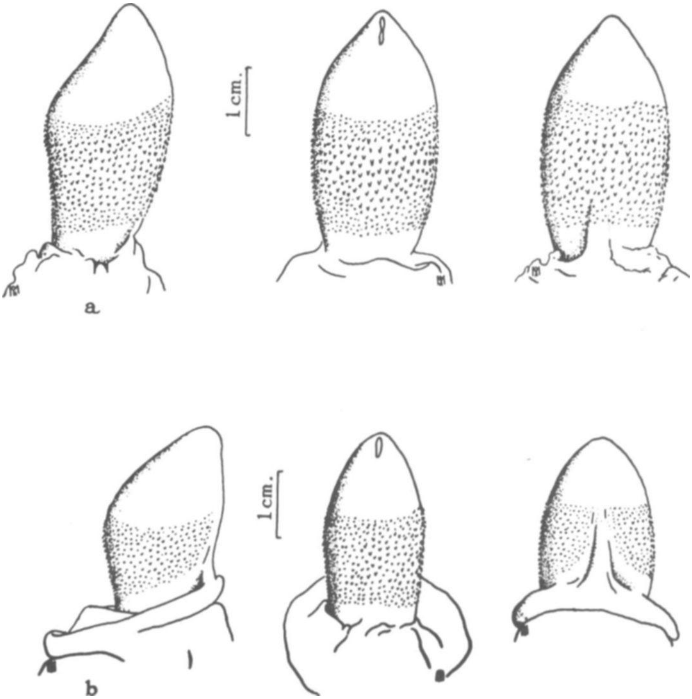
But hyenas also had some formidable defenders against this particular calumny. Aristotle himself had declared in the *Historia animalium:* "The statement is made that the hyena has both male and female sexual organs; but this is untrue."

Aristotle—and not for the first time—was right of course. But the legend had arisen for a good reason. Female hyenas are virtually indistinguishable from males. Their clitoris is enlarged and extended to form an organ of the same size, shape, and position as the male penis. It can also be erected. Their labia have folded up and fused to form a false scrotum that is not discernibly different in external form or location from the true scrotum of males. It even contains fatty tissue forming two swellings easily mistaken for testicles. Authors of the most recent paper on spotted hyenas found the appearance of males and females "so close that sex could only be determined with certainty by palpation of the scrotum. Testes could be located in the scrotum of the male compared with soft adipose tissue in the false scrotum of the female."

British zoologist L. Harrison Matthews wrote the most extensive anatomical description of the hyena's sexual anatomy in 1939. He described the peniform clitoris, emphasizing that it is no smaller than the male penis, is equally constricted to a single slitlike opening at the tip, and is as subject to erection as its male counterpart. He concluded his dry and precise pages of description with as forceful a statement of wonder as measured British scientific prose would allow: "It is probably one of the most unusual of the forms which the external orifice of the urogenital canal takes amongst female mammals."

Harrison Matthews also investigated the interesting question of how hyenas do it, given a female orifice no larger than the slit of a male's penis. "In the pre-pubertal state," he writes, "these functions are obviously impossible, owing to the minute size of the opening." But as the female matures the slit gradually lengthens and "creeps down round the ventral surface... travelling down the midline" until it forms an orifice 1.5 cm long and extending from the tip of the clitoris to its base. This lengthening of the slit and a subsequent enlargement of the nipples following pregnancy and parturition help distinguish older females from males. We can now understand the basis for ancient myths that hyenas were either simultaneous hermaphrodites (bearing male and female organs at the same time) or male for part of their life and then female.

Nature's oddities cry out for explanation, and we therefore ask what advantages females gain from looking like males. Immediately, we come upon the other most striking oddity of hyena biology: females not only resemble males, they are also larger than males, contrary to the usual pattern in mammals, including humans (but see essay 1 for a discussion of the reverse pattern in most other animals). Females in Kruuk's East African clans averaged 120 pounds in body



Similarity of male and female genitalia in the spotted hyena. Top row, views of the male penis. Bottom row, similar views of the female clitoris, FROM HARRISON MATTHEWS, 1939.

weight versus 107 pounds for males. Moreover, they lead the clans in hunting and defense of territory and are generally dominant over males in individual contacts. Dominance is not merely a result of larger size because females also rank higher than larger males if the discrepancy in size is not too great.

Although the female hyena's assumption of what are usually male roles in mammals is probably related to its evolution of sexual structures that mimic male organs, the link between these phenomena is not immediately clear. It cannot have much to do with sexual performance itself for, if anything, the female "penis" is a hindrance to copulation until its opening enlarges and its form departs from that of the male.

Kruuk suggests that the strong mimicry arose in connection with a common behavior in hyenas called the "meeting ceremony." Hyenas live in clans that defend territories and engage in communal hunting. But individuals also spend much of their time as solitary wanderers searching the landscape for carrion. To maintain cohesion in clans and to keep strangers away, hyenas must develop a mechanism for recognizing each other and reintegrating solitary wanderers into their proper clan.

When two hyenas of the same clan meet, they stand side

External genitalia of female spotted hyena, showing peniform clitoris and false scrotum, FROM HARRISON MATTHEWS, 1939.

to side, facing in opposite directions. Each lifts its inside hind leg, subordinate individual first, exposing either an erect penis or clitoris, one of the most vulnerable parts of the body, to its partner's teeth. They then sniff and lick each other's genitals for ten to fifteen seconds, primarily at the base of the penis or clitoris and in front of the scrotum or false scrotum.

Kruuk believes that the female clitoris and false scrotum evolved to provide a conspicuous structure serving for recognition in the meeting ceremony. He writes:

> It is impossible to think of any other purpose for this special female feature than for use in the meeting ceremony. ... It may also be, then, that an individual with a familiar but relatively complex and conspicuous structure sniffed at during the meeting has an advantage over others; the structure would often facilitate this reestablishment of social bonds by keeping partners together over a longer meeting period. This could be the selective advantage that has caused the evolution of the females' and cubs' genital structure.

Speculation about adaptive significance is a favorite, and surely entertaining, ploy among evolutionary biologists. But the question, "What is it for?" often diverts attention from the more mundane but often more enlightening issue, "How is it built?" In this case, speculations about adaptive significance have been in the literature for a long time, yet no one bothered to tread the obvious path for hypotheses of anatomical construction until 1979: What sexual hormones are maintained at what levels by female hyenas from conception to maturity? (See Racey and Skinner, 1979, in bibliography).

Racey and Skinner found, in short, that two androgens (male-producing hormones) had higher concentrations in testicles than in ovaries of adult spotted hyenas (scarcely surprising). Yet, when they investigated levels of the same hormones in blood plasma, they detected *no differences* between males and females. One female contained twin female fetuses, and both had about the same level of testosterone as adult females. Racey and Skinner therefore conclude "that high foetal androgen levels are responsible for the appearance of the male sexual fades in adult female spotted hyenas."

Racey and Skinner affirmed their hypothesis by studying brown and striped hyenas, the other two species of the family Hyaenidae. Neither brown nor striped hyenas develop peniform clitorises or false scrotums. In both species, androgen levels in blood plasma are much lower for females than for males. (Aristotle, by the way, defended hyenas against the charge of hermaphroditism by correctly describing the genitalia of these other species—something of a dodge with respect to the spotted hyena, the source of the legend; but "the master of them that know" was right in any case.)

But why should high levels of androgenic hormones lead to the construction of false penises and scrotums? The animals that form them are still, after all, genetically female. How can female genes produce mimics of male structures, even in a milieu of high androgenic hormones? A look at the developmental basis of sexual anatomy resolves this dilemma.

Mammals share a common pattern for the embryology of sexual organs, and we may therefore use humans as an example. The early embryo is sexually indifferent and contains all precursors and structures necessary for the development of either male or female organs. After about the eighth week following conception, the gonads begin to differentiate as either ovaries or testes. The developing testes secrete androgens, which induce the development of male genitalia. If androgens are absent, or present at low levels, female genitalia are formed.

The internal and external genitalia develop in different ways. For internal genitalia, the early embryo contains precursors of both sexes: the Miillerian ducts (which form the Fallopian tubes and ovaries of females) and the Wolffian ducts (which form the vas deferens—the ducts that carry sperm from the testes to the penis—in males). In females, the Wolffian ducts degenerate and the Miillerian ducts differentiate; males develop by the opposite route.

The external genitalia follow a markedly different pattern. Individuals do not begin with two distinct sets of precursors and then lose one while strengthening the other. Rather, the different organs of male and female develop along diverging routes from the *same* precursor. The male's penis is the same organ as the female's clitoris—they form from the same tissues, are indistinguishable in the early embryo, and follow different pathways later. The male's scrotum is the same organ as the female's labia majora. The two lips simply grow longer, fold over and fuse along the midline, forming the scrotal sac.

The female course of development is, in a sense, biologically intrinsic to all mammals. It is the pattern that unfolds in the absence of any hormonal influence. The male route is a modification induced by secretion of androgens from the developing testes.

The mystery of male mimicry in female hyenas may be solved, in large part, by recognizing these fundamental facts of developmental anatomy. We know from the work of Racey and Skinner that female hyenas maintain high levels of androgenic hormones. We may therefore conclude that the striking and complex peculiarities of sexual anatomy in female spotted hyenas are simply, indeed almost automatically, produced by a single, underlying effect: the secretion of unusually large amounts of androgens by females.

The automatic nature of peniform clitorises and false scrotums in female mammals with high androgen levels can be illustrated by unusual patterns of human development. The adrenal glands also secrete androgens, usually in small amounts. In some genetic females, adrenals are abnormally enlarged and produce high levels of androgens. These baby girls are born with a penis and false scrotum. Several years ago a drug was placed on the market to prevent miscarriages. It had the unfortunate side effect of mimicking the action of natural androgens. Female babies were born with a greatly enlarged clitoris and an empty scrotal sac formed from the fused labia.

I believe that these facts of developmental anatomy must force a revision in the usual interpretation of male mimicry in female spotted hyenas. Evolutionary biologists have too often slipped into a seductively appealing mode of argument about the phenomenon of adaptation. We tend to view every structure as designed for a definite purpose, thus building (in our imagination) a world of perfect design not much different from that concocted by eighteenth-century natural theologians who "proved" God's existence by the perfect architecture of organisms. Adaptationists might allow a little flexibility for tiny and apparently inconsequential structures, but surely anything big, complex, and obviously useful must be built directly by natural selection. Indeed, previous literature on spotted hyenas has assumed that female sexual organs evolved directly for a definite function—as in Kruuk's speculation about the adaptive advantages of conspicuous external genitalia for recognition in the meeting ceremony.

But another scenario is possible and strikes me as more likely. I don't doubt that the basic peculiarity of hyena social organization—the larger size and dominance of females—is an adaptation to something. The easiest pathway to such an adaptation would be a marked rise in the production of androgenic hormones by females (these exist in small amounts in all female mammals). High levels of androgens would entail complex secondary effects as automatic consequences—among them, a peniform clitoris and a false scrotum (we cannot, after all, label the same condition in some abnormal human baby girls as an adaptation). Once these effects are present, some use might be evolved for them—as in the meeting ceremony. But their current utility does not imply that they were built directly by natural selection for the purpose they now serve. (Yes, I know that my scenario might be run in reverse: conspicuous female genitalia are required for the meeting ceremony and are evolved by enhanced androgen levels, thus yielding large female size and dominance as a consequence. I do, however, point out that under our usual preferences for seeing direct adaptation everywhere, my scenario would not even be considered. Indeed, it wasn't in the major works on spotted hyenas.)

We do not inhabit a perfected world where natural selection ruthlessly scrutinizes all organic structures and then molds them for optimal utility. Organisms inherit a body form and a style of embryonic development; these impose constraints upon future change and adaptation. In many cases, evolutionary pathways reflect inherited patterns more than current environmental demands. These inheritances constrain, but they also provide opportunity. A potentially minor genetic change—a rise of androgen level in this case—entails a host of complex, nonadaptive consequences. The primary flexibility of evolution may arise from nonadaptive by-products that occasionally permit organisms to strike out in new and unpredictable directions. What "play" would evolution have if each structure were built for a restricted purpose and could be used for nothing else? How could humans learn to write if our brain had evolved for hunting, social cohesion, or whatever, and could not transcend the adaptive boundaries of its original purpose?

In the second show of his *Cosmos* series, Carl Sagan told the tale of a Japanese crab that carries a portrait of a samurai warrior on its back. He argued that humans have built this face after their own image because local fisherman have been throwing back the most facelike crabs for centuries, thus imposing strong selection pressure for samurai look-alikes (the others get eaten). He used this example as a lead-in for a rapturous discourse on the pervasive power of natural selection.

I doubt this story very much and suspect that the conventional explanation is correct—that the resemblance is accidental and, at best, only slightly strengthened by human intervention. But even if Sagan were right, I believe that he is marveling at the wrong item (or at least failing to give equal time to another remarkable aspect of the case). I am most impressed by a crab's ability to do such an uncrablike thing in the first place—just as the capacity of an inherited developmental system to produce (and so easily) such marked changes in the sexual anatomy of female hyenas grabs me far more than any putative adaptive significance for the change.

The capacity of crabs to make a face on their back did not arise from any selective value such a face might have, since crabs so rarely use this latent ability. Rather, this capacity reflects several deeper facts of crab biology: the bilateral symmetry of the carapace (corresponding by analogy with the bilateral symmetry of the human face), and the fact that many crabs are ornamented by creases along the midline (where a "nose" might form) and perpendicular to it (where "eyes" and "mouths" might be constructed).

The accidental production of a human portrait represents a stunning example of the evolutionary flexibility arising from consequences of an inherited design. Organic material is not putty and natural selection is not omnipotent. Each organic design is pregnant with evolutionary possibilities, but restricted in its paths of potential change. Fishermen might throw back selected starfishes with their five-part symmetry, or snails with their spiral design, for tens of millions of years and never carve a samurai into their hard parts.

Peter Medawar has described science as the "art of the soluble." Evolution might be labeled "the transformation of the possible."

Kingdoms Without Wheels

SISERA'S MOTHER thought fondly of the booty that her son might bring back—"a prey of divers colors of needlework"—after meeting the armies of Israel led by Deborah and Barak (Judges, chapters 4-5). Yet he was overdue, and she began to worry: "Why tarry the wheels of his chariots?" she inquired anxiously. And rightly did she fear, for Sisera would never return. The Canaanite armies had been routed, while Jael had just transfixed Sisera through the head with a nail (a tent post in modern translations)—ranking her second to Judith among Jewish heroines for the gory dispatch of enemies.

Generals of the biblical armies rode on chariots; their apparatus traveled on carts. But two thousand years later, by the sixth century **A.D.**, the question posed by Sisera's mother could no longer be asked, for wheels virtually disappeared as a means of transportation from Morocco to Afghanistan. They were replaced by camels (Richard W. Bulliet, *The Camel and the Wheel,* 1975).

Bulliet cites several reasons for this counterintuitive switch. The Roman roads had begun to deteriorate and camels were not bound to them. Craftsmanship in harnesses and wagons had suffered a sharp decline. But, most important, camels (as pack animals) were more efficient than carts pulled by draft animals (even by camels). In a long list of reasons for favoring camels to nonmechanized transport by wheels, Bulliet includes their longevity, endurance, ability to ford rivers and traverse rough ground, and savings in manpower (a wagon requires a man for every two animals, but three to six pack camels can be tended by a single person).

We are initially surprised by Bulliet's tale because wheels have come to symbolize in our culture the sine qua non of intelligent exploitation and technological progress. Once invented, their superiority cannot be gainsaid or superseded. Indeed, "reinventing the wheel" has become our standard metaphor for deriding the repetition of such obvious truths. In an earlier era of triumphant social Darwinism, wheels stood as an ineluctable stage of human progress. The "inferior" cultures of Africa slid to defeat; their conquerors rolled to victory. The "advanced" cultures of Mexico and Peru might have repulsed Cortes and Pizarro if only a clever artisan had thought of turning a calendar stone into a cartwheel. The notion that carts could ever be replaced by pack animals strikes us not only as backward but almost sacrilegious.

The success of camels reemphasizes a fundamental theme of these essays. Adaptation, be it biological or cultural, represents a better fit to specific, local environments, not an inevitable stage in a ladder of progress. Wheels were a formidable invention, and their uses are manifold (potters and millers did not abandon them, even when cartwrights were eclipsed). But camels may work better in some circumstances. Wheels, like wings, fins, and brains, are exquisite devices for certain purposes, not signs of intrinsic superiority.

The haughty camel may provide enough embarrassment for any modern Ezekiel, yet this column might seem to represent still another blot on the wheel's reputation (though it does not). For I wish to pose another question that seems to limit the wheel. So much of human technology arose by recreating the good designs of organisms. If art mirrors nature and if wheels are so successful an invention, why do animals walk, fly, swim, leap, slither, and creep, but never roll (at least not on wheels)? It is bad enough that wheels, as human artifacts, are not always superior to nature's handiwork. Why has nature, so multifarious in her ways, shunned the wheel as well? Are wheels a poor or rarely efficient way to make progress after all?

In this case, however, the limit lies with animals, not with the efficiency of wheels. A vulgarization of evolution, presented in many popular accounts, casts natural selection as a perfecting principle, so accurate in its operation, so unconstrained in its action, that animals come to embody a set of engineering blueprints for optimal form (see essay 11). Instead of replacing the older "argument from design"—the notion that God's existence can be proved by the harmonies of nature and the clever construction of organisms—natural selection slips into God's old role as perfecting principle.

But the proof that evolution, and not the fiat of a rational agent, has built organisms lies in the imperfections that record a *history* of descent and refute creation from nothing. Animals cannot evolve many advantageous forms because inherited architectural patterns preclude them. Wheels are not flawed as modes of transport; I am sure that many animals would do far better with them. (The one creature clever enough to build them, after all, has gotten some mileage from the invention, the superiority of camels in certain circumstances notwithstanding.) But animals cannot construct wheels from the parts that nature provides.

As its basic structural principle, a true wheel must spin freely without physical fusion to the solid object it drives. If wheel and object are physically linked, then the wheel cannot turn freely for very long and must rotate back, lest connecting elements be ruptured by the accumulated stress. But animals must maintain physical connections between their parts. If the ends of our legs were axles and our feet were wheels, how could blood, nutrients, and nerve impulses cross the gap to nurture and direct the moving parts of our natural roller skates? The bones of our arms may be unconnected, but we need the surrounding envelopes of muscle, blood vessels, and skin—and therefore cannot rotate our arms even once around our shoulders.

We study animals to illuminate or exemplify nature's laws. The highest principle of all may be nature's equivalent of the axiom that for every hard-won and comforting regularity, we can find an exception. Sure enough—somebody out there has a wheel. In fact, at this very moment, wheels are rotating by the millions in your own gut.

Escherichia coll, the common bacillus of the human gut, is about two micrometers long (a micrometer is one-thousandth of a millimeter). Propelled by long whiplike threads called flagella (singular, flagellum), an *E. coli* can swim about ten times its own length in a second. Lest swimming seem easy for a creature virtually unaffected by gravitational forces and moving through a supporting and easily yielding fluid, I caution against extrapolating our view to a bacterium's world. The perceived viscosity of a fluid depends upon an organism's dimensions. Decrease a creature's size and water quickly turns to molasses. Howard C. Berg, the Colorado biologist who demonstrated how flagella operate, compares a bacterium moving in water to a man trying to swim through asphalt. A bacterium cannot coast. If its flagella stop moving, a bacterium comes to an abrupt halt within about a millionth of its body length. The flagella work wonderfully well in trying circumstances.

After Berg had modified his microscope to track individual bacteria, he noted that an *E. coli* moves in two ways. It may "run," swimming steadily for a time in a straight or slightly curved path. Then it stops abruptly and jiggles about—a "twiddle" in Berg's terminology. After twiddling, it runs off again in another direction. Twiddles last a tenth of a second and occur on an average of once a second. The timing of twiddles and the directions of new runs seem to be random unless a chemical attractant exists at high concentration in one part of the medium. A bacterium will then move up-gradient toward the attractant by decreasing the probability of twiddling when a random run carries it in the right direction. When a random run moves in the wrong direction, twiddling frequency remains at its normal, higher level. The bacteria therefore drift toward an attractant by increasing the lengths of runs in favored directions.

The bacterial flagellum is built in three parts: a long helical filament, a short segment (called a hook) connecting the filament to the flagellar base, and a basal structure embedded in the cell wall. Biologists have argued about how bacteria move since Leeuwenhoek first saw them in 1676. Most models assumed that Hagella are fixed rigidly to the cell wall and that they propel bacteria by waving to and fro. When such models had little success in explaining the rapid transition between runs and twiddles, some biologists suggested that flagella might tag passively along and that some other (and unknown) mechanism might move bacteria.

Berg's observations revealed something surprising, hinted at and proposed in theory before, but never adequately demonstrated: the bacterial flagellum operates as a wheel. It rotates rigidly like a propeller, driven by a rotatory "motor" in the basal portion embedded in the cell wall. Moreover, the motor is reversible. *E. coli* runs by rotating the flagella in one direction; it twiddles by abruptly stopping and rotating the flagella the other way!

Berg could observe the rotation and correlate its direction with runs and twiddles by following free-swimming bacteria in his machine, but S. H. Larsen and others, working in Julius Adler's laboratory at the University of Wisconsin, provided an even more striking demonstration. They isolated two mutant strains of *E. coli*—one that runs and never twiddles and another that twiddles incessantly. They "tethered" these mutant bacteria to glass slides, using antibodies that attach either to the hook or filament of the flagella and also, fortunately, to glass. Thus, the bacteria are affixed to the slide by their flagella. Larsen noted that the tethered bacteria rotate continually about their immobilized flagella. The running mutants turn counterclockwise (as viewed from outside the cell), while the twiddling mutants turn clockwise. The flagellar wheel has a reversible motor.

The biochemical basis of rotation has not yet been elucidated, but the morphology can be resolved. Berg proposes that the bottom end of the flagellum expands out to form a thin ring rotating freely in the cytoplasmic membrane of the cell wall. Just above, another ring surrounds the flagellar base, without attaching to it. This second ring is mounted rigidly on the cell wall. The lower ring (and entire flagellum) rotates freely, held in position by the surrounding upper ring and the cell wall itself.

Some exceptions in nature are dispiriting—the nasty, ugly, little facts that spoil great theories, in Huxley's aphorism. Others are enlightening and serve only to reinforce a regularity by identifying both its scope and its reasons. These are the exceptions that prove (or probe) rules—and the flagellar wheel falls into this happy class.

Is it accidental that wheels only occur in nature's smallest creatures? Organic wheels require that two parts be juxtaposed without physical connection. I argued previously that this cannot be accomplished in creatures familiar to us because connection between parts is an integral property of living systems. Substances and impulses must be able to move from one segment to another. Yet, in the smallest organisms—and in them alone—substances can move between two unconnected parts by diffusing through membranes. Thus, single cells, including all of ours of course, contain organelles lying within the cytoplasm and communicating with other parts of the cell, not by physical connection, but by passage of molecules through bounding membranes. Such structures could, in principle, be designed to rotate like wheels.

The principle that restricts such communication without physical connection to the smallest organisms (or to similarly sized parts of larger organisms) embodies a theme that has circulated extensively throughout these essays (see sections in *Ever Since Darwin* and *The Panda's Thumb):* the correlation of size and shape through the changing relationship of surfaces and volumes. With surfaces (length^2) increasing so much more slowly than volumes (length^3) as an object grows, any process regulated by surfaces but essential to volumes must become less efficient unless the enlarging object changes its shape to produce more surface. The external boundary is surface enough for communication between the organelles of a single cell with their minuscule volumes. But the surface of a wheel as large as a human foot could not provision the wheelful of organic matter within.

Large organisms must evolve channels—physical connections—to convey the nutrients and oxygen that can no longer diffuse through external surfaces.

Wheels work well, but animals are debarred from building them by structural constraints inherited as an evolutionary legacy. Adaptation does not follow the blueprints of a perfect engineer. It must work with parts available. Yet when I survey animals in all their stunning, if wheel-less, variety, I can only marvel at the diversity and good design that a few basic and highly constrained organic patterns have produced. Forced to make do, we do rather well.

Postscript

I did not know how many artists and writers of fiction had made up for nature's limitations until readers began to submit their favorite stories. To choose just one example in each category, G. W. Chandler told me that one of the *Oz* novels featured some four-legged rollers known as wheelers. They were, in fact, built in just the way I argued an animal could not work—with wheels for feet and the ends of legs for axles. D. Roper sent me a print of M. C. Escher's "curl-up," a lithograph showing hundreds of curious creatures wandering through a typical Escher landscape of impossible staircases. They climb by dragging a segmented body along on three pairs of humanoid legs. When they hit a flat surface, they roll up and roll along. These, of course, are permissible "one part" wheels, (like tumbling tumbleweeds), not the impossible wheel and axle combination. Still, Escher specifically created them to make up for nature's limitation since he writes that the lithograph was inspired by his "dissatisfaction concerning nature's lack of any wheelshaped living creatures. . . . So the little animal shown here . . . is an attempt to fill a long-felt want."

Still, as usual, nature wins again. Robert LaPorta and Joseph Frankel both wrote to tell me that I had missed another of nature's real wheels. They directed me to the work of Sidney Tamm, which, I am ashamed to say, I did not know when I wrote the original article. Dr. Tamm has found wheels in single-celled creatures that live in the guts of termites. They therefore (whew!) fall into the category of permissible exceptions at small dimensions.

The body of this protist contains an axostyle (a kind of axis running the length of its body) that rotates continuously in one direction. The organelles of the anterior end (including the nucleus) are attached to the axostyle and rotate with it—"much like turning a lollipop by the stick," as Tamm notes. But, and we now encounter the more curious and wheel-like point, the entire anterior end, including the cell surface, rotates along with the axostyle relative to the rest of the body.

Tamm demonstrated this peculiar motion with an ingenious experiment in which he attached small bacteria all over the cell's outer surface. Those attached to the front end rotated continuously with respect to those adhering to the back end. But bacteria did not attach to a narrow band between front and back, and this band must therefore represent a zone of shear. Tamm then studied the structure of the cell-membrane by freeze-fracture electron microscopy and found it to be continuous across the shear zone. Tamm concludes that the entire surface must be fluid and that shear zones could, in theory, form anywhere upon it. A very strange creature! "Prais'd be the fathomless universe," Whitman wrote, "for life and joy, and for objects and knowledge curious."

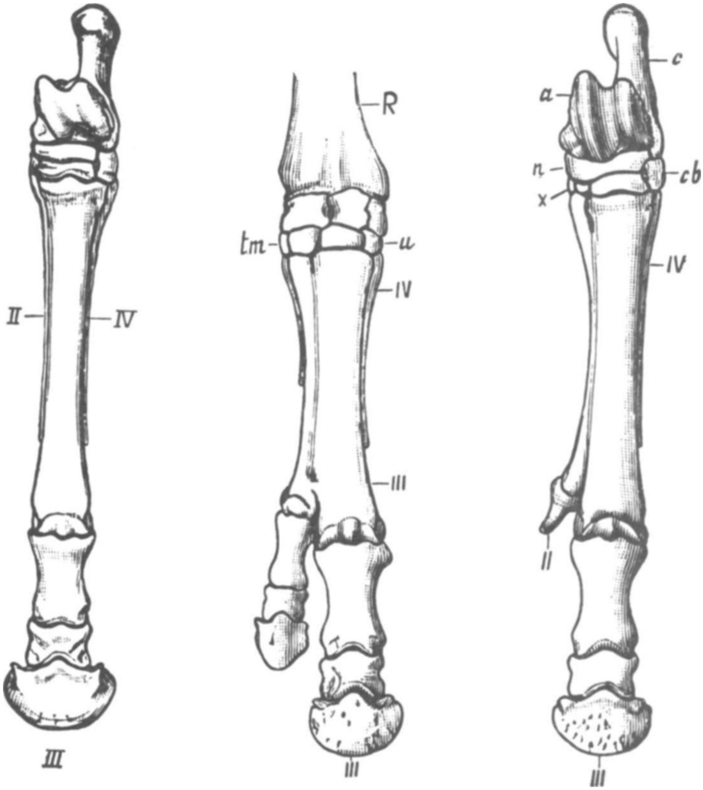
Hen's Teeth and Horse's Toes

VANITY LICENSE PLATES are the latest expression of an old conviction that distinctive conveyances reflect status or, at least, compel notice. We can build our modern machines to order, but nature has narrower limits. Horses of unusual size or color commanded great favor, but Julius Caesar ventured beyond the mere accentuation of normality in choosing his favorite mount. The historian Suetonius writes that Caesar

> used to ride a remarkable horse, which had feet that were almost human, the hoofs being cleft like toes. It was born in his own stables, and as the soothsayers declared that it showed its owner would be lord of the world, he reared it with great care, and was the first to mount it; it would allow no other rider.

Normal horses represent the limit of evolutionary trends for the reduction of toes. Ancestral *Hyracotheiium* (popularly, but incorrectly, known as *Eohippus)* had four toes in front and three in back, while some earlier forebear undoubtedly possessed the original mammalian complement of five on each foot. Modern horses retain but a single toe, the third of an original five. They also develop vestiges of the old second and fourth toes as short splints of bone, mounted high and inconspicuously above the hoof.

Abnormal horses with extra digits have been admired and studied since Caesar's time. O. C. Marsh, a founder of vertebrate paleontology in America, took a special interest in these aberrant animals and published a long article on "Recent polydactyle horses" in April 1892. Marsh had two major claims upon fame, one dubious—his acrimonious battles with E. D. Cope in collecting and describing vertebrate fossils from the American West—and one unambiguous—his success in deciphering the evolution of horses, the first



Marsh's 1892 figures of polydactyl horses. Left, a normal horse. Note the splint remnants of side toes labeled II and IV. Middle: Polydactyly by duplication. The side splints are still present and the extra toe is a duplicated third digit. Right: Polydactyly by atavism. The extra toe is an enlarged side splint.

Marsh's 1892 figure of a polydactyl horse, the "horned horse from Texas."

adequate demonstration of descent provided by the fossil record of vertebrates, and an important support in Darwin's early battles.

Marsh was puzzled and fascinated by these aberrant horses with extra toes. In most cases, the additional toe is merely a duplicate copy of the functional third digit. But Marsh found that many two- and three-toed horses had harkened back to their ancestors by developing either or both of the side splints into functional (or nearly functional) hoofed toes. (A later, and particularly thorough, German monograph of 1918 concluded that about two-thirds of horses with extra toes had simply duplicated the functional third digit, while about one-third had resuscitated an ancestral feature by developing the vestigial splints of their second or fourth toe into complete, hoofed digits.)

These apparent reversions to previous evolutionary states are called atavisms, after the Latin *atavus:* literally, great-great-great-grandfather; more generally, simply ancestor. The biological literature is studded with examples of the genre, but they have generally been treated anecdotally as mere curiosities bearing no important evolutionary message. If anything, they are surrounded with the odor of slight embarrassment, as if the progressive process of evolution did not care to be reminded so palpably of its previous imperfections. The synonyms of European colleagues express this feeling directly—"throwback" in England, *pas-en-arnere* ("backward step") in France, and *Riickschlag* ("set-back") in Germany. When granted any general significance, atavisms have been treated as marks of constraint, as indications that an organism's past lurks just below its present surface and can hold back its future advance.

I would suggest an opposite view—that atavisms teach an important lesson about potential results of small genetic changes, and that they suggest an unconventional approach to the problem of major transitions in evolution. In the traditional view, major transitions are a summation of the small changes that adapt populations ever more finely to their local environments. Several evolutionists, myself in-eluded, have become dissatisfied with this vision of smooth extrapolation. Must one group always evolve from another through an insensibly graded series of intermediate forms? Must evolution proceed gene by gene, each tiny change producing a correspondingly small alteration of external appearance? The fossil record rarely records smooth transitions, and it is often difficult even to imagine a function for all hypothetical intermediates between ancestors and their highly modified descendants.

One promising solution to this dilemma recognizes that certain kinds of small genetic changes may have major, discontinuous effects upon morphology. We can make no one-to-one translation between extent of genetic change and degree of alteration in external form. Genes are not attached to independent bits of the body, each responsible for building one small item. Genetic systems are arranged hierarchically; controllers and master switches often activate large blocks of genes. Small changes in the timing of action for these controllers often translate into major and discontinuous alterations of external form. Most dramatic are the so-called homeotic mutants discussed in the following essay.

The current challenge to traditional gradualistic accounts of evolutionary transitions will take root only if genetic systems contain extensive, hidden capacities for expressing small changes as large effects. Atavisms provide the most striking demonstration of this principle that I know. If genetic systems were beanbags of independent items, each responsible for building a single part of the body, then evolutionary change could only occur piece by piece. But genetic systems are integrated products of an organism's history, and they retain extensive, latent capacities that can often be released by small changes. Horses have never lost the genetic information for producing side toes even though their ancestors settled on a single toe several million years ago. What else might their genetic system maintain, normally unexpressed, but able to serve, if activated, as a possible focus for major and rapid evolutionary change? Atavisms reflect the enormous, latent capacity of genetic systems, not primarily the constraints and limitations imposed by an organism's past.

My latent interest in atavism was recently kindled by a report of something that has no right to exist if one of our most venerable similes expresses literal truth—hen's teeth. On February 29, 1980 (enough of a rarity in itself). E.J. Kollar and C. Fisher reported an ingenious technique for coaxing chickens to reveal some surprising genetic flexibility retained from a distant past.

They took epithelial (outer) tissue from the first and second gill arches of a five-day-old chick embryo and combined it with mesenchyme (inner embryonic tissue) of sixteen- to eighteen-day-old mouse embryos taken from the region where first molar teeth form. A fascinating evolutionary tale lies hidden in this simple statement as well. Jaws evolved from bones supporting the anterior gills of ancestral fishes. All vertebrate embryos still develop the anterior gill arches first (as ancestral embryos did) and then transform them during development into jaws (as ancestors did not in retaining the forward gills throughout life). Thus, if the embryonic tissues of chickens still retain any capacity for forming teeth, the epithelium of the anterior gill arches is the place to look.

Kollar and Fisher took the combined embryonic tissue of mouse and chicken and grew it in what might strike readers as a bizarre and unlikely place—the anterior chambers of the eyes of adult nude mice (but where else in an animal's body can one find an open space, filled with liquid that is not circulating?). In ordinary teeth, made by a single animal, the outer enamel layer forms from epithelial tissue and the underlying dentin and bone from mesenchyme. But mesenchyme cannot form dentin (although it can produce bone) unless it can interact directly with epithelium destined to form enamel. (In embryological jargon, epithelium is a necessary inducer, although only mesenchyme can form dentin.)

When Kollar and Fisher grafted mouse mesenchyme alone into the eyes of their experimental animals, no dentin developed, but only spongy bone—the normal product of mesenchyme when deprived of contact with enamel epithelium as an inducer. But among fifty-five combined grafts of mouse mesenchyme and chick epithelium, ten produced dentin. Thus, chick epithelium is still capable of inducing mesenchyme (from another species in another vertebrate class yet!) to form dentin. *Archaeopteryx,* the first bird, still possessed teeth, as did several fossils from the early history of birds. But no fossil bird has produced teeth during the past sixty million years, while the toothlessness of all modern birds ranks with wings and feathers as defining characters of the class. Nonetheless, although the system has not been used on its home ground for perhaps a hundred million generations, chick epithelium can still induce the formation of dentin when combined with appropriate mesenchyme (chick mesenchyme itself has probably lost the ability to form dentin, hence the toothlessness of hens and the necessity for using mice).

Kollar and Fisher then found something even more interesting. In four of their grafts, complete teeth had developed! Chick epithelium had not only induced mouse mesenchyme to form dentin; it had also been able to generate enamel matrix proteins. (Dentin must be induced by epithelium, but this epithelium cannot differentiate into enamel unless it, in turn, can interact with the very dentin it has induced. Since chick mesenchyme cannot form dentin, chick epithelium never gets the chance to show its persistent stuff in nature.)

One final point stunned me even more. Kollar and Fisher write of their best tooth: "The entire tooth structure was well formed, with root development in proper relation to the crown, but the latter did not have the typical first-molar morphology, since it lacked the cusp pattern usually present in intraocular grafts of first-molar rudiments." In other words, the tooth looks normal, but it does not have the form of a mouse's molar. The odd form may, of course, simply result from the peculiar interaction of two systems not meant to be joined in nature. But is it possible that we are seeing, in part, the actual form of a latent bird's tooth—the potential structure that chick epithelium has encoded for sixty million years but has not expressed in the absence of dentin to induce it?

Kollar and Fisher's work recalled another experiment from the opposite end of a chick, a famous story usually misreported by evolutionary biologists (once, I am embarrassed to say, by myself), as I discovered in tracking down the original source. In 1959, the French embryologist Armand Hampe reported some experiments on the development of leg bones in chick embryos. In ancestral reptiles, the tibia and fibula (the bones between your kneecap and ankle) are equal in length; the ankle region below includes a series of small bones. In *Archaeopleryx,* the first bird, tibia and fibula are still equal in length, but the ankle bones below have been reduced to two, one articulating with the tibia, the other with the fibula. In most modern birds, however, the fibula has been reduced to a splint. It never reaches the ankle region, while the two ankle bones are "engulfed" by the rapidly growing tibia and fuse with it. Thus, modern birds develop a single structure (the tibia with ankle bones fused to it and the rudimentary fibula at its side), articulating with bones of the foot below.

Hampe reasoned that the fibula might well maintain its capacity for attaining full, ancestral length, but that competition for material by the rapidly growing tibia might deprive it of any opportunity to express this potential. He therefore performed three types of experiments, all directed toward giving the fibula some relief from its imperialistic and normally victorious neighboring bone. In all cases, the fibula attained its ancestral length, equal to the tibia and reaching the ankle region below. In the first, Hampe simply grafted more embryonic tissue into the region of the growing leg bones. The tibia reached its characteristic length, but the region now had enough material "left over" for the fibula. In the second, he altered the direction of growth for tibia and fibula so that the two bones did not remain in intimate contact. In the third, he inserted a mica plate between the two bones; the developing tibia could no longer "grab" material from its less vigorous neighbor and the fibula achieved its full length.

Thus, Hampe recreated an ancestral relationship between two bones by a series of simple manipulations. And this alteration engendered an even more interesting consequence. In normal chicks, the fibula begins its growth in contact with one of the small ankle bones below. But as the tibia enlarges and predominates, this contact breaks at about the fifth day of development. The fibula then retreats to form its splint, while the expanding tibia engulfs both ankle bones to form a single structure. In one case during Hampe's manipulations, the two ankle bones remained separate and did not fuse with either tibia or fibula (while both ankle bones fused with the tibia, as usual, in the other leg of the same embryo—an untreated control allowed to develop normally). In this bird, Hampe's simple manipulation not only produced its intended result (expression of an ancestral relationship in leg bones); it also evoked the ancestral pattern of ankle bones as well.

Hampe was able to produce these impressive atavisms by simple manipulations that amount to minor, quantitative changes in timing of development or placement of embryonic tissue. Adding more tissue doesn't simply make a bigger part with the same proportions; it leads to differential growth of one bone (the fibula) and a change in arrangement of the entire ankle area (two ankle bones, articulating separately to tibia and fibula in some cases, rather than a single tibia with both ankle bones fused to it).

Developmental patterns of an organism's past persist in latent form. Chicks no longer develop teeth because their own mesenchyme does not form dentin, even though their epithelium can still produce enamel and induce dentin in other animals. Chicks no longer develop separate ankle bones because their fibula no longer keeps pace with the tibia during growth, but the ankle bones develop and retain their identity when fibulas are coaxed to reach their ancestral length. An organism's past not only constrains its future; it also provides as legacy an enormous reservoir of potential for rapid morphological change based upon small genetic alterations.

Charles Darwin constructed his theory as a two-stage process: variation to supply raw material and natural selection to impart direction. It is frequently (and incorrectly) stated that he said little about variation, embarrassed as he was by ignorance about the mechanism of heredity. Many people believe that he simply treated variation as a "black box," something to be assumed, mentioned in passing, and then forgotten. After all, if there is always enough variation for natural selection to use, why worry about its nature and causes?

Yet Darwin was obsessed with variation. His books, considered as an ensemble, devote much more attention to variation than to natural selection, for he knew that no satisfactory theory of major evolutionary change could be constructed until the causes of variation and the empirical rules of its form and amount had been elucidated. His longest book is devoted entirely to problems of variation—the two-volume *Variation of Animals and Plants Under Domestication* (1868). Darwin felt that atavism held the key to many mysteries of variation, and he devoted an entire chapter to it, closing (as I will) with these words:

> The fertilized germ of one of the higher animals ... is perhaps the most wonderful object in nature. . . . On the doctrine of reversion [atavism] . . . the germ becomes a far more marvellous object, for, besides the visible changes which it undergoes, we must believe that it is crowded with invisible characters . . . separated by hundreds or even thousands of generations from the present time: and these characters, like those written on paper with invisible ink, lie ready to be evolved whenever the organization is disturbed by certain known or unknown conditions.

Helpful Monsters

MY GRANDFATHER, who taught me to play poker and watched the Friday night fights with me every week, once took me to one of the cruelest, yet most fascinating spectacles of decades now thankfully past—the rows of malformed people forced (by an absence of other opportunities) to display themselves to a gawking public at the Ringling Brothers sideshow.

The genteel and legitimate counterpart to such public cruelty is the vast scientific literature on deformed births—a subject dignified with its own formal name as teratology, literally, the study of monsters. Although scientists are as subject as all people to the mixture of awe, horror, and curiosity that draws people to sideshows, teratology has an important rationale beyond primal fascination.

The laws of normal growth are best formulated and understood when the causes of their exceptions can be established. The experimental method itself, a touchstone of scientific procedure, rests upon the notion that induced and controlled departures from the ordinary can lay bare the laws of order. Congenitally malformed bodies are nature's experiments, uncontrolled by intentional human art to be sure, but sources of insight nonetheless.

The early teratologists sought to understand malformations by classifying them. In the decades before Darwin, French medical anatomists developed three categories: missing parts *(monstres par defaut),* extra parts *(monstres par* *exces),* and normal parts in the wrong places. The folklore of monsters had long recognized the last category in tales of anthropophagi, maneaters with eyes in their shoulders and a, mouth on their breast. Shakespeare alluded both to them and to some related colleagues in *Othello* when he spoke of "The Anthropophagi and men whose heads/Do grow beneath their shoulders."

But a classification is no more than a set of convenient pigeonholes until the causes of ordering can be specified. And here nineteenth-century teratology got becalmed in its own ignorance of heredity. The establishment of genetics in our century revived a waning interest in teratology, as early Mendelians discovered the mutational basis of several common deformities.

Geneticists had particular success with one common category in the old classification—normal parts in the wrong places. They studied their favorite animal, the fruit fly, *Drosophila melanogaster,* and found a variety of bizarre transpositions. In the first of two famous examples, the halteres (organs of balance) are transformed into wings, restoring to the aberrant fly its ancestral complement of four (normal flies, as members of the order Diptera, have two wings). In the second, legs or parts of legs replace a variety of structures in the head—antennae and parts of the mouth in particular. Mutations of this sort are called homeotic.

Not all misplacements of parts represent homeosis, and this restriction is a key to the evolutionary message I shall draw further on. William Bateson, who later invented the term genetics, defined as "homeotic" only those parts that replace an organ having the same developmental or evolutionary origin (the word comes from a Greek root for "similar"). Thus, halteres are the evolutionary descendants of wings, while insect antennae, mouthparts, and legs all differentiate from similar precursors in the embryonic segments, and all presumably evolved from an ancestor with a pair of simple and similar appendages on each adult body segment. We might refer to homeosis if a human developed a second pair of arms where his legs should be, but an extra pair of arms on the chest would not qualify.

Homeotic mutants are found on all four pairs of chromosomes in *D. melanogaster.* A 1976 review by W.J. Ouweneel includes a list that runs to three full pages. But the two most famous, best studied, and elaborate sets of homeotic mutations both reside on the right arm of the third chromosome.

The first set, called the bithorax complex and abbreviated BX-C, regulates the normal development and differentiation of the fly's posterior body segments. The larval fly is already divided into a series of segments, initially quite similar, that will differentiate into specialized adult structures. The first five larval segments build the adult head (the first forms anterior parts of the head; the second, the eyes and antennae; and the third through fifth, the various parts of the mouth). The next three segments, T_1, T_2, and T_3, form the thorax. Each will bear a pair of legs in the adult, building the normal insect complement of six. The single pair of wings will differentiate in T_2.

The next eight segments (A_1 through A_8) form the adult's abdomen, while the final, or caudal, segment (A_9 and A_{10}) will build the adult's posterior end. The presence of normal BX-C genes appears to be a precondition for the ordinary development of all segments behind the second thoracic. If all the genes of BX-C are deleted from the third chromosome, all larval segments behind the second thoracic (T_2) fail to differentiate along their normal route and seem to become second thoracic segments themselves. If the adult survived, it would be a wonder to behold, with (presumably) a pair of legs on each of its numerous posterior segments. But this deletion is, in geneticist's jargon, "lethal," and the fly dies while still a larva. We know that the posterior segments of such aberrant flies are slated to develop as second thoracics because incipient differentiation within the larval segments serves as a sure guide to their later fate.

The bithorax complex includes at least eight genes, all located in sequence right next to each other. Edward B. Lewis (see bibliography), the distinguished geneticist from CalTech who has spent twenty years probing the complexities of BX-C, believes that these eight genes arose as repetitions of a single ancestral gene and then evolved in different directions. Just as the entire deletion of BX-C produces the striking homeotic effect of converting all posterior segments to second thoracics, several mutations in the eight genes produce homeotic results as well. The most famous mutation, called bithorax and commandeered as a name for the entire complex, converts the third thoracic segment into a second thoracic. Thus, the adult fly develops with two second thoracics and two pairs of wings, instead of one pair and a pair of halteres behind. (It is misleading to state that halteres "turn into" wings. Rather, the entire segment normally destined to be a third thoracic, and to produce halteres, develops as a second thoracic and builds wings.) In another mutation, called bithoraxoid, the first abdominal segment develops as a third thoracic, builds a pair of legs, and produces a fly with more than the usual insect number of six.

Lewis has proposed an interesting hypothesis for the normal action of BX-C genes. He believes that they are initially repressed (turned off) in the larval fly. As the fly develops, BX-C genes are progressively derepressed (turned on). The BX-C genes act as regulators—that is, they do not build parts of the body themselves but are responsible for turning on the structural genes that do code for building blocks. Adult form reflects the amount of BX-C gene-product in an embryonic segment; the more BX-C, the more posterior in appearance the segment. Lewis then argues that BX-C genes are derepressed in sequence, from the anterior point of their action (the third thoracic segment) to the back end of the animal. When a BX-C gene turns on, its product accumulates in a given segment and, simultaneously, in all segments posterior to it. BX-C first turns on in the third thoracic, and its product accumulates in all segments from the third thoracic to the posterior end. The next BX-C gene turns on in the next posterior segment, the first abdominal, and its product accumulates in all segments from the first abdominal to the posterior end. The next gene turns on in the second abdominal, and so forth. Thus, a gradient of BX-C product forms, with lowest concentration in the second thoracic and increasing amounts in a posterior direction. The more gene product, the more posterior in appearance the form of a resultant segment.

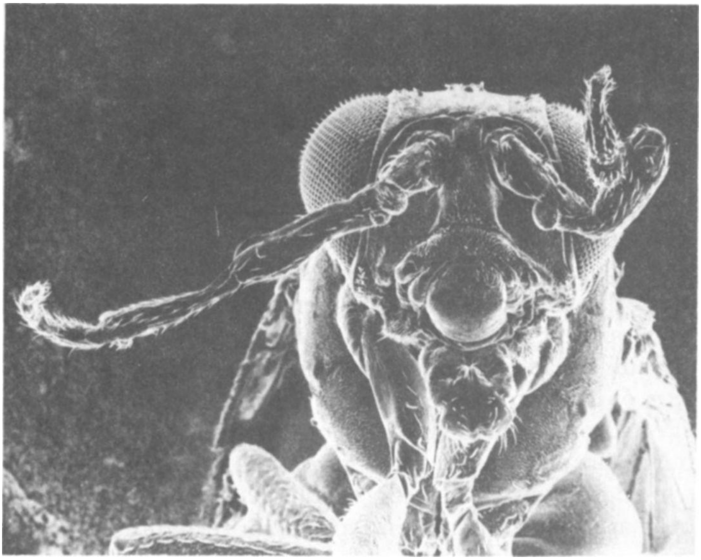
This hypothesis is consistent with the known homeotic effects of BX-C mutations. If BX-C is deleted entirely, it supplies no gene product, and all segments behind the second thoracic differentiate as second thoracics. In a mutation with opposite effect, all the BX-C genes are turned on at the same time in all segments—and all segments affected by BX-C then differentiate as eighth abdominals.

The second outstanding set of homeotics is also named for its most famous mutation—the antennapedia complex, or ANT-C. The fine structure of this complex has recently been elucidated in a series of remarkable experiments by Thomas C. Kaufman, Ricki Lewis, Barbara Wakimoto, and Tulle Hazelrigg in Kaufman's laboratory at the University of Indiana. (I thank Dr. Kaufman for introducing me to the literature of homeosis and for patient and lucid explanations of his own work.) The BX-C genes regulate the morphology of segmentation from the third thoracic to the posterior end; ANT-C also affects the third thoracic, but then regulates development in the five segments anterior to it (the other two thoracics and the three that produce parts of the mouth). If the entire complex is deleted, then all three thoracic segments begin to differentiate as first thoracics (while the abdominals, regulated by BX-C, develop normally). Apparently, the genes of ANT-C normally turn on in the second thoracic segment and trigger the proper development of the second and third thoracics.

Kaufman and his colleagues have found that ANT-C consists of at least seven genes, not all with known homeotic effects, lying right next to each other on the right arm of the third chromosome in *D. melanogaster.* The genes are not named for their normal effects (which, after all, just yield an ordinary fly bearing nothing special for recognition) but for their rare homeotic mutations. The first, the antennapedia gene, regulates differentiation of the second thoracic segment, and normally turns on there to accomplish its appointed function. A series of mutations has been detected at this locus, all with homeotic effects consistent with this interpretation of normal function.

One dominant mutation, antennapedia itself, has the bizarre effect (as its name implies) of producing a leg where an antenna ought to be. This wayward appendage is not any old leg, but clearly a second thoracic. The antennapedia mutation apparently works by turning on in the wrong place —the antennal segment—rather than in the second thoracic segment.

Another dominant mutation, called extra sex combs, leads to the appearance of sex combs on all three pairs of legs, not only on the first as in normal flies. This morphology is not simply the result of a gene that makes sex combs (contrary to popular belief, very few genes simply "make" individual parts without series of complex and coordinated effects). It is a homeotic mutation. All three thoracic segments differenti-



A fly with antennapedia mutation, in which legs form where the antenna should be. SCANNING ELECTRON MICROSCOPE PHOTO BY F. R. TURNER.

ate as first thoracics, and the fly has, literally, three pairs of first legs with their attendant sex combs. (The entire deletion of ANT-C also causes the three thoracics to differentiate as first thoracics, but this deletion is lethal and the fly dies in its larval stage. Flies with the extra sex comb mutation do live to become adults.) The extra sex comb mutation probably operates by suppressing the normal action of its gene. Since normal action causes the second thoracic segment to differentiate properly, suppression induces all three thoracics to develop as first thoracics.

The second gene of ANT-C is named for its prominent mutation, reduced sex comb. This homeotic mutation, contrary to the effect of its neighbor extra sex comb, causes the first thoracic segment to differentiate as a second thoracic. Only first thoracic legs bear sex combs in *D. melanogaster.* The next three genes do not have known homeotic effects, and their inclusion within ANT-C is something of a puzzle. One deletes a number of embryonic segments in its most prominent mutation, another interferes with normal development of the maxilla and mandible of the mouth, while the third produces a curiously wrinkled embryo.

The sixth gene of ANT-C is named for the other famous homeotic mutant of this complex—proboscipedia, discovered in 1933 by two of the century's most famous geneticists, Calvin Bridges and Theodosius Dobzhansky. Six mutations have been detected at this locus; most, like proboscipedia itself, produce legs where parts of the mouth should develop. The seventh and last (known) gene of ANT-C lacks homeotic effects in its mutant form and produces severe constrictions at segment boundaries in the larva. It is lethal.

Homeosis is not peculiar to fruit flies, but seems to be a general phenomenon, at least in arthropods. A set of mutations analogous (or even homologous) with the bithorax homeotics of *Drosophila* occurs in the silk moth *Bombyx* (order Lepidoptera; flies belong to the order Diptera). Two species of *Tribolium,* the flour beetle (order Coleoptera), exhibit mutations with effects that mimic the ANT-C homeotics of *Drosophila.* One set, in *Tribolium castaneum,* acts like antennapedia and produces a graded series of partial replacements of antennae by legs, ranging from tarsal claws on the eleventh antennal segment to the virtual replacement of an entire antenna with a foreleg. Another, in *T. confusum,* acts like proboscipcdia and substitutes legs of the first thoracic segment for mouth structures known as labial palps. In the cockroach *Blatella germamca,* a homeotic mutant produces rudimentary wings on the first thoracic segment. No modern insect normally bears wings on its first thoracic segment, but the earliest winged fossil insects did!

Homeosis is easiest to demonstrate in arthropods with their characteristic body plan of discrete segments with different and definite fates in normal development, but common embryological and evolutionary origins. Yet analogous phenomena have been noted again and again in other animals and plants with repeated parts. In fact, Bateson's first example after defining the term cited vertebrae in the human backbone. All mammals (except sloths, but including giraffes) have seven cervical, or neck, vertebrae (they are awfully large in giraffes). These are followed by dorsal, or rib-bearing, vertebrae. Bateson noted numerous cases of humans with ribs on the seventh, and even a few with ribs on the sixth, cervical vertebra.

Homeotic mutants are gripping in their weirdness, but what do they teach us about evolution? We must avoid, I believe, the tempting but painfully naive idea that they represent the long-sought "hopeful monsters" that might validate extreme saltationist views of major evolutionary transitions in single steps (a notion that I, despite my predilections for rapid change, regard as a fantasy born of insufficient appreciation for organisms as complex and integrated entities). First of all, most homeotic mutations produce hopeless creatures. The legs that extend from antennal sockets or surround mouths in afflicted flies are useless appendages without proper neural and muscular hookups. Even if they did work, what could they accomplish in such odd positions? Secondly, the viable homeotics mimicking ancestral forms are not really forebears reborn. A bithorax fly bears the ancestral complement of four wings, but it attains this state by growing two second thoraxes, not by recovering an ancient pattern.

I believe that the lessons of homeosis lie first in embryology and then cycle back to evolution. As Tom Kaufman pointed out to me, they demonstrate in a dramatic way how few genes are responsible for regulating the basic order of developing parts in a fruit fly's body. Together, the ANT-C and BX-C complexes of *D. melanogaster* specify the normal development of all the mouth, thoracic, and abdominal segments—only the two anterior segments are not subject to their control. Each complex contains only a handful of genes and each handful may have evolved from a single ancestral gene that repeated itself several times. When these genes mutate or are deleted, peculiar homeotic effects arise that usually throw development awry and lead to death.

Most importantly perhaps, these homeotic complexes display the hierarchical way in which genetic programs regulate the immense complexity of embryonic development, recognized since Aristotle's time as biology's greatest mystery. The homeotic genes do not build the different structures of each body segment themselves. This is the role of so-called structural genes that direct the assembly of proteins. The homeotics are switches or regulators; they produce some signal (of utterly unknown nature) that turns on whole blocks of structural genes.

Yet, at a higher level, some master regulator must be responsible for turning on the homeotics at the right time and in the right place, for we know that many homeotic mutations are mistakes in placement and timing. Perhaps this master regulator is no more than a gradient of some substance running from the front to the back end of a larval fly; perhaps the homeotic regulators can "read" this gradient and turn on in the right place by assessing its concentration. In any case, we have three hierarchical levels of control: the structural genes that build different parts in each segment, the homeotic regulators that switch on the blocks of structural genes, and the higher regulators that turn on instead of piercing, they would be no match for the normal kind because they have longer larval lives, increased pupal mortality, and a significant decrease in adult longevity. Still, these are the curious facts that nurture hope in parlous times—in this case, and with only a little poetic license, an enormous advantage (if only for another long-suffering creature) of putting a foot in one's mouth.

Evolution as Fact and Theory*

KIRTLEY MATHER, who died last year at age ninety, was a pillar of both science and Christian religion in America and one of my dearest friends. The difference of a half-century in our ages evaporated before our common interests. The most curious thing we shared was a battle we each fought at the same age. For Kirtley had gone to Tennessee with Clarence Darrow to testify for evolution at the Scopes trial of 1925. When I think that we are enmeshed again in the same struggle for one of the best documented, most compelling and exciting concepts in all of science, I don't know whether to laugh or cry.

According to idealized principles of scientific discourse, the arousal of dormant issues should reflect fresh data that give renewed life to abandoned notions. Those outside the current debate may therefore be excused for suspecting that creationists have come up with something new, or that evolutionists have generated some serious internal trouble. But nothing has changed; the creationists have presented not a single new fact or argument. Darrow and Bryan were at least more entertaining than we lesser antagonists today. The rise of creationism is politics, pure and simple; it represents one issue (and by no means the major concern) of the resurgent evangelical right. Arguments that seemed kooky just a decade ago have reentered the mainstream.

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The basic attack of modern creationists falls apart on two general counts before we even reach the supposed factual details of their assault against evolution. First, they play upon a vernacular misunderstanding of the word "theory" to convey the false impression that we evolutionists are covering up the rotten core of our edifice. Second, they misuse a popular philosophy of science to argue that they are behaving scientifically in attacking evolution. Yet the same philosophy demonstrates that their own belief is not science, and that "scientific creationism" is a meaningless and self-contradictory phrase, an example of what Orwell called "newspeak."

In the American vernacular, "theory" often means "imperfect fact"—part of a hierarchy of confidence running downhill from fact to theory to hypothesis to guess. Thus, creationists can (and do) argue: evolution is "only" a theory, and intense debate now rages about many aspects of the theory. If evolution is less than a fact, and scientists can't even make up their minds about the theory, then what confidence can we have in it? Indeed, President Reagan echoed this argument before an evangelical group in Dallas when he said (in what I devoutly hope was campaign rhetoric): "Well, it is a theory. It is a scientific theory only, and it has in recent years been challenged in the world of science—that is, not believed in the scientific community to be as infallible as it once was."

Well, evolution *is* a theory. It is also a fact. And facts and theories are different things, not rungs in a hierarchy of increasing certainty. Facts are the world's data. Theories are structures of ideas that explain and interpret facts. Facts do not go away while scientists debate rival theories for explaining them. Einstein's theory of gravitation replaced Newton's, but apples did not suspend themselves in mid-air pending the outcome. And human beings evolved from apelike ancestors whether they did so by Darwin's proposed mechanism or by some other, yet to be discovered.

Moreover, "fact" does not mean "absolute certainty." The final proofs of logic and mathematics flow deductively from stated premises and achieve certainty only because they are *not* about the empirical world. Evolutionists make no claim for perpetual truth, though creationists often do (and then attack us for a style of argument that they themselves favor). In science, "fact" can only mean "confirmed to such a degree that it would be perverse to withhold provisional assent." I suppose that apples might start to rise tomorrow, but the possibility does not merit equal time in physics classrooms.

Evolutionists have been clear about this distinction between fact and theory from the very beginning, if only because we have always acknowledged how far we are from completely understanding the mechanisms (theory) by which evolution (fact) occurred. Darwin continually emphasized the difference between his two great and separate accomplishments: establishing the fact of evolution, and proposing a theory—natural selection—to explain the mechanism of evolution. He wrote in *The Descent of Man:* "I had two distinct objects in view; firstly, to show that species had not been separately created, and secondly, that natural selection had been the chief agent of change . . . Hence if I have erred in ... having exaggerated its [natural selection's] power ... I have at least, as I hope, done good service in aiding to overthrow the dogma of separate creations."

Thus Darwin acknowledged the provisional nature of natural selection while affirming the fact of evolution. The fruitful theoretical debate that Darwin initiated has never ceased. From the 1940s through the 1960s, Darwin's own theory of natural selection did achieve a temporary hegemony that it never enjoyed in his lifetime. But renewed debate characterizes our decade, and, while no biologist questions the importance of natural selection, many now doubt its ubiquity. In particular, many evolutionists argue that substantial amounts of genetic change may not be subject to natural selection and may spread through populations at random. Others are challenging Darwin's linking of natural selection with gradual, imperceptible change through all intermediary degrees; they are arguing that most evolutionary events may occur far more rapidly than Darwin envisioned.

Scientists regard debates on fundamental issues of theory as a sign of intellectual health and a source of excitement. Science is—and how else can I say it?—most fun when it plays with interesting ideas, examines their implications, and recognizes that old information may be explained in surprisingly new ways. Evolutionary theory is now enjoying this uncommon vigor. Yet amidst all this turmoil no biologist has been led to doubt the fact that evolution occurred; we are debating *how* it happened. We are all trying to explain the same thing: the tree of evolutionary descent linking all organisms by ties of genealogy. Creationists pervert and caricature this debate by conveniently neglecting the common conviction that underlies it, and by falsely suggesting that we now doubt the very phenomenon we are struggling to understand.

Secondly, creationists claim that "the dogma of separate creations," as Darwin characterized it a century ago, is a scientific theory meriting equal time with evolution in high school biology curricula. But a popular viewpoint among philosophers of science belies this creationist argument. Philosopher Karl Popper has argued for decades that the primary criterion of science is the falsifiability of its theories. We can never prove absolutely, but we can falsify. A set of ideas that cannot, in principle, be falsified is not science.

The entire creationist program includes little more than a rhetorical attempt to falsify evolution by presenting supposed contradictions among its supporters. Their brand of creationism, they claim, is "scientific" because it follows the Popperian model in trying to demolish evolution. Yet Popper's argument must apply in both directions. One does not become a scientist by the simple act of trying to falsify a rival and truly scientific system; one has to present an alternative system that also meets Popper's criterion—it too must be falsifiable in principle.

"Scientific creationism" is a self-contradictory, nonsense phrase precisely because it cannot be falsified. I can envision observations and experiments that would disprove any evolutionary theory I know, but I cannot imagine what potential data could lead creationists to abandon their beliefs. Unbeatable systems are dogma, not science. Lest I seem harsh or rhetorical, I quote creationism's leading intellectual, Duane Gish, Ph.D., from his recent (1978) book, *Evolution? The Fossils Say No!* "By creation we mean the bringing into being by a supernatural Creator of the basic kinds of plants and animals by the process of sudden, or fiat, creation. We do not know how the Creator created, what processes He used, *for He used processes which are not now operating anywhere in the natural universe* [Gish's italics]. This is why we refer to creation as special creation. We cannot discover by scientific investigations anything about the creative processes used by the Creator." Pray tell, Dr. Gish, in the light of your last sentence, what then is "scientific" creationism?

Our confidence that evolution occurred centers upon three general arguments. First, we have abundant, direct, observational evidence of evolution in action, from both field and laboratory. This evidence ranges from countless experiments on change in nearly everything about fruit flies subjected to artificial selection in the laboratory to the famous populations of British moths that became black when industrial soot darkened the trees upon which the moths rest. (Moths gain protection from sharp-sighted bird predators by blending into the background.) Creationists do not deny these observations; how could they? Creationists have tightened their act. They now argue that God only created "basic kinds," and allowed for limited evolutionary meandering within them. Thus toy poodles and Great Danes come from the dog kind and moths can change color, but nature cannot convert a dog to a cat or a monkey to a man.

The second and third arguments for evolution—the case for major changes—do not involve direct observation of evolution in action. They rest upon inference, but are no less secure for that reason. Major evolutionary change requires too much time for direct observation on the scale of recorded human history. All historical sciences rest upon inference, and evolution is no different from geology, cosmology, or human history in this respect. In principle, we cannot observe processes that operated in the past. We must infer them from results that still surround us: living and fossil organisms for evolution, documents and artifacts for human history, strata and topography for geology.

The second argument—that the imperfection of nature reveals evolution—strikes many people as ironic, for they feel that evolution should be most elegantly displayed in the nearly perfect adaptation expressed by some organisms—the camber of a gull's wing, or butterflies that cannot be seen in ground litter because they mimic leaves so precisely. But perfection could be imposed by a wise creator or evolved by natural selection. Perfection covers the tracks of past history. And past history—the evidence of descent—is the mark of evolution.

Evolution lies exposed in the *imperfections* that record a history of descent. Why should a rat run, a bat fly, a porpoise swim, and I type this essay with structures built of the same bones unless we all inherited them from a common ancestor? An engineer, starting from scratch, could design better limbs in each case. Why should all the large native mammals of Australia be marsupials, unless they descended from a common ancestor isolated on this island continent? Marsupials are not "better," or ideally suited for Australia; many have been wiped out by placental mammals imported by man from other continents. This principle of imperfection extends to all historical sciences. When we recognize the etymology of September, October, November, and December (seventh, eighth, ninth, and tenth), we know that the year once started in March, or that two additional months must have been added to an original calendar of ten months.

The third argument is more direct: transitions are often found in the fossil record. Preserved transitions are not common—and should not be, according to our understanding of evolution (see next section)—but they are not entirely wanting, as creationists often claim. The lower jaw of reptiles contains several bones, that of mammals only one. The non-mammalian jawbones are reduced, step by step, in mammalian ancestors until they become tiny nubbins located at the back of the jaw. The "hammer" and "anvil" bones of the mammalian ear are descendants of these nubbins. How could such a transition be accomplished? the creationists ask. Surely a bone is either entirely in the jaw or in the ear. Yet paleontologists have discovered two transitional lineages of therapsids (the so-called mammal-like reptiles) with a double jaw joint—one composed of the old quadrate and articular bones (soon to become the hammer and anvil), the other of the squamosal and dentary bones (as in modern mammals). For that matter, what better transitional form could we expect to find than the oldest human, *Australopithecus afarensis,* with its apelike palate, its human upright stance, and a cranial capacity larger than any ape's of the same body size but a full 1,000 cubic centimeters below ours? If God made each of the half-dozen human species discovered in ancient rocks, why did he create in an unbroken temporal sequence of progressively more modern features—increasing cranial capacity, reduced face and teeth, larger body size? Did he create to mimic evolution and test our faith thereby?

Faced with these facts of evolution and the philosophical bankruptcy of their own position, creationists rely upon distortion and innuendo to buttress their rhetorical claim. If I sound sharp or bitter, indeed I am—for I have become a major target of these practices.

I count myself among the evolutionists who argue for a jerky, or episodic, rather than a smoothly gradual, pace of change. In 1972 my colleague Niles Eldredge and I developed the theory of punctuated equilibrium. We argued that two outstanding facts of the fossil record—geologically "sudden" origin of new species and failure to change thereafter (stasis)—reflect the predictions of evolutionary theory, not the imperfections of the fossil record. In most theories, small isolated populations are the source of new species, and the process of speciation takes thousands or tens of thousands of years. This amount of time, so long when measured against our lives, is a geological microsecond. It represents much less than 1 per cent of the average lifespan for a fossil invertebrate species—more than ten million years. Large, widespread, and well established species, on the other hand, are not expected to change very much. We believe that the inertia of large populations explains the stasis of most fossil species over millions of years.

We proposed the theory of punctuated equilibrium largely to provide a different explanation for pervasive trends in the fossil record. Trends, we argued, cannot be attributed to gradual transformation within lineages, but must arise from the differential success of certain kinds of species. A trend, we argued, is more like climbing a flight of stairs (punctuations and stasis) than rolling up an inclined plane.

Since we proposed punctuated equilibria to explain trends, it is infuriating to be quoted again and again by creationists—whether through design or stupidity, I do not know—as admitting that the fossil record includes no transitional forms. Transitional forms are generally lacking at the species level, but they are abundant between larger groups. Yet a pamphlet entitled "Harvard Scientists Agree Evolution Is a Hoax" states: "The facts of punctuated equilibrium which Gould and Eldredge . . . are forcing Darwinists to swallow fit the picture that Bryan insisted on, and which God has revealed to us in the Bible."

Continuing the distortion, several creationists have equated the theory of punctuated equilibrium with a caricature of the beliefs of Richard Goldschmidt, a great early geneticist. Goldschmidt argued, in a famous book published in 1940, that new groups can arise all at once through major mutations. He referred to these suddenly transformed creatures as "hopeful monsters." (I am attracted to some aspects of the non-caricatured version, but Goldschmidt's theory still has nothing to do with punctuated equilibrium—see essays in section 3 and my explicit essay on Goldschmidt in *The Panda's Thumb.*) Creationist Luther Sunderland talks of the "punctuated equilibrium hopeful monster theory" and tells his hopeful readers that "it amounts to tacit admission that anti-evolutionists are correct in asserting there is no fossil evidence supporting the theory that all life is connected to a common ancestor." Duane Gish writes, "According to Goldschmidt, and now apparently according to Gould, a reptile laid an egg from which the first bird, feathers and all, was produced." Any evolutionist who believed such nonsense would rightly be laughed off the intellectual stage; yet the only theory that could ever envision such a scenario for the origin of birds is creationism—with God acting in the egg.

I am both angry at and amused by the creationists; but mostly I am deeply sad. Sad for many reasons. Sad because so many people who respond to creationist appeals are troubled for the right reason, but venting their anger at the wrong target. It is true that scientists have often been dogmatic and elitist. It is true that we have often allowed the white-coated, advertising image to represent us—"Scientists say that Brand X cures bunions ten times faster than . . ." We have not fought it adequately because we derive benefits from appearing as a new priesthood. It is also true that faceless and bureaucratic state power intrudes more and more into our lives and removes choices that should belong to individuals and communities. I can understand that school curricula, imposed from above and without local input, might be seen as one more insult on all these grounds. But the culprit is not, and cannot be, evolution or any other fact of the natural world. Identify and fight your legitimate enemies by all means, but we are not among them.

I am sad because the practical result of this brouhaha will not be expanded coverage to include creationism (that would also make me sad), but the reduction or excision of evolution from high school curricula. Evolution is one of the half dozen "great ideas" developed by science. It speaks to the profound issues of genealogy that fascinate all of us—the "roots" phenomenon writ large. Where did we come from? Where did life arise? How did it develop? How are organisms related? It forces us to think, ponder, and wonder. Shall we deprive millions of this knowledge and once again teach biology as a set of dull and unconnected facts, without the thread that weaves diverse material into a supple unity?

But most of all I am saddened by a trend I am just beginning to discern among my colleagues. I sense that some now wish to mute the healthy debate about theory that has brought new life to evolutionary biology. It provides grist for creationist mills, they say, even if only by distortion. Perhaps we should lie low and rally round the flag of strict Darwinism, at least for the moment—a kind of old-time religion on our part.

But we should borrow another metaphor and recognize that we too have to tread a straight and narrow path, surrounded by roads to perdition. For if we ever begin to suppress our search to understand nature, to quench our own intellectual excitement in a misguided effort to present a united front where it does not and should not exist, then we are truly lost.

A Visit to Dayton

IN HIS SUMMATION to the court, Clarence Darrow talked for three full days to save the lives of Nathan Leopold and Richard Loeb. Guilty they clearly were, of perhaps the most brutal and senseless murder of the 1920s. By arguing that they were victims of their upbringing, Darrow sought only to mitigate their personal responsibility and substitute a lifetime in jail for the noose. He won, as he usually did.

John Thomas Scopes, defendant in Darrow's next famous case, recalled his attorney's theory of human behavior in the opening lines of an autobiography published long after the famous "monkey trial" (see bibliography): "Clarence Darrow spent his life arguing teaching, really—that a man is the sum of his heredity and his environment." The world may seem capricious, but events have their reasons, however complex. These reasons conspire to drive events forward; Leopold and Loeb were not free agents when they bludgeoned Bobby Franks and stuffed his body into a culvert, all to test the idea that a perfect crime might be committed by men of sufficient intelligence.

We wish to find reasons for the manifest senselessness that surrounds us. But deterministic theories, like Darrow's, leave out the genuine randomness of our world, a chanciness that gives meaning to the old concept of human free will. Many events, although they move forward with accelerating inevitability after their inception, begin as a concatenation of staggering improbabilities. And so we all began, as one sperm among billions vying for entry; a microsecond later, I might have been the Stephanie my mother wanted.

The Scopes trial in Dayton, Tennessee, occurred as the outcome of accumulated improbability. The Butler Act, passed by the Tennessee legislature and signed by Gov. Austin Peay on March 21,1925, declared it "unlawful for any teacher in any of the Universities, Normals and all other public schools of the state—which are supported in whole or in part by the public school funds of the State, to teach any theory that denies the story of the Divine Creation of man as taught in the Bible, and to teach instead that man has descended from a lower order of animals." The bill could have been beaten with little trouble had the opposition bothered to organize and lobby (as they had the previous year in Kentucky, when a similar bill in similar circumstances went down to easy defeat). The senate passed it with no enthusiasm, assuming a gubernatorial veto. One member said of Mr. Butler: "The gentleman from Macon wanted a bill passed; he had not had much during the session and this did not amount to a row of pins; let him have it." But Peay, admitting the bill's absurdity and protesting that the legislature should have saved him from embarrassment by defeating it, signed the act as an innocuous statement of Christian principles: "After a careful examination," wrote Peay, "I can find nothing of consequence in the books now being taught in our schools with which this bill will interfere in the slightest manner. Therefore it will not put our teachers in any jeopardy. Probably the law will never be applied.... Nobody believes that it is going to be an active statute." (See Ray Ginger's *Six Days or Forever?* for a fine account of the legislative debate.)

If the bill itself was improbable, Scopes's test of it was even more unlikely. The American Civil Liberties Union (ACLU) offered to supply council and provide legal costs for any teacher willing to challenge the act by courting an arrest for teaching evolution. The test was set for the favorable urban setting of Chattanooga, but plans fell through.

Scopes didn't even teach biology in the small, inappropriate, fundamentalist town of Dayton, located forty miles north of Chattanooga. He had been hired as an athletic coach and physics teacher but had substituted in biology when the regular instructor (and principal of the school) fell ill. He had not actively taught evolution at all, but merely assigned the offending textbook pages as part of a review for an exam. When some town boosters decided that a test of the Butler Act might put Dayton on the map—none showed much interest in the intellectual issues—Scopes was available only by another quirk of fate. (They would not have asked the principal, an older, conservative family man, but they suspected that Scopes, a bachelor and free thinker, might go along.) The school year was over, and Scopes had intended to depart immediately for a summer with his family. But he stayed on because he had a date with "a beautiful blonde" at a forthcoming church social.

Scopes was playing tennis on a warm afternoon in May, when a small boy appeared with a message from "Doc" Robinson, the local pharmacist and owner of Dayton's social center, Robinson's Drug Store. Scopes finished his game, for there is no urgency in Dayton, and then ambled on down to Robinson's, where he found Dayton's leading citizens crowded around a table, sipping Coke and arguing about the Butler Act. Within a few minutes, Scopes had offered himself as the sacrificial lamb. From that point, events accelerated and began to run along a predictable track. William Jennings Bryan, who had stirred millions with his "Cross of Gold" speech and almost become president as a result, was passing his declining years as a fundamentalist stumper—"a tinpot pope in the Coca-Cola belt," as H. L. Mencken remarked. He volunteered his services for the prosecution, and Clarence Darrow responded in kind for the defense. The rest, as they say, is history. Of late, it has, alas, become current events as well.

Robinson's Drug Store is still the social center of Dayton, although it moved in 1928 to its present location in the shadow of the Rhea County courthouse, where Scopes faced the wrath of Bryan's God. "Sonny" Robinson, Doc's

Robinson's Drug Store, where it all began, moved to its present location in the late 1920s, PHOTO BY DEBORAH COULD.

boy, has run the store for decades, dispensing pills to the local citizenry and thoughts about Dayton's moment of fame to the pilgrims and gawkers who stop by to see where it all started. The little round table, with its wire-backed chairs, occupies a central place, as it did when Scopes, Doc Robinson, and George Rappelyea (who made the formal "arrest") laid their plans in May 1925. The walls are covered with pictures and other memorabilia, including Sonny Robinson's only personal memory of the trial: a photograph of a five-year-old boy, sitting in a carriage and pouting because a chimpanzee had received the Coke he had expected. (The chimp was a prominent member in the motley entourage of camp followers, many of comparable intelligence, that descended upon Dayton during the trial, in search of ready cash rather than eternal enlightenment.)

I was visiting Robinson's Drug Store in June 1981, when a San Francisco paper called with a request for photos of modern Dayton. Sonny Robinson, who claims to be a shy

The interior of Robinson's is covered with photos and other mementos of the Scopes trial, PHOTO BY DEBORAH COULD.

man, began a flurry of calls to exploit the moment. Up north in the big town, you wouldn't keep a man waiting, at least not without a request or an explanation: "Excuse me, I know you must be in a hurry, but would you mind, it won't be more than a few minutes. . . ." But it was 97° outside and cool in Sonny Robinson's store. And where would a man be going anyway? Half an hour later, his personages assembled, Sonny Robinson pulled out the famous table and brought three Cokes in some old-fashioned five-cent glasses. I sat in the middle ("the biology professor from Harvard who just happened to walk in," as Robinson had told his callers). On one side sat Ted Mercer, president of Bryan College, the fundamentalist school begun as a legacy to the "Great Commoner's" last battle. On the other side sat Mr. Robinson, son of the man who had started it all around the same table fifty-six years before. The fundamentalist editor of the Dayton *Herald* snapped our pictures and we sipped our Cokes.

Dayton has remained a small and inconspicuous town. If you're coming from Knoxville via Decatur, you still have to cross the Tennessee River on a six-car ferry. The older

A proper way to treat the issues that divide us. Three men of divergent views chat and sip Coke aound the "original" table in Robinson's Drug Store. Left, Ted Mercer, president of fundamentalist Bryan College; center, yours truly; right, Sonny Robinson. PHOTO BY DEBORAH GOULD.

houses are well kept, with four white pillars in front, the vernacular imitation of plantation style. (As a regional marker of the South, these pillars are architecture's equivalent of the dependable gastronomical criterion: when the beverage simply labeled "tea" on the menu invariably comes iced.) H. L. Mencken, not known for words of praise, confessed (in surprise) his liking for Dayton:

> I had expected to find a squalid Southern village . . . with pigs rooting under the houses and the inhabitants full of hookworm and malaria. What I found was a country town full of charm and even beauty. . . . The

> houses are surrounded by pretty gardens, with cool green lawns and stately trees.... The stores carry good stocks and have a metropolitan air, especially the drug, book, magazine, sporting goods and soda-water emporium of the estimable Robinson.

Some things have changed, of course. Trailers now rooted to their turf and houses of undressed concrete block reflect the doubling of Dayton's population to nearly 4,000. The older certainties may have eroded somewhat. A banner headline in this week's Dayton *Herald* tells of a $200-million marijuana crop confiscated and destroyed in Rhea and neighboring Bledsoe counties. And a quarter gets you a condom—"sold for the prevention of disease only," of course—at vending machines in restrooms of local service stations. At least they can't blame evolution for this, as one evangelical minister did a few months back when he cited Darwin as a primary supporter of the four "p's": prostitu-

The Rhea County Court House in Dayton, Tennessee, scene of the Scopes trial, PHOTO BY DEBORAH COULD.

tion, perversion, pornography, and permissiveness. They taught creationism in Dayton before John Scopes arrived, and they teach it today.

For all these muted changes, Dayton remains a two-street town, dwarfed at the crossroad by the Rhea County courthouse, a Renaissance Revival building of the 1890s seemingly too large by half for a small town in a small county. Yet even this courtroom failed in its moment of glory, as Judge Raulston, noting that the weight of humanity had opened cracks in the ceiling below, reconvened his court on the side lawn, where Darrow grilled Bryan alfresco. (It is a meaningless and tangential irony to be sure, but I thought I'd mention it. Rhea was the daughter of Uranus and the mother of Zeus. Her name also applies to the South American "ostrich." On the *Beagle* voyage, Darwin rediscovered a second species, the lesser, or Darwin's, rhea, living in a different part of South America. In one of his first evolutionary speculations, Darwin surmised that the spatial difference between these two rheas might be analogous to the temporal distinction between extinct species and their living relatives.)

The Scopes trial is surrounded by misconceptions, and their exposure provides as good a way as any for recounting the basic story. In the heroic version, John Scopes was persecuted, Darrow rose to Scopes's defense and smote the antediluvian Bryan, and the antievolution movement then dwindled or ground to at least a temporary halt. All three parts of this story are false.

For the first, we have already noted that Austin Peay and the legislators of Tennessee did not intend to enforce their law. In fact, Bryan himself had lobbied the legislature (unsuccessfully) with advice that the act prescribe no penalty for noncompliance. It was, after all, only a symbolic statement; any teeth in the act might lead to its upset on constitutional grounds. The ACLU advertised in Tennessee papers for a test case. George Rappelyea read their offer in the Chattanooga *Times* and moseyed on down to Robinson's with his plan. Later, John Scopes remembered: "It was just a drugstore discussion that got past control." For once, the tale of outside (even Yankee) agitators tells at least a half-truth.

Bryan was vanquished and embarrassed during the trial, but not primarily by Darrow. The trial itself, with its foregone conclusion, was something of a bore. (Scopes *had* violated the law and the defense wanted a quick conviction for an advantageous move to a higher court.) It dragged on in interminable legal wrangling and had only two moments of high drama. The first occurred during a legal argument about the admissibility of expert testimony. The defense had brought to Dayton an impressive array of men prominent both in evolutionary biology and Christian conviction. The prosecution urged that their testimony be excluded. The law plainly forbade the teaching of human evolution, and Scopes just as plainly had violated the law. The potential truth of evolution was not at issue. Judge Raulston agreed with the prosecution, and the assembled experts took to their typewriters instead. With benefit of a weekend recess to hone their statements, the experts produced some formidable documents. They were printed in newspapers throughout the country, and Judge Raulston finally did admit them into the printed record of the trial.

Bryan, who had sat in uncharacteristic silence for several days, used this procedural argument as a springboard for his prepared excoriation of evolution. In a grandiloquent speech clearly directed to his constituents (witnesses remarked that he stood with his back to the judge), Bryan virtually denied that humans were mammals and argued that the case of Messrs. Leopold and Loeb amply demonstrated that too much learning is a dangerous thing. The defense's rebuttal provided Bryan's first humiliation; for in this rural land, before the advent of television, no art commanded more respect than speechifying. And Bryan was just plain outspoken, outgestured, and outshouted—not by Darrow, but by another defense attorney, Dudley Field Malone, a prominent New York divorce lawyer and former subordinate to Bryan in the State Department (where Bryan had been secretary under Woodrow Wilson). H. L. Mencken wrote:

> I doubt that any louder speech has ever been heard in a court of law since the days of Gog and Magog. It

> roared out of the open windows like the sound of artillery practice, and alarmed the moonshiners and catamounts on distant peaks. . . . In brief, Malone was in good voice. It was a great day for Ireland. And for the defense. For Malone not only out-yelled Bryan, he also plainly out-generaled and out-argued him. . . . It conquered even the fundamentalists. At its end they gave it a tremendous cheer—a cheer at least four times as hearty as that given to Bryan. For these rustics delight in speechifying, and know when it is good. The devil's logic cannot fetch them, but they are not above taking a voluptuous pleasure in his lascivious phrases.

Nonetheless, Judge Raulston ruled against the defense and excluded expert testimony the next morning. It was Friday and all seemed over, including the shouting. Scopes would be convicted summarily on Monday morning; he had violated the law and Raulston's narrow construction of the case had excluded all other issues. Virtually all the journalists, including H. L. Mencken, left town to avoid both the lull of a weekend recess and the expected anticlimax to follow. Thus, when Darrow induced Bryan to take the stand as an expert witness on the Bible, he spoke to a depleted local crowd and a skeleton crew of journalists. The reconstructions of *Inherit the Wind* and other accounts dramatize what was only an afterthought.

It is not even clear why Raulston allowed Bryan to appear (since he had excluded experts of opposite persuasion). The other prosecuting attorneys tried to dissuade Bryan, and Raulston finally expunged the entire exchange from the record. Bryan viewed the occasion as a desperate attempt to recover from Malone's drubbing, but Darrow exposed him as a pompous fool. Still, the most famous moment of the exchange—when Bryan deserted strict fundamentalist tenets by admitting that the days of Genesis might have lasted far longer than twenty-four hours—was not, as legend has it, a reluctant admission drawn forth by Darrow's ruthless logic. Bryan offered this statement freely, as an initial response to a series of questions. He did not seem to appreciate that local fundamentalists would regard it as a betrayal, and the surrounding world as a fatal inconsistency.

Scope's conviction was eventually quashed on a technicality. Judge Raulston had set the fine of $100 himself, but Tennessee law required that all fines greater than $50 be recommended by the jury. With Bryan humiliated and the conviction quashed, the legend of victory for the defense arose, thus completing the heroic version. But the Scopes trial was a defeat (or a victory so Pyrrhic that it scarcely deserves the name) for several reasons. First, Bryan recouped by involuntarily taking the only option left for an immediate restoration of prestige: he died in Dayton a week after the trial ended. Ted Mercer's Bryan College, a thriving fundamentalist institution in Dayton, is his local legacy. Second, the quashing of Scopes's conviction was a bitter pill for the defense. Suddenly, there was no case left to appeal. All that effort down the tubes of a judge's $50 error.

The Butler Act remained on the books until its repeal in 1967. It was not enforced, but who can tell how many teachers muted or suppressed their views and how many children never learned one of the most exciting and expansive ideas ever developed by scientists. In 1973, a "Genesis Bill" passed the senate of Tennessee, 69 to 16. It legislated equal time for evolution and creation and required a disclaimer in all texts that any stated idea about "the origin and creation of man and his world ... is not represented to be scientific fact." The Bible, however, was declared a reference work, not a text, and therefore exempt from the requirement for a printed disclaimer. This bill was declared unconstitutional a few years later.

Third, and sadly, any hope that the issues of Scopes's trial had been banished to the realm of nostalgic Americana have been swept aside by our current creationist resurgence—the climate that inspired my own detour across the Tennessee River.

Late in his life, I came to know Kirtley Mather, emeritus professor of geology at Harvard, pillar of the Baptist church, lonely defender of academic freedom during the worst days of McCarthyism, and perhaps the finest man I have ever known. Kirtley was also a defense witness in Dayton. Each year, from the late 1960s to the mid 1970s, Kirtley gave a lecture to my class recalling his experiences at Dayton. It seemed a wonderful echo of times gone by, for Kirtley, in his late eighties, could still weave circles around the finest orators at Harvard. The lecture didn't change much from year to year. I viewed it first as a charming evocation, later as mildly related to current affairs, finally as a vital statement of pressing realities. This year, I will dust off the videotape and show it to my class as a disquisition on immediate dangers.

In 1965, John Scopes permitted himself this hope in retrospect:

> I believe that the Dayton trial marked the beginning of the decline of fundamentalism.... I feel that restrictive legislation on academic freedom is forever a thing of the past, that religion and science may now address one another in an atmosphere of mutual respect and of a common quest for truth. I like to think that the Dayton trial had some part in bringing to birth this new era.

(Scopes, by the way, later went to the University of Chicago and became a geologist. He lived quietly in Shreveport, Louisiana, for most of his life, working, as do so many geologists, for the petroleum industry. This splendid man of quiet integrity refused to capitalize on his transient and accidental fame in any way. His silence betokened no crisis of confidence or any departure from the principles that led to his momentary renown. He simply chose to make his own way on his own merits.)

Today, Jerry Falwell has donned Bryan's mantle, and Scopes's hopes for a "new era" have been thwarted. Of course, we will not replay Scopes's drama in exactly the same way; we have advanced somewhere in fifty-six years. Evolution is now too strong to exclude entirely, and current proposals for legislation mandate "equal time" for evolution and for old-time religion masquerading under the self-contradictory title of "scientific creationism." But the similarities between 1925 and 1981 are more disconcerting than the differences are comforting.

As in 1925, creationists are not battling for religion. They have been disowned by leading churchmen of all persuasions, for they debase religion even more than they misconstrue science. They are a motley collection to be sure, but their core of practical support lies with the evangelical right, and creationism is a mere stalking horse or subsidiary issue in a political program that would ban abortion, erase the political and social gains of women by reducing the vital concept of the family to an outmoded paternalism, and reinstitute all the jingoism and distrust of learning that prepares a nation for demagoguery.

As in 1925, they use the same methods of willful misquotation to impart a "scientific" patina to creationism. I am now a major victim of these efforts because my views on rapid evolutionary bursts followed by long periods of stasis can be distorted to apparent support for creation by fiat and unchanging persistence of immutable types (see last essay). I was therefore amused (or soothed) to read that, in 1925, Bryan and company were using the same strategy to exploit the forthright address that William Bateson had delivered to the American Association for the Advancement of Science in 1922. Bateson had expressed his confidence in the fact of evolution, but had honestly admitted that, despite reigning pomposity and textbook pap, we knew rather little about the mechanisms of evolutionary change. Scopes's prosecutors had cited Bateson as "proof that scientists had admitted the tenuousness of evolution itself. In his written affidavit to Judge Raulston, W. C. Curtis, a zoologist from the University of Missouri, submitted a letter from Bateson:

> I have looked through my Toronto address again. I see nothing in it which can be construed as expressing doubt as to the main fact of evolution. . . . I took occasion to call the attention of my colleagues to the loose thinking and unproven assumptions which pass current as to the actual processes of evolution. We do

> know that the plants and animals, including most certainly man, have been evolved from other and very different forms of life. As to the nature of this process of evolution, we have many conjectures but little positive knowledge.

Curtis also submitted a letter from Bryan's old boss Woodrow Wilson: "Of course, like every other man of intelligence and education, I do believe in organic evolution. It surprises me that at this late date such questions should be raised." Ronald Reagan, however, raised them on the stump before a fundamentalist crowd in Dallas.

I learned something in Dayton, or rather, remembered something I should never have forgotten, while sipping that five-cent Coke around the original table in Robinson's Drug Store. The enemy is not fundamentalism; it is intolerance. In this case, the intolerance is perverse since it masquerades under the "liberal" rhetoric of "equal time." But mistake it not. Creationists are trying to impose a specific religious view by legislative fiat upon teachers who reject it both by conscience and training. For all their talk about weighing both sides (a mere question of political expediency), they would also substitute biblical authority for free scientific inquiry as a source of empirical knowledge.

All the commentators at Dayton, including the caustic H. L. Mencken himself, noted that the local people, although secure in their creationist beliefs, showed no intolerance or even discourtesy to the opposition. They feted Bryan when he arrived in town, and they provided a spread of equal size for Darrow. They applauded Malone on the merits of his speech. Mencken wrote:

> Nor is there any evidence in the town of that poisonous spirit which usually shows itself when Christian men gather to defend the great doctrine of their faith. I have heard absolutely no whisper that Scopes is in the pay of the Jesuits, or that the whisky trust is backing him, or that he is egged on by the Jews who manufacture

> lascivious moving pictures. On the contrary, the Evolutionists and the Anti-Evolutionists seem to be on the best of terms and it is hard in a group to distinguish one from the other.

Dayton has persevered in its geniality. I encountered warm disagreement with my evolutionary views, but I sensed no disrespect for my opinions and no inclination to demote me as a person because I disagreed with a favored belief. Geniality of this sort is widespread but, alas, so fragile. A few seeds of ugliness and intolerance can generate the cover for an entire field. We have nothing to fear from the vast majority of fundamentalists who, like many citizens of Dayton, live by a doctrine that is legitimately indigenous to their area. Rather, we must combat the few yahoos who exploit the fruits of poor education for ready cash and larger political ends.

Bryan was easy prey for ridicule, since he was such a fool in his political dotage. Mencken wrote in his sharpest prose:

> Once he had one leg in the White House and the nation trembled under his roars. Now he is a tinpot pope in the Coca-Cola belt and a brother to the forlorn pastors who belabor half-wits in galvanized iron tabernacles behind the railroad yards. . . . It is a tragedy, indeed, to begin life as a hero and to end it as a buffoon.

Many current creationists seem equally pitiable in their pronouncements: can anyone take seriously a link between Darwinism and the four evil p's?

But Mencken also understood the dangers, for he wrote in his final lines:

> Let no one mistake it for comedy, farcical though it may be in all its details. It serves notice on the country that Neanderthal man is organizing in these forlorn backwaters of the land, led by a fanatic, rid of sense and devoid of conscience. Tennessee, challenging him too timor-

> ously and too late, now sees its courts converted into camp meetings and its Bill of Rights made a mock of by its sworn officers of the law.

Do movements of intolerance ever start in any other way, given our pervasive tendencies toward geniality? Do they not always begin in comedy and end, when successful, in carnage? Who did not regard Hitler as an object of pitiful derision after the beer hall putsch. And who can read the famous words of Protestant theologian Martin Niemoller without a shudder:

> First the Nazis went after the Jews, but I wasn't a Jew, so I did not react. Then they went after the Catholics, but I wasn't a Catholic, so I didn't object. Then they went after the workers, so I didn't stand up. Then they went after the Protestant clergy and by then it was too late for anybody to stand up.

Clarence Darrow understood the roots of intolerance only too well when he said in Dayton:

> If today you can take a thing like evolution and make it a crime to teach it in the public schools, tomorrow you can make it a crime to teach it in the private schools and next year you can make it a crime to teach it to the hustings or in the church. At the next session you may ban books and the newspapers. . . . Ignorance and fanaticism are ever busy and need feeding. Always feeding and gloating for more. Today it is the public school teachers; tomorrow the private. The next day the preachers and the lecturers, the magazines, the books, the newspapers. After a while, Your Honor, it is the setting of man against man and creed against creed until with flying banners and beating drums we are marching backward to the glorious ages of the sixteenth century when bigots lighted fagots to burn the men who dared to bring any intelligence and enlightenment and culture to the human mind.

Ever the cynic, H. L. Mencken evaluated this impassioned plea: "The net effect of Clarence Darrow's great speech yesterday seems to be precisely the same as if he had bawled it up a rainspout in the interior of Afghanistan." We had better proclaim the same message today into a downspout that resonates across the nation.

The Panda's Thumb

FEW HEROES LOWER their sights in the prime of their lives; triumph leads inexorably on, often to destruction. Alexander wept because he had no new worlds to conquer; Napoleon, overextended, sealed his doom in the depth of a Russian winter. But Charles Darwin did not follow the *Origin of Species* (1859) with a general defense of natural selection or with its evident extension to human evolution (he waited until 1871 to publish *The Descent of Man).* Instead, he wrote his most obscure work, a book entitled: *On the Various Contrivances by Which British and Foreign Orchids Are Fertilized by Insects* (1862).

Darwin's many excursions into the minutiae of natural history—he wrote a taxonomy of barnacles, a book on climbing plants, and a treatise on the formation of vegetable mold by earthworms—won him an undeserved reputation as an old-fashioned, somewhat doddering describer of curious plants and animals, a man who had one lucky insight at the right time. A rash of Darwinian scholarship has laid this myth firmly to rest during the past twenty years (see essay 2). Before then, one prominent scholar spoke for many ill-informed colleagues when he judged Darwin as a "poor joiner of ideas ... a man who does not belong with the great thinkers."

In fact, each of Darwin's books played its part in the grand and coherent scheme of his life's work—demonstrating the fact of evolution and defending natural selection as its primary mechanism. Darwin did not study orchids solely for their own sake. Michael Ghiselin, a California biologist who finally took the trouble to read all of Darwin's books (see his *Triumph of the Darwinian Method*), has correctly identified the treatise on orchids as an important episode in Darwin's campaign for evolution.

Darwin begins his orchid book with an important evolutionary premise: continued self-fertilization is a poor strategy for long-term survival, since offspring carry only the genes of their single parent, and populations do not maintain enough variation for evolutionary flexibility in the face of environmental change. Thus, plants bearing flowers with both male and female parts usually evolve mechanisms to ensure cross-pollination. Orchids have formed an alliance with insects. They have evolved an astonishing variety of "contrivances" to attract insects, guarantee that sticky pollen adheres to their visitor, and ensure that the attached pollen comes in contact with female parts of the next orchid visited by the insect.

Darwin's book is a compendium of these contrivances, the botanical equivalent of a bestiary. And, like the medieval bestiaries, it is designed to instruct. The message is paradoxical but profound. Orchids manufacture their intricate devices from the common components of ordinary flowers, parts usually fitted for very different functions. If God had designed a beautiful machine to reflect his wisdom and power, surely he would not have used a collection of parts generally fashioned for other purposes. Orchids were not made by an ideal engineer; they are jury-rigged from a limited set of available components. Thus, they must have evolved from ordinary flowers.

Thus, the paradox, and the common theme of this trilogy of essays: Our textbooks like to illustrate evolution with examples of optimal design—nearly perfect mimicry of a dead leaf by a butterfly or of a poisonous species by a palatable relative. But ideal design is a lousy argument for evolution, for it mimics the postulated action of an omnipotent creator. Odd arrangements and funny solutions are the proof of evolution—paths that a sensible God would never tread but that a natural process, constrained by history, follows perforce. No one understood this better than Darwin. Ernst Mayr has shown how Darwin, in defending evolution, consistently turned to organic parts and geographic distributions that make the least sense. Which brings me to the giant panda and its "thumb."

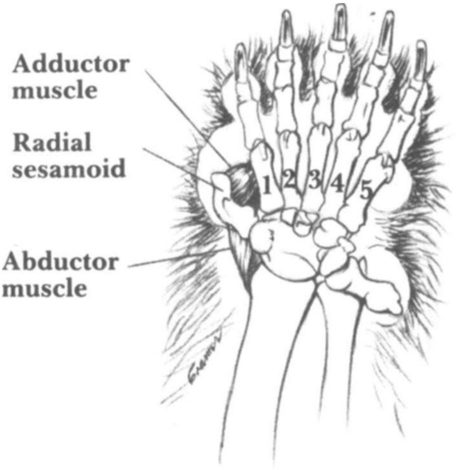
Giant pandas are peculiar bears, members of the order Carnivora. Conventional bears are the most omnivorous representatives of their order, but pandas have restricted this catholicity of taste in the other direction—they belie the name of their order by subsisting almost entirely on bamboo. They live in dense forests of bamboo at high elevations in the mountains of western China. There they sit, largely unthreatened by predators, munching bamboo ten to twelve hours each day.

As a childhood fan of Andy Panda, and former owner of a stuffed toy won by some fluke when all the milk bottles actually tumbled at the county fair, I was delighted when the first fruits of our thaw with China went beyond ping pong to the shipment of two pandas to the Washington zoo. I went and watched in appropriate awe. They yawned, stretched, and ambled a bit, but they spent nearly all their time feeding on their beloved bamboo. They sat upright and manipulated the stalks with their forepaws, shedding the leaves and consuming only the shoots.

I was amazed by their dexterity and wondered how the scion of a stock adapted for running could use its hands so adroitly. They held the stalks of bamboo in their paws and stripped off the leaves by passing the stalks between an apparently flexible thumb and the remaining fingers. This puzzled me. I had learned that a dexterous, opposable thumb stood among the hallmarks of human success. We had maintained, even exaggerated, this important flexibility of our primate forebears, while most mammals had sacrificed it in specializing their digits. Carnivores run, stab, and scratch. My cat may manipulate me psychologically, but he'll never type or play the piano.

So I counted the panda's other digits and received an even greater surprise: there were five, not four. Was the "thumb" a separately evolved sixth finger? Fortunately, the giant panda has its bible, a monograph by D. Dwight Davis, late curator of vertebrate anatomy at Chicago's Field Museum of Natural History. It is probably the greatest work of modern evolutionary comparative anatomy, and it contains more than anyone would ever want to know about pandas. Davis had the answer, of course.

The panda's "thumb" is not, anatomically, a finger at all. It is constructed from a bone called the radial sesamoid, normally a small component of the wrist. In pandas, the radial sesamoid is greatly enlarged and elongated until it almost equals the metapodial bones of the true digits in length. The radial sesamoid underlies a pad on the panda's forepaw; the five digits form the framework of another pad, the palmar. A shallow furrow separates the two pads and serves as a channelway for bamboo stalks.



D. L. CRAMER

The panda's thumb comes equipped not only with a bone to give it strength but also with muscles to sustain its agility. These muscles, like the radial sesamoid bone itself, did not arise *de novo.* Like the parts of Darwin's orchids, they are familiar bits of anatomy remodeled for a new function. The abductor of the radial sesamoid (the muscle that pulls it away from the true digits) bears the formidable name *abduc-*

torpollicis longus ("the long abductor of the thumb"—*pollicis* is the genitive of *pollex,* Latin for "thumb"). Its name is a giveaway. In other carnivores, this muscle attaches to the first digit, or true thumb. Two shorter muscles run between the radial sesamoid and the pollex. They pull the sesamoid "thumb" towards the true digits.

Does the anatomy of other carnivores give us any clue to the origin of this odd arrangement in pandas? Davis points out that ordinary bears and raccoons, the closest relatives of giant pandas, far surpass all other carnivores in using their forelegs for manipulating objects in feeding. Pardon the backward metaphor, but pandas, thanks to their ancestry, began with a leg up for evolving greater dexterity in feeding. Moreover, ordinary bears already have a slightly enlarged radial sesamoid.

In most carnivores, the same muscles that move the radial sesamoid in pandas attach exclusively to the base of the pollex, or true thumb. But in ordinary bears, the long abductor muscle ends in two tendons: one inserts into the base of the thumb as in most carnivores, but the other attaches to the radial sesamoid. The two shorter muscles also attach, in part, to the radial sesamoid in bears. "Thus," Davis concludes, "the musculature for operating this remarkable new mechanism—functionally a new digit—required no intrinsic change from conditions already present in the panda's closest relatives, the bears. Furthermore, it appears that the whole sequence of events in the musculature follows automatically from simple hypertrophy of the sesamoid bone."

The sesamoid thumb of pandas is a complex structure formed by marked enlargement of a bone and an extensive rearrangement of musculature. Yet Davis argues that the entire apparatus arose as a mechanical response to growth of the radial sesamoid itself. Muscles shifted because the enlarged bone blocked them short of their original sites. Moreover, Davis postulates that the enlarged radial sesamoid may have been fashioned by a simple genetic change, perhaps a single mutation affecting the timing and rate of growth.

In a panda's foot, the counterpart of the radial sesamoid, called the tibial sesamoid, is also enlarged, although not so much as the radial sesamoid. Yet the tibial sesamoid supports no new digit, and its increased size confers no advantage, so far as we know. Davis argues that the coordinated increase of both bones, in response to natural selection upon one alone, probably reflects a simple kind of genetic change. Repeated parts of the body are not fashioned by the action of individual genes—there is no gene "for" your thumb, another for your big toe, or a third for your pinky. Repeated parts are coordinated in development; selection for a change in one element causes a corresponding modification in others. It may be genetically more complex to enlarge a thumb and *not* to modify a big toe, than to increase both together. (In the first case, a general coordination must be broken, the thumb favored separately, and correlated increase of related structures suppressed. In the second, a single gene may increase the rate of growth in a field regulating the development of corresponding digits.)

The panda's thumb provides an elegant zoological counterpart to Darwin's orchids. An engineer's best solution is debarred by history. The panda's true thumb is committed to another role, too specialized for a different function to become an opposable, manipulating digit. So the panda must use parts on hand and settle for an enlarged wrist bone and a somewhat clumsy, but quite workable, solution. The sesamoid thumb wins no prize in an engineer's derby. It is, to use Michael Ghiselin's phrase, a contraption, not a lovely contrivance. But it does its job and excites our imagination all the more because it builds on such improbable foundations.

Darwin's orchid book is filled with similar illustrations. The marsh Epipactus, for example, uses its labellum—an enlarged petal—as a trap. The labellum is divided into two parts. One, near the flower's base, forms a large cup filled with nectar—the object of an insect's visit. The other, near the flower's edge, forms a sort of landing stage. An insect alighting on this runway depresses it and thus gains entrance to the nectar cup beyond. It enters the cup, but the

Marsh ***Epipactis,*** lower sepals removed

a. Runway of labellum depressed after insect lands.

D. L. CRAMER

b. Runway of labellum raised after insect crawls into **cup** below. **D. L. CRAMER** runway is so elastic that it instantly springs up, trapping the insect within the nectar cup. The insect must then back out through the only available exit—a path that forces it to brush against the pollen masses. A remarkable machine but all developed from a conventional petal, a part readily available in an orchid's ancestor.

Darwin then shows how the same labellum in other orchids evolves into a series of ingenious devices to ensure cross-fertilization. It may develop a complex fold that forces an insect to detour its proboscis around and past the pollen masses in order to reach nectar. It may contain deep channels or guiding ridges that lead insects both to nectar and pollen. The channels sometimes form a tunnel, producing a tubular flower. All these adaptations have been built from a part that began as a conventional petal in some ancestral form. Yet nature can do so much with so little that it displays, in Darwin's words, "a prodigality of resources for gaining the very same end, namely, the fertilization of one flower by pollen from another plant."

Darwin's metaphor for organic form reflects his sense of wonder that evolution can fashion such a world of diversity and adequate design with such limited raw material:

> Although an organ may not have been originally formed for some special purpose, if it now serves for this end we are justified in saying that it is specially contrived for it. On the same principle, if a man were to make a machine for some special purpose, but were to use old wheels, springs, and pulleys, only slightly altered, the whole machine, with all its parts, might be said to be specially contrived for that purpose. Thus throughout nature almost every part of each living being has probably served, in a slightly modified condition, for diverse purposes, and has acted in the living machinery of many ancient and distinct specific forms.

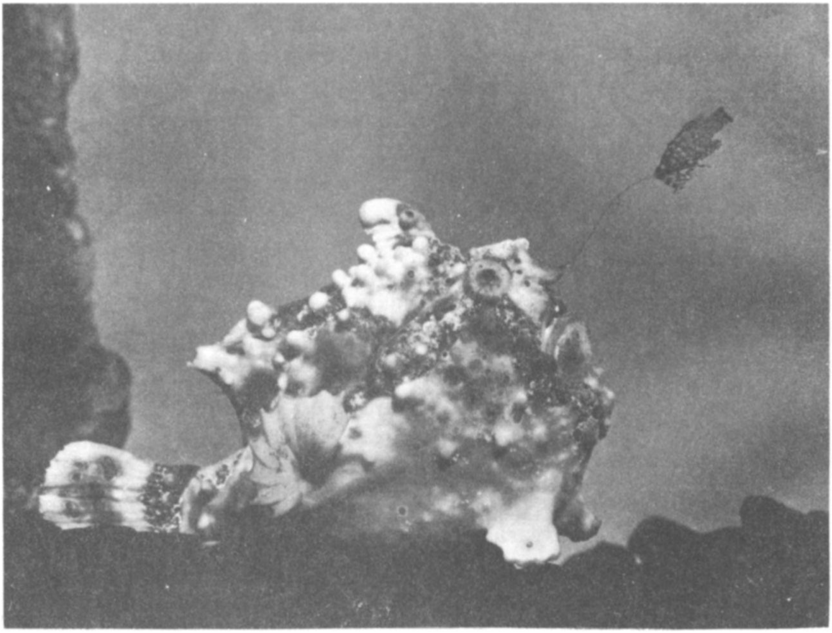
We may not be flattered by the metaphor of refurbished wheels and pulleys, but consider how well we work. Nature is, in biologist Francois Jacob's words, an excellent tinkerer, not a divine artificer. And who shall sit in judgment between these exemplary skills?

Double Trouble

NATURE MARKS Izaak Walton as a rank amateur more often than I had imagined. In 1654, the world's most famous fisherman before Ted Williams wrote of his favorite lure: "I have an artificial minnow . . . so curiously wrought, and so exactly dissembled that it would beguile any sharpsighted trout in a swift stream."

An essay in my previous book, *Ever Since Darwin,* told the tale of *Lampsilis,* a freshwater clam with a decoy "fish" mounted on its rear end. This remarkable lure has a streamlined "body," side flaps simulating fins and tail, and an eyespot for added effect; the flaps even undulate with a rhythmic motion that imitates swimming. This "fish," constructed from a brood pouch (the body) and the clam's outer skin (fin and tails), attracts the real item and permits a mother clam to shoot her larvae from the brood pouch toward an unsuspecting fish. Since the larvae of *Lampsilis* can only grow as parasites on a fish's gill, this decoy is a useful device indeed.

I was astounded recently to learn that *Lampsilis* is not alone. Ichthyologists Ted Pietsch and David Grobecker recovered a single specimen of an amazing Philippine anglerfish, not as a reward for intrepid adventures in the wilds, but from that source of so much scientific novelty—the local aquarium retailer. (Recognition, rather than *machismo,* is often the basis of exotic discovery.) Anglerfish lure their dinner, rather than a free ride for their larvae. They carry a highly modified dorsal fin spine affixed to the tips of their snouts. At the end of this spine, they mount an appropriate lure. Some deep-sea species, living in a dark world untouched by light from the surface, fish with their own source of illumination: they gather phosphorescent bacteria in their lures. Shallow-water species tend to have colorful, bumpy bodies, and look remarkably like rocks encrusted with sponges and algae. They rest inert on the bottom and wave or wiggle their conspicuous lures near their mouths. "Baits" differ among species, but most resemble—often imperfectly—a variety of invertebrates, including worms and crustaceans.



Anglerfish DAVID B. CROBECKER

Pietsch and Grobecker's anglerfish, however, has evolved a fish lure every bit as impressive as the decoy mounted on *Lampsilis's* rear—a first for anglerfish. (Their report bears as its appropriate title "The Compleat Angler" and cites as an epigraph the passage from Walton quoted above.) This exquisite fake also sports eyelike spots of pigment in the right place. In addition, it bears compressed filaments representing pectoral and pelvic fins along the bottom of the body, extensions from the back resembling dorsal and anal fins, and even an expanded rear projection looking for all the world like a tail. Pietsch and Grobecker conclude: "The bait is nearly an exact replica of a small fish that could easily belong to any of a number of percoid families common to the Philippine region." The angler even ripples its bait through the water, "simulating the lateral undulations of a swimming fish."

These nearly identical artifices of fish and clam might seem, at first glance, to seal the case for Darwinian evolution. If natural selection can do this twice, surely it can do anything. Yet—continuing the theme of the last two essays and bringing this trilogy to a close—perfection works as well for the creationist as the evolutionist. Did not the psalmist proclaim: "The heavens declare the glory of God; and the firmament showeth his handiwork." The last two essays argued that imperfection carries the day for evolution. This one discusses the Darwinian response to perfection.

The only thing more difficult to explain than perfection is repeated perfection by very different animals. A fish on a clam's rear end *and* another in front of an anglerfish's nose—the first evolved from a brood pouch and outer skin, the second from a fin spine—more than doubles the trouble. I have no difficulty defending the origin of both "fishes" by evolution. A plausible series of intermediate stages can be identified for *Lampsilis.* The fact that anglerfish press a fin spine into service as a lure reflects the jury-rigged, parts-available principle that made the panda's thumb and the orchid's labellum speak so strongly for evolution (see the first essay of this trilogy). But Darwinians must do more than demonstrate evolution; they must defend the basic mechanism of random variation and natural selection as the primary cause of evolutionary change.

Anti-Darwinian evolutionists have always favored the *re-*

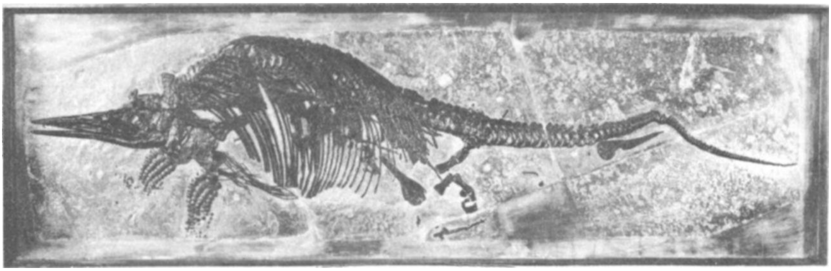
peuted development of very similar adaptations in different lineages as an argument against the central Darwinian notion that evolution is unplanned and undirected. If different organisms converge upon the same solutions again and again, does this not indicate that certain directions of change are preset, not established by natural selection working on random variation? Should we not look upon the repeated form itself as a cause of the numerous evolutionary events leading toward it?

Throughout his last half-dozen books, for example, Arthur Koestler has been conducting a campaign against his own misunderstanding of Darwinism. He hopes to find some ordering force, constraining evolution to certain directions and overriding the influence of natural selection. Repeated evolution of excellent design in separate lineages is his bulwark. Again and again, he cites the "nearly identical skulls" of wolves and the "Tasmanian wolf." (This marsupial carnivore looks like a wolf but is, by genealogy, more closely related to wombats, kangaroos, and koalas.) In *Janus,* his latest book, Koestler writes: "Even the evolution of a single species of wolf by random mutation plus selection presents, as we have seen, insurmountable difficulties. To duplicate this process independently on island and mainland would mean squaring a miracle."

The Darwinian response involves both a denial and an explanation. First, the denial: it is emphatically not true that highly convergent forms are effectively identical. Louis Dollo, the great Belgian paleontologist who died in 1931, established a much misunderstood principle—"the irreversibility of evolution" (also known as Dollo's law). Some ill-informed scientists think that Dollo advocated a mysterious directing force, driving evolution forward, never permitting a backward peek. And they rank him among the non-Darwinians who feel that natural selection cannot be the cause of nature's order.

In fact, Dollo was a Darwinian interested in the subject of convergent evolution—the repeated development of similar adaptations in different lineages. Elementary probability theory, he argued, virtually guarantees that convergence can never yield anything close to perfect resemblance. Organisms cannot erase their past. Two lineages may develop remarkable, superficial similarities as adaptations to a common mode of life. But organisms contain so many complex and independent parts that the chance of all evolving twice toward exactly the same result is effectively nil. Evolution is irreversible; signs of ancestry are always preserved; convergence, however impressive, is always superficial.

Consider my candidate for the most astounding convergence of all: the ichthyosaur. This sea-going reptile with terrestrial ancestors converged so strongly on fishes that it actually evolved a dorsal fin and tail in just the right place and with just the right hydrological design. These structures are all the more remarkable because they evolved from nothing—the ancestral terrestrial reptile had no hump on its back or blade on its tail to serve as a precursor. Nonetheless, the ichthyosaur is no fish, either in general design or in intricate detail. (In ichthyosaurs, for example, the vertebral column runs through the lower tail blade; in fish with tail vertebrae, the column runs into the upper blade.) The ichthyosaur remains a reptile, from its lungs and surface breathing to its flippers made of modified leg bones, not fin rays.



Ichthyosaur

COURTESY OF THE AMERICAN MUSEUM OF NATURAL HISTORY

Koestler's carnivores tell the same tale. Both placental wolf and marsupial "wolf are well designed to hunt, but no expert would ever mistake their skulls The numerous, small marks of marsupiality are not obliterated by convergence in outward form and function.

Second, the explanation: Darwinism is not the theory of capricious change that Koestler imagines. Random variation may be the raw material of change, but natural selection builds good design by rejecting most variants while accepting and accumulating the few that improve adaptation to local environments.

The basic reason for strong convergence, prosaic though it may seem, is simply that some ways of making a living impose exacting criteria of form and function upon any organism playing the role. Mammalian carnivores must run and stab; they do not need grinding molar teeth since they tear and swallow their food. Both placental and marsupial wolves are built for sustained running, have long, sharp, pointed canine teeth and reduced molars. Terrestrial vertebrates propel themselves with their limbs and may use their tails for balance. Swimming fish balance with their fins and propel from the rear with their tails. Ichthyosaurs, living like fish, evolved a broad propulsive tail (as whales did later —although the horizontal flukes of a whale's tail beat up and down, while the vertical flukes offish and ichthyosaurs beat from side to side).

No one has treated this biological theme of repeated, exquisite design more eloquently than D'Arcy Wentworth Thompson in his 1942 treatise, *On Growth and Form,* still in print and still as relevant as ever. Sir Peter Medawar, a man who eschews hype and exaggeration, describes it as "beyond comparison the finest work of literature in all the annals of science that have been recorded in the English tongue." Thompson, zoologist, mathematician, classical scholar, and prose stylist, won accolades as an old man but spent his entire professional life in a small Scottish university because his views were too unorthodox to win prestigious London and Oxbridge jobs.

Thompson was more a brilliant reactionary than a visionary. He took Pythagoras seriously and worked as a Greek geometrician. He took special delight in finding the abstract forms of an idealized world embodied again and again in the products of nature. Why do repeated hexagons appear in the cells of a honeycomb and in the interlocking plates of some turtle shells? Why do the spirals in a pine cone and a sunflower (and often of leaves on a stem) follow the Fibonacci series? (A system of spirals radiating from a common point can be viewed either as a set of left- or right-handed spirals. Left and right spirals are not equal in number, but represent two consecutive figures of the Fibonacci series. The Fibonacci series is constructed by adding the previous two numbers to form the next: 1, 1, 2, 3, 5, 8, 13, 21, etc. The pine cone may, for example, have 13 left spirals and 21 right spirals.) Why do so many snail shells, ram's horns, and even the path of a moth to light follow a curve called the logarithmic spiral?

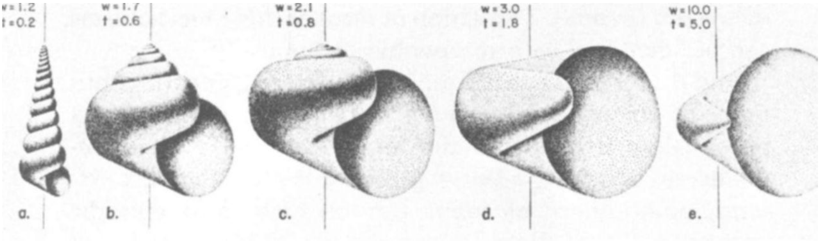
Thompson's answer was the same in each case: these abstract forms are optimal solutions for common problems. They are evolved repeatedly in disparate groups because they are the best, often the only, path to adaptation. Triangles, parallelograms, and hexagons are the only plane figures that fill space completely without leaving holes. Hexagons are often favored because they approximate a circle and maximize area within relative to the supporting walls (minimum construction for greatest storage of honey, for example). The Fibonacci pattern emerges automatically in any system of radiating spirals built by adding new elements at the apex, one at a time in the largest space available. The logarithmic spiral is the only curve that does not change its shape as it grows in size. I can identify the abstract Thompsonian forms as optimal adaptations, but to the larger metaphysical issue of why "good" form often exhibits such simple, numerical regularity, I plead only ignorance and wonder.

So far, I have only spoken to half the issue embodied in the problem of repeated perfection. I have discoursed on the "why." I have argued that convergence never renders two complex organisms completely identical (a circumstance that would strain Darwinian processes beyond their reasonable power) and I have tried to explain close repeats as optimal adaptations to common problems with few solutions.

But what about the "how?" We may know what the fish of *Lampsilis* and the lure of the anglerfish are for, but how did they arise? This problem becomes particularly acute when the final adaptation is complex and peculiar but built from familiar parts of different ancestral function. If the angler's fishlike lure required 500 entirely separate modifications to attain its exquisite mimicry, then how did the process begin? And why did it continue, unless some non-Darwinian force, cognizant of the final goal, drove it on? Of what possible benefit is step one alone? Is a five-hundredth of a fake enough to inspire the curiosity of any real item?

D'Arcy Thompson's answer to this problem was overextended but characteristically prophetic. He argued that organisms are shaped directly by physical forces acting upon them: optima of form are nothing more than the natural states of plastic matter in the presence of appropriate physical forces. Organisms jump suddenly from one optimum to another when the regime of physical forces alters. We now know that physical forces are too weak, in most cases, to build form directly—and we look to natural selection instead. But we are derailed if selection can only act in a patient and piecemeal way—step by sequential step to build any complex adaptation.

I believe that a solution lies in the essence of Thompson's insight, shorn of his unsubstantiated claim that physical forces shape organisms directly. Complex forms are often built by a much simpler (often a very simple) system of generating factors. Parts are connected in intricate ways through growth, and alteration of one may resound through the entire organism and change it in a variety of unsuspected ways. David Raup, of Chicago's Field Museum of Natural History, adapted D'Arcy Thompson's insight to a modern computer, and showed that the basic forms of coiled shells—from nautiloid to clam to snail—can all be generated by varying only three simple gradients of growth. Using Raup's program, I can change a garden-variety snail into a common clam by modifying just two of the three gradients. And, believe it or not, a peculiar genus of modern snails does carry a bivalved shell so like a conventional



In these computer-drawn figures (they are not real snails, despite the similarities), a form (right) looking much like certain clams can be converted into a "snail" (left figures) simply by decreasing the rate at which the generating ellipse increases as the "shell" grow, and by increasing the rate of translation of this ellipse down the axis of coiling. All these figures are drawn by specifying just four parameters.
PHOTO COURTESY OF D. M. RAUP

clam's that I gasped when I saw a snail's head poking out between the valves in a striking close-up movie.

This closes my trilogy on the issue of perfection and imperfection as signs of evolution. But the entire set is really an extended disquisition on the panda's "thumb," a single, concrete object that spawned all three essays, despite their subsequent wanderings and musings. The thumb, built of a wrist bone, imperfect as a sign of history, constructed from parts available. Dwight Davis faced the dilemma of potential impotence for natural selection if it must work step by countless step to make a panda from a bear. And he advocated D'Arcy Thompson's solution of reduction to a simple system of generating factors. He showed how the complex apparatus of the thumb, with all its muscles and nerves, may arise as a set of automatic consequences following a simple enlargement of the radial sesamoid bone. He then argued that the complex changes in form and function of the skull—the transition from omnivory to nearly exclusive munching on bamboo—could be expressed as consequences of one or two underlying modifications. He concluded that "very few genetic mechanisms—perhaps no more than half a dozen—were involved in the primary adaptive shift from *Ursus* [bear] to

Ailuropoda [panda]. The action of most of these mechanisms can be identified with reasonable certainty."

And thus we may pass from the underlying genetic continuity of change—an essential Darwinian postulate—to a potentially episodic alteration in its manifest result—a sequence of complex, adult organisms. Within complex systems, smoothness of input can translate into episodic change in output. Here we encounter a central paradox of our being and of our quest to understand what made us. Without this level of complexity in construction, we could not have evolved the brains to ask such questions. With this complexity, we cannot hope to find solutions in the simple answers that our brains like to devise.

Death Before Birth, or a Mite's *Nunc Dimittis*

CAN ANYTHING BE more demoralizing than parental incompetence before the most obvious and innocent of children's questions: why is the sky blue, the grass green? Why does the moon have phases? Our embarrassment is all the more acute because we thought we knew the answer perfectly well, but hadn't rehearsed it since we ourselves had received a bumbled response in similar circumstances a generation earlier. It is the things we think we know—because they are so elementary, or because they surround us—that often present the greatest difficulties when we are actually challenged to explain them.

One such question, with an obvious and incorrect answer, lies close to our biological lives: why, in humans (and in most species familiar to us), are males and females produced in approximately equal numbers? (Actually, males are more common than females at birth in humans, but differential mortality of males leads to a female majority in later life. Still, the departures from a one to one ratio are never great.) At first glance, the answer seems to be, as in Rabelais's motto, "plain as the nose on a man's face." After all, sexual reproduction requires a mate; equal numbers imply universal mating—the happy Darwinian status of maximal reproductive capacity. At second glance, it isn't so clear at all, and we are drawn in confusion to Shakespeare's recasting of the simile: "A jest unseen, inscrutable, invisible, as a nose on a man's face." If maximal reproductive capacity is the optimal state for a species, then why make equal numbers of males and females. Females, after all, set the limit upon numbers of offspring, since eggs are invariably so much larger and less abundant than sperm in species familiar to us—that is, each egg can make an offspring, each sperm cannot. A male can impregnate several females. If a male can mate with nine females and the population contains a hundred individuals, why not make ten males and ninety females? Reproductive capacity will certainly exceed that of a population composed of fifty males and fifty females. Populations made predominantly of females should, by their more rapid rates of reproduction, win any evolutionary race with populations that maintain equality in numbers between the sexes.

What appeared obvious is therefore rendered problematical and the question remains: why do most sexual species contain approximately equal numbers of males and females? The answer, according to most evolutionary biologists, lies in a recognition that Darwin's theory of natural selection speaks only of struggle among *individuals* for reproductive success. It contains no statement about the good of populations, species, or ecosystems. The argument for ninety females and ten males was framed in terms of advantages for populations as a whole—the usual, congenial, and dead wrong, way in which most people think of evolution. If evolution worked for the good of populations as a whole, then sexual species would contain relatively few males.

The observed equality of males and females, in the face of obvious advantages for female predominance if evolution worked upon groups, stands as one of our most elegant demonstrations that Darwin was right—natural selection works by the struggle of individuals to maximize their own reproductive success. The Darwinian argument was first framed by the great British mathematical biologist R.A. Fisher. Suppose, Fisher argued, that either sex began to predominate. Let us say, for example, that fewer males than females are born. Males now begin to leave more offspring than females since their opportunities for mating increase as they become rarer—that is, they impregnate more than one female on average. Thus, if any genetic factors influence the relative proportion of males born to a parent (and such factors do exist), then parents with a genetic inclination to produce males will gain a Darwinian advantage—they will produce more than an average number of grandchildren thanks to the superior reproductive success of their predominantly male offspring. Thus, genes that favor the production of males will spread and male births will rise in frequency. But, this advantage for males fades out as male births increase and it disappears entirely when males equal females in number. Since the same argument works in reverse to favor female births when females are rare, the sex ratio is driven by Darwinian processes to its equilibrium value of one to one.

But how would a biologist go about testing Fisher's theory of sex ratio? Ironically, the species that confirm its predictions are no great help beyond the initial observation. Once we frame the basic argument and determine that the species we know best have approximately equal numbers of males and females, what do we achieve by finding that the next thousand species are similarly ordered? Sure, it all fits, but we do not gain an equal amount of confidence each time we add a new species. Perhaps the one to one ratio exists for another reason?

To test Fisher's theory, we must look for exceptions. We must seek unusual situations in which the premises of Fisher's theory are not met—situations that lead to a specific prediction about how sex ratio should depart from one to one. If change of premises leads to a definite and successful prediction of altered outcome, then we have an independent test that strongly boosts our confidence. This method is embodied in the old proverb that "the exception proves the rule," although many people misunderstand the proverb because it embodies the less common meaning of "prove." Prove comes from the Latin *probare*—to test or to try. Its usual, modern meaning refers to final and convincing demonstration and the motto would seem to say that exceptions establish indubitable validity. But in another sense, closer to its root, "prove" (as in "proving ground" or printer's "proof) is more like its cognate "probe"—a test or an exploration. It is the exception that probes the rule by testing and exploring its consequences in altered situations.

Here nature's rich diversity comes to our aid. The stereotyped image of a birder assiduously adding the rufous-crowned, peg-legged, speckle-backed, cross-billed and cross-eyed towhee to his life list gives, in unwarranted ridicule, a perverted twist to the actual use made by naturalists of life's diversity. It is nature's richness that permits us to establish a science of natural history in the first place—for the variety virtually guarantees that appropriate exceptions can be found to probe any rule. Oddities and weirdnesses are tests of generality, not mere peculiarities to describe and greet with awe or a chuckle.

Fortunately, nature has been profligate in providing species and modes of life that violate the premises of Fisher's argument. In 1967, British biologist W.D. Hamilton (now at the University of Michigan) gathered the cases and arguments into an article entitled "Extraordinary sex ratios." I will discuss in this essay only the clearest and most important of these probing violations.

Nature rarely heeds our homilies in all cases. We are told, and with good reason, that mating of brothers and sisters should be avoided, lest too many unfavorable recessive genes gain an opportunity to express themselves in double dose. (Such genes tend to be rare, and chances are small that two unrelated parents will both carry them. But the probability that two sibs carry the same gene is usually fifty percent.) Nonetheless, some animals never heard the rule and indulge, perhaps exclusively, in sib mating.

Exclusive sib mating destroys the major premise of Fisher's argument for one to one sex ratios. If females are always fertilized by their brothers, then the same parents manufacture both partners of any mating. Fisher assumed that the males had different parents and that an undersupply of males awarded genetic advantages to those parents that could produce males preferentially. But if the same parents produce *both* the mothers and fathers of their grandchildren, then they have an equal genetic investment in each grandchild, no matter what percentage of males and females they produce among their children. In this case, the reason for an equal balance of males and females disappears and the previous argument for female predominance reasserts itself. If each pair of grandparents has a limited store of energy to invest in offspring, and if grandparents producing more offspring gain a Darwinian edge, then grandparents should make as many daughters as possible, and produce only enough sons to ensure that all their daughters will be fertilized. In fact, if their sons can muster sufficient sexual prowess, then parents should make just one son and use every bit of remaining energy to produce as many daughters as they can. As usual, bountiful nature comes to our aid with numerous exceptions to probe Fisher's rule: indeed, species with sib mating also tend to produce a minimal number of males.

Consider the curious life of a male mite in the genus *Adactylidium,* as described by E.A. Albadry and M.S.F. Tawfik in 1966. It emerges from its mother's body and promptly dies within a few hours, having done apparently nothing during its brief life. It attempts, while outside its mother, neither to feed nor to mate. We know about creatures with short adult lives—the mayfly's single day after a much lengthier larval life, for example. But the mayfly mates and insures the continuity of its kind during these few precious hours. The males of *Adactylidium* seem to do nothing at all but emerge and die.

To solve the mystery, we must study the entire life cycle and look inside the mother's body. The impregnated female of *Adactylidium* attaches to the egg of a thrips. That single egg provides the only source of nutrition for rearing all her offspring—for she will feed on nothing else before her death. This mite, so far as we know, engages exclusively in sib mating; thus, it should produce a minimal number of males. Moreover, since total reproductive energy is so strongly constrained by the nutritional resources of a single thrips' egg, progeny are strictly'limited, and the more females the better. Indeed, *Adactylidium* matches our prediction by raising a brood of five to eight sisters accompanied by a single male who will serve as both brother and husband to them all. But producing a single male is chancy; if it dies, all sisters will remain virgins and their mother's evolutionary life is over.

If the mite takes a chance on producing but a single male, thus maximizing its potential brood of fertile females, two other adaptations might lessen the risk—providing both protection for the male and guaranteed proximity to his sisters. What better than to rear the brood entirely within a mother's body, feeding both larvae and adults within her, and even allowing copulation to occur inside her protective shell. Indeed, about forty-eight hours after she attaches to the thrips' egg, six to nine eggs hatch within the body of a female *Adactylidium.* The larvae feed on their mother's body, literally devouring her from inside. Two days later, the offspring reach maturity, and the single male copulates with all his sisters. By this time, the mother's tissues have disintegrated, and her body space is a mass of adult mites, their feces, and their discarded larval and nymphal skeletons. The offspring then cut holes through their mother's body wall and emerge. The females must now find a thrips' egg and begin the process again, but the males have already fulfilled their evolutionary role before "birth." They emerge, react however a mite does to the glories of the outside world, and promptly die.

But why not carry the process one stage further? Why should the male be born at all? After copulating with its sisters, its work is done. It is ready to chant the acarine version of Simeon's prayer, *Nunc dimittu*—Oh Lord, now lettest thou thy servant depart in peace. Indeed, since everything that is possible tends to occur at least once in the multifarious world of life, a close relative of *Adactylidium* does just this. *Acarophenax tribolii* also indulges exclusively in sib mating. Fifteen eggs, including but a single male, develop within the mother's body. The male emerges within his mother's shell, copulates with all his sisters and dies before birth. It may not sound like much of a life, but the male *Acarophenax* does as much for its evolutionary continuity as Abraham did in fathering children into his tenth decade.

Nature's oddities are more than good stories. They are material for probing the limits of interesting theories about life's history and meaning.

Piltdown Revisited

NOTHING IS QUITE so fascinating as a well-aged mystery. Many connoisseurs regard Josephine Tey's *The Daughter of Time* as the greatest detective story ever written because its protagonist is Richard III, not the modern and insignificant murderer of Roger Ackroyd. The old chestnuts are perennial sources for impassioned and fruitless debate. Who was Jack the Ripper? Was Shakespeare Shakespeare?

My profession of paleontology offered its entry to the first rank of historical conundrums a quarter-century ago. In 1953, Piltdown man was exposed as a certain fraud perpetrated by a very uncertain hoaxer. Since then, interest has never flagged. People who cannot tell *Tyrannosaurus* from *Allosaurus* have firm opinions about the identity of Piltdown's forger. Rather than simply ask "whodunit?" this column treats what I regard as an intellectually more interesting issue: why did anyone ever accept Piltdown man in the first place? I was led to address the subject by recent and prominent news reports adding—with abysmally poor evidence, in my opinion—yet another prominent suspect to the list. Also, as an old mystery reader, I cannot refrain from expressing my own prejudice, all in due time.

In 1912, Charles Dawson, a lawyer and amateur archeologist from Sussex, brought several cranial fragments to Arthur Smith Woodward, Keeper of Geology at the British Museum (Natural History). The first, he said, had been unearthed by workmen from a gravel pit in 1908. Since then, he had searched the spoil heaps and found a few more fragments. The bones, worn and deeply stained, seemed indigenous to the ancient gravel; they were not the remains of a more recent interment. Yet the skull appeared remarkably modern in form, although the bones were unusually thick.

Smith Woodward, excited as such a measured man could be, accompanied Dawson to Piltdown and there, with Father Teilhard de Chardin, looked for further evidence in the spoil heaps. (Yes, believe it or not, the same Teilhard who, as a mature scientist and theologian, became such a cult figure some fifteen years ago with his attempt to reconcile evolution, nature, and God in *The Phenomenon of Man.* Teilhard had come to England in 1908 to study at the Jesuit College in Hastings, near Piltdown. He met Dawson in a quarry on May 31, 1909; the mature solicitor and the young French Jesuit became warm friends, colleagues, and coexplorers.)

On one of their joint expeditions, Dawson found the famous mandible, or lower jaw. Like the skull fragments, the jaw was deeply stained, but it seemed to be as apish in form as the cranium was human. Nonetheless, it contained two molar teeth, worn flat in a manner commonly encountered in humans, but never in apes. Unfortunately, the jaw was broken in just the two places that might have settled its relationship with the skull: the chin region, with all its marks of distinction between ape and human, and the area of articulation with the cranium.

Armed with skull fragments, the lower jaw, and an associated collection of worked flints and bone, plus a number of mammalian fossils to fix the age as ancient, Smith Woodward and Dawson made their splash before the Geological Society of London on December 18, 1912. Their reception was mixed, although on the whole favorable. No one smelled fraud, but the association of such a human cranium with such an apish jaw indicated to some critics that remains of two separate animals might have been mixed together in the quarry.

During the next three years, Dawson and Smith Woodward countered with a series of further discoveries that, in retrospect, could not have been better programmed to dispel doubt. In 1913, Father Teilhard found the all-important lower canine tooth. It, too, was apish in form but strongly worn in a human manner. Then, in 1915, Dawson convinced most of his detractors by finding the same association of two thick-skulled human cranial fragments with an apish tooth worn in a human manner at a second site two miles from the original finds.

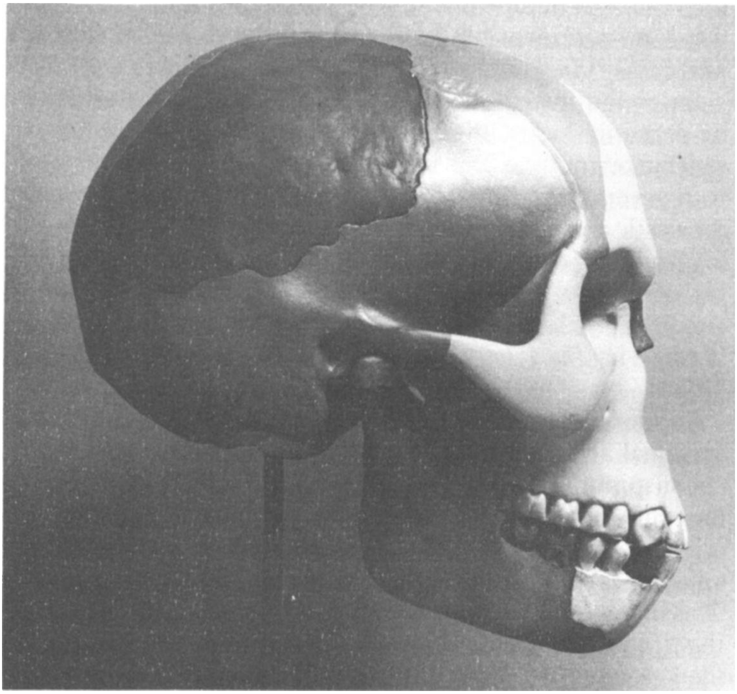
Henry Fairfield Osborn, leading American paleontologist and converted critic, wrote:

> If there is a Providence hanging over the affairs of prehistoric men, it certainly manifested itself in this case, because the three fragments of the second Piltdown man found by Dawson are exactly those which we would have selected to confirm the comparison with the original type. . . . Placed side by side with the corresponding fossils of the first Piltdown man they agree precisely; there is not a shadow of a difference.

Providence, unbeknown to Osborn, walked in human form at Piltdown.

For the next thirty years, Piltdown occupied an uncomfortable but acknowledged place in human prehistory. Then, in 1949, Kenneth P. Oakley applied his fluorine test to the Piltdown remains. Bones pick up fluorine as a function of their time of residence in a deposit and the fluorine content of surrounding rocks and soil. Both the skull and jaw of Piltdown contained barely detectable amounts of fluorine; they could not have lain long in the gravels. Oakley still did not suspect fakery. He proposed that Piltdown, after all, had been a relatively recent interment into ancient gravels.

But a few years later, in collaboration with J.S. Weiner and W.E. le Gros Clark, Oakley finally considered the obvious alternative—that the "interment" had been made in this century with intent to defraud. He found that the skull



Skull of Piltdown Man.
COURTESY OF THE AMERICAN MUSEUM OF NATURAL HISTORY

and jaw had been artificially stained, the flints and bone worked with modern blades, and the associated mammals, although genuine fossils, imported from elsewhere. Moreover, the teeth had been filed down to simulate human wear. The old anomaly—an apish jaw with a human cranium—was resolved in the most parsimonious way of all. The skull *did* belong to a modern human; the jaw was an orangutan's.

But who had foisted such a monstrous hoax upon scientists so anxious for such a find that they remained blind to an obvious resolution of its anomalies? Of the original trio, Teilhard was dismissed as a young and unwitting dupe. No one has ever (and rightly, in my opinion) suspected Smith Woodward, the superstraight arrow who devoted his life to the reality of Piltdown and who, past eighty and blind, dictated in retirement his last book with its chauvinistic title, *The Earliest Englishman* (1948).

Suspicion instead has focused on Dawson. Opportunity he certainly had, although no one has ever established a satisfactory motive. Dawson was a highly respected amateur with several important finds to his credit. He was overenthusiastic and uncritical, perhaps even a bit unscrupulous in his dealings with other amateurs, but no direct evidence of his complicity has ever come to light. Nevertheless, the circumstantial case is strong and well summarized by JS. Weiner in *The Piltdown Forgery* (Oxford University Press, 1955).

Supporters of Dawson have maintained that a more professional scientist must have been involved, at least as a coconspirator, because the finds were so cleverly faked. I have always regarded this as a poor argument, advanced by scientists largely to assuage their embarrassment that such an indifferently designed hoax was not detected sooner. The staining, to be sure, had been done consummately. But the "tools" had been poorly carved and the teeth crudely filed—scratch marks were noted as soon as scientists looked with the right hypothesis in mind. Le Gros Clark wrote: 'The evidences of artificial abrasion immediately sprang to the eye. Indeed so obvious did they seem it may well be asked—how was it that they had escaped notice before." The forger's main skill consisted in knowing what to leave out—discarding the chin and articulation.

In November 1978, Piltdown reappeared prominently in the news because yet another scientist had been implicated as a possible coconspirator. Shortly before he died at age ninety-three, J.A. Douglas, emeritus professor of geology at Oxford, made a tape recording suggesting that his predecessor in the chair, W.J. Sollas, was the culprit. In support of this assertion, Douglas offered only three items scarcely ranking as evidence in my book: (1) Sollas and Smith Woodward were bitter enemies. (So what. Academia is a den of vipers, but verbal sparring and elaborate hoaxing are responses of differing magnitude.) (2) In 1910, Douglas gave

Sollas some mastodon bones that could have been used as part of the imported fauna. (But such bones and teeth are not rare.) (3) Sollas once received a package of potassium bichromate and neither Douglas nor Sollas's photographer could figure out why he had wanted it. Potassium bichromate was used in staining the Piltdown bones. (It was also an important chemical in photography, and I do not regard the alleged confusion of Sollas's photographer as a strong sign that the professor had some nefarious usages in mind.) In short, I find the evidence against Sollas so weak that I wonder why the leading scientific journals of England and the United States gave it so much space. I would exclude Sollas completely, were it not for the paradox that his famous book, *Ancient Hunters,* supports Smith Woodward's views about Piltdown in terms so obsequiously glowing that it could be read as subtle sarcasm.

Only three hypotheses make much sense to me. First, Dawson was widely suspected and disliked by some amateur archeologists (and equally acclaimed by others). Some compatriots regarded him as a fraud. Others were bitterly jealous of his standing among professionals. Perhaps one of his colleagues devised this complex and peculiar form of revenge. The second hypothesis, and the most probable in my view, holds that Dawson acted alone, whether for fame or to show up the world of professionals we do not know.

The third hypothesis is much more interesting. It would render Piltdown as a joke that went too far, rather than a malicious forgery. It represents the "pet theory" of many prominent vertebrate paleontologists who knew the man well. I have sifted all the evidence, trying hard to knock it down. Instead, I find it consistent and plausible, although not the leading contender. A.S. Romer, late head of the museum I inhabit at Harvard and America's finest vertebrate paleontologist, often stated his suspicions to me. Louis Leakey also believed it. His autobiography refers anonymously to a "second man," but internal evidence clearly implicates a certain individual to anyone in the know.

It is often hard to remember a man in his youth after old age imposes a different persona. Teilhard de Chardin became an austere and almost Godlike figure to many in his later years; he was widely hailed as a leading prophet of our age. But he was once a fun-loving young student. He knew Dawson for three years before Smith Woodward entered the story. He may have had access, from a previous assignment in Egypt, to mammalian bones (probably from Tunisia and Malta) that formed part of the "imported" fauna at Piltdown. I can easily imagine Dawson and Teilhard, over long hours in field and pub, hatching a plot for different reasons: Dawson to expose the gullibility of pompous professionals; Teilhard to rub English noses once again with the taunt that their nation had no legitimate human fossils, while France reveled in a superabundance that made her the queen of anthropology. Perhaps they worked together, never expecting that the leading lights of English science would fasten upon Piltdown with such gusto. Perhaps they expected to come clean but could not.

Teilhard left England to become a stretcher bearer during World War I. Dawson, on this view, persevered and completed the plot with a second Piltdown find in 1915. But then the joke ran away and became a nightmare. Dawson sickened unexpectedly and died in 1916. Teilhard could not return before the war's end. By that time, the three leading lights of British anthropology and paleontology—Arthur Smith Woodward, Grafton Elliot Smith, and Arthur Keith—had staked their careers on the reality of Piltdown. (Indeed they ended up as two Sir Arthurs and one Sir Grafton, largely for their part in putting England on the anthropological map.) Had Teilhard confessed in 1918, his promising career (which later included a major role in describing the legitimate Peking man) would have ended abruptly. So he followed the Psalmist and the motto of Sussex University, later established just a few miles from Piltdown—"Be still, and know. . . ."—to his dying day. Possible. Just possible.

All this speculation provides endless fun and controversy, but what about the prior and more interesting question: why had anyone believed Piltdown in the first place? It was an improbable creature from the start. Why had anyone admitted to our lineage an ancestor with a fully modern cranium and the unmodified jaw of an ape?

Indeed, Piltdown never lacked detractors. Its temporary reign was born in conflict and nurtured throughout by controversy. Many scientists continued to believe that Piltdown was an artifact composed of two animals accidentally commingled in the same deposit. In the early 1940s, for example, Franz Weidenreich, perhaps the world's greatest human anatomist, wrote (with devastating accuracy in hindsight): "*Eoanthropus* ['dawn man,' the official designation of Piltdown] should be erased from the list of human fossils. It is the artificial combination of fragments of a modern human braincase with orang-utanglike mandible and teeth." To this apostasy, Sir Arthur Keith responded with bitter irony: "This is one way of getting rid of facts which do not fit into a preconceived theory; the usual way pursued by men of science is, not to get rid of facts, but frame theory to fit them."

Moreover, had anyone been inclined to pursue the matter, there were published grounds for suspecting fraud from the start. A dental anatomist, C.W. Lyne, stated that the canine found by Teilhard was a young tooth, just erupted before Piltdown's death, and that its intensity of wear could not be reconciled with its age. Others voiced strong doubts about the ancient manufacture of Piltdown's tools. In amateur circles of Sussex, some of Dawson's colleagues concluded that Piltdown must be a fake, but they did not publish their beliefs.

If we are to learn anything about the nature of scientific inquiry from Piltdown—rather than just reveling in the joys of gossip—we will have to resolve the paradox of its easy acceptance. I think that I can identify at least four categories of reasons for the ready welcome accorded to such a misfit by all the greatest English paleontologists. All four contravene the usual mythology about scientific practice—that facts are "hard" and primary and that scientific understanding increases by patient collection and sifting of these objective bits of pure information. Instead, they display science as a human activity, motivated by hope, cultural prejudice.

and the pursuit of glory, yet stumbling in its erratic path toward a better understanding of nature.

The imposition of strong hope upon dubious evidence. Before Piltdown, English paleoanthropology was mired in a limbo now occupied by students of extraterrestrial life: endless fields for speculation and no direct evidence. Beyond some flint "cultures" of doubtful human workmanship and some bones strongly suspected as products of recent interments into ancient gravels, England knew nothing of its most ancient ancestors. France, on the other hand, had been blessed with a superabundance of Neanderthals, Cro-Magnons and their associated art and tools. French anthropologists delighted in rubbing English noses with this marked disparity of evidence. Piltdown could not have been better designed to turn the tables. It seemed to predate Neanderthal by a considerable stretch of time. If human fossils had a fully modern cranium hundreds of thousands of years before beetle-browed Neanderthal appeared, then Piltdown must be our ancestor and the French Neanderthals a side branch. Smith Woodward proclaimed: "The Neanderthal race was a degenerate offshoot of early man while surviving modern man may have arisen directly from the primitive source of which the Piltdown skull provides the first discovered evidence." This international rivalry has often been mentioned by Piltdown's commentators, but a variety of equally important factors have usually escaped notice.

Reduction of anomaly by fit with cultural biases. A human cranium with an ape's jaw strikes us today as sufficiently incongruous to merit strong suspicion. Not so in 1913. At that time, many leading paleontologists maintained an a priori preference largely cultural in origin, for "brain primacy" in human evolution. The argument rested on a false inference from contemporary importance to historical priority: we rule today by virtue of our intelligence. Therefore, in our evolution, an enlarged brain must have preceded and inspired all other alterations of our body. We should expect to find human ancestors with enlarged, perhaps nearly modern, brains and a distinctly simian body. (Ironically, nature followed an opposite path. Our earliest ancestors, the australopithecines, were fully erect but still small brained.) Thus, Piltdown neatly matched a widely anticipated result. Grafton Elliot Smith wrote in 1924:

> The outstanding interest of the Piltdown skull is in the confirmation it affords of the view that in the evolution of Man the brain led the way. It is the veriest truism that Man has emerged from the simian state in virtue of the enrichment of the structure of his mind. . . . The brain attained what may be termed the human rank at a time when the jaws and face, and no doubt the body also, still retained much of the uncouthness of Man's simian ancestors. In other words, Man at first . . . was merely an Ape with an overgrown brain. The importance of the Piltdown skull lies in the fact that it affords tangible confirmation of these inferences.

Piltdown also buttressed some all too familiar racial views among white Europeans. In the 1930s and 1940s, following the discovery of Peking man in strata approximately equal in age with the Piltdown gravels, phyletic trees based on Piltdown and affirming the antiquity of white supremacy began to appear in the literature (although they were never adopted by Piltdown's chief champions, Smith Woodward, Smith, and Keith). Peking man (originally called *Sinanthropus,* but now placed in *Homo erectus)* lived in China with a brain two-thirds modern size, while Piltdown man, with its fully developed brain, inhabited England. If Piltdown, as the earliest Englishman, was the progenitor of white races, while other hues must trace their ancestry to *Homo erectus,* then whites crossed the threshold to full humanity long before other people. As longer residents in this exalted state, whites must excel in the arts of civilization.

Reduction of anomaly by matching fact to expectation. We know, in retrospect, that Piltdown had a human cranium and an ape's jaw. As such, it provides an ideal opportunity for testing what scientists do when faced with uncomfortable anomaly. G.E. Smith and others may have advocated an evolutionary head start for the brain, but no one dreamed of an independence so complete that brains might become fully human before jaws changed at all! Piltdown was distressingly too good to be true.

If Keith was right in his taunt to Weidenreich, then Piltdown's champions should have modeled their theories to the uncomfortable fact of a human cranium and an ape's jaw. Instead, they modeled the "facts"—another illustration that information always reaches us through the strong filters of culture, hope, and expectation. As a persistent theme in "pure" description of the Piltdown remains, we learn from all its major supporters that the skull, although remarkably modern, contains a suite of definitely simian characters! Smith Woodward, in fact, originally estimated the cranial capacity at a mere 1,070 cc (compared with a modern average of 1,400 to 1,500), although Keith later convinced him to raise the figure nearer to the low end of our modern spectrum. Grafton Elliot Smith, describing the brain cast in the original paper of 1913, found unmistakable signs of incipient expansion in areas that mark the higher mental faculties in modern brains. He concluded: "We must regard this as being the most primitive and most simian human brain so far recorded; one, moreover, such as might reasonably have been expected to be associated in one and the same individual with the mandible which so definitely indicates the zoological rank of its original possessor." Just a year before Oakley's revelation, Sir Arthur Keith wrote in his last major work (1948): "His forehead was like that of the orang. devoid of a supraorbital torus; in its modeling his frontal bone presented many points of resemblance to that of the orang of Borneo and Sumatra." Modern *Homo sapiens,* I hasten to add, also lacks a supraorbital torus, or brow ridge.

Careful examination of the jaw also revealed a set of remarkably human features for such an apish jaw (beyond the forged wear of the teeth). Sir Arthur Keith repeatedly emphasized, for example, that the teeth were inserted into the jaw in a human, rather than a simian, fashion.

Prevention of discovery by practice. In former years, the British Museum did not occupy the vanguard in maintaining open and accessible collections—a happy trend of recent years, and one that has helped to lift the odor of mustiness (literally and figuratively) from major research museums. Like the stereotype of a librarian who protects books by guarding them from use, Piltdown's keepers severely restricted access to the original bones. Researchers were often permitted to look but not touch; only the set of plaster casts could be handled. Everyone praised the casts for their accuracy of proportion and detail, but the detection of fraud required access to the originals—artificial staining and wear of teeth cannot be discovered in plaster. Louis Leakey writes in his autobiography:

> As I write this book in 1972 and ask myself how it was that the forgery remained unmasked for so many years, I have turned my mind back to 1933, when I first went to see Dr. Bather, Smith Woodward's successor. . . . I told him that I wished to make a careful examination of the Piltdown fossils, since I was preparing a textbook on early man. I was taken into the basement to be shown the specimens, which were lifted out of a safe and laid on a table. Next to each fossil was an excellent cast. I was not allowed to handle the originals in any way, but merely to look at them and satisfy myself that the casts were really good replicas. Then, abruptly, the originals were removed and locked up again, and I was left for the rest of the morning with only the casts to study.
>
> It is my belief now that it was under these conditions that all visiting scientists were permitted to examine the Piltdown specimens, and that the situation changed only when they came under the care of my friend and contemporary Kenneth Oakley. He did not see the necessity of treating the fragments as if they were the crown jewels but, rather, considered them simply as important fossils—to be looked after carefully, but from which the maximum scientific evidence should be obtained.

Henry Fairfield Osborn, although not known as a generous man, paid almost obsequious homage to Smith Woodward in his treatise on the historical path of human progress, *Man Rises to Parnassus* (1927). He had been a skeptic before his visit to the British Museum in 1921. Then, on Sunday morning, July 24, "after attending a most memorable service in Westminster Abbey,'' Osborn "repaired to the British Museum to see the fossil remains of the now thoroughly vindicated Dawn Man of Great Britain." (He, at least, as head of the American Museum of Natural History, got to see the originals.) Osborn swiftly converted and proclaimed Piltdown "a discovery of transcendent importance to the prehistory of man." He then added: "We have to be reminded over and over again that Nature is full of paradoxes and that the order of the universe is not the human order." Yet Osborn had seen little but the human order on two levels—the comedy of fraud and the subtler, yet ineluctable, imposition of theory upon nature. Somehow, I am not distressed that the human order must veil all our interactions with the universe, for the veil is translucent, however strong its texture.

Postscript

Our fascination with Piltdown never seems to abate. This article, published originally in March, 1979, elicited a flurry of correspondence, some acerbic, some congratulatory. It centered, of course, upon Teilhard. I was not trying to be cute by writing at length about Teilhard while stating briefly that Dawson acting alone accounts best for the facts. The case against Dawson had been made admirably by Weiner, and I had nothing to add to it. I continued to regard Weiner's as the most probable hypothesis. But I also believed that the only reasonable alternative (since the second Piltdown site established Dawson's complicity in my view) was a coconspiracy—an accomplice for Dawson. The other current proposals, involving Sollas or even G.E. Smith himself, seemed to me so improbable or off-the-wall that I wondered why so little attention had focussed upon the only recognized scientist who had been with Dawson from the start—especially since several of Teilhard's prominent colleagues in vertebrate paleontology harbored private thoughts (or had made cryptically worded public statements) about his possible role.

Ashley Montagu wrote on December 3, 1979, and told me that he had broken the news to Teilhard himself after Oakley's revelation of the fraud—and that Teilhard's astonishment seemed too genuine to represent dissembling: "I feel sure you're wrong about Teilhard. I knew him well, and, in fact, was the first to tell him, the day after it was announced in *The Xew York Times,* of the hoax. His reaction could hardly have been faked. I have not the slightest doubt that the faker was Dawson." In Paris last September, I spoke with several of Teilhard's contemporaries and scientific colleagues, including Pierre P. Grasse and Jean Piveteau; all regarded any thought of his complicity as monstrous. Pere Francois Russo, S.J., later sent me a copy of the letter that Teilhard wrote to Kenneth P. Oakley after Oakley had exposed the fraud. He hoped that this document would assuage my doubts about his coreligionist. Instead my doubts intensified; for, in this letter, Teilhard made a fatal slip. Intrigued by my new role as sleuth, I visited Kenneth Oakley in England on April 16. 1980. He showed me additional documents of Teilhard, and shared other doubts with me. I now believe that the balance of evidence clearly implicates Teilhard as a coconspirator with Dawson in the Piltdown plot. I will present the entire case in Natural History Magazine in the summer or fall of 1980; but for now, let me mention the internal evidence from Teilhard's first letter to Oakley alone.

Teilhard begins the letter by expressing satisfaction. "I congratulate you most sincerely on your solution of the Piltdown problem . . . I am fundamentally pleased by your conclusions, in spite of the fact that, sentimentally speaking, it spoils one of my brightest and earliest paleontological memories." He continues with his thoughts on "the psychological riddle," or whodunit, he agrees with all others in dismissing Smith Woodward, but he also refuses to implicate Dawson, citing his thorough knowledge of Dawson's character and abilities: "He was a methodical and enthusiastic character . . . In addition, his deep friendship for Sir Arthur makes it almost unthinkable that he should have systematically deceived his associate several years. When we were in the field, I never noticed anything suspicious in his behavior." Teilhard ends by proposing, halfheartedly by his own admission, that the whole affair might have been an accident engendered when an amateur collector threw out some ape bones onto a spoil heap that also contained some human skull fragments, (although Teilhard does not tell us how such a hypothesis could possibly account for the same association two miles away at the second Piltdown site).

Teilhard's slip occurs in his description of the second Piltdown find. Teilhard writes: "He just brought me to the site of Locality 2 and explained me (sic) that he had found the isolated molar and the small pieces of skull in the heaps of rubble and pebbles raked at the surface of the field." Now we know (see Weiner, p. 142) that Dawson did take Teilhard to the second site for a prospecting trip in 1913. He also took Smith Woodward there in 1914. But neither visi* led to any discovery; no fossils were found at the second site until 1915. Dawson wrote to Smith Woodward on January 20, 1915 to announce the discovery of two cranial fragments. In July 1915, he wrote again with good news about the discovery of a molar tooth. Smith Woodward assumed (and stated in print) that Dawson had unearthed the specimens in 1915 (see Weiner, p. 144). Dawson became seriously ill later in 1915 and died the next year. Smith Woodward never obtained more precise information from him about the second find. Now, the damning point: Teilhard states explicitly, in the letter quoted above, that Dawson told him about both the tooth and the skull fragments of the second site. But Claude Cuenot, Teilhard's biographer, states that Teilhard was called up for service in December, 1914; and we know that he was at the front on January 22, 1915 (pp. 22-23). But if Dawson did not "officially" discover the molar until July, 1915, how could Teilhard have known about it *unless he was involved in the hoax.* I regard it as unlikely that Dawson would show the material to an innocent Teilhard in 1913 and then withold it from Smith Woodward for two years (especially after taking Smith Woodward to the second site for two days of prospecting in 1914). Teilhard and Smith Woodward were friends and might have compared notes at any time; such an inconsistency on Dawson's part could have blown his cover entirely.

Second, Teilhard states in his letter to Oakley that he did not meet Dawson until 1911: "I knew Dawson very well, since I worked with him and Sir Arthur three or four times at Piltdown (after a chance meeting in a quarry near Hastings in 1911)." Yet it is certain that Teilhard met Dawson during the spring or summer of 1909 (see Weiner, p. 90). Dawson introduced Teilhard to Smith Woodward, and Teilhard submitted some fossils he had found, including a rare tooth of an early mammal, to Smith Woodward late in 1909. When Smith Woodward described this material before the Geological Society of London in 1911, Dawson, in the discussion following Smith Woodward's talk, paid tribute to the "patient and skilled assistance" given to him by Teilhard and another priest since 1909. I don't regard this as a damning point. A first meeting in 1911 would still be early enough for complicity (Dawson "found" his first piece of the Piltdown skull in the autumn of 1911, although he states that a workman had given him a fragment "some years" earlier), and I would never hold a mistake of two years against a man who tried to remember the event forty years later. Still, a later (and incorrect) date, right upon the heels of Dawson's find, certainly averts suspicion.

Moving away from the fascination of whodunit to the theme of my original essay (why did anyone ever believe it in the first place), another colleague sent me an interesting article from *Nature* (the leading scientific periodical in England), November 13, 1913, from the midst of the initial discussions. In it, David Waterston of King's College, University of London, correctly (and definitely) stated that the skull was human, the jaw an ape's. He concludes: "It seems to me to be as inconsequent to refer the mandible and the cranium to the same individual as it would be to articulate a chimpanzee foot with the bones of an essentially human thigh and leg." The correct explanation had been available from the start, but hope, desire, and prejudice prevented its acceptance.

Our Greatest Evolutionary Step

IN MY PREVIOUS book, *Ever Since Darwin,* I began an essay on human evolution with these words:

> New and significant prehuman fossils have been unearthed with such unrelenting frequency in recent years that the fate of any lecture notes can only be described with the watchword of a fundamentally irrational economy—planned obsolescence. Each year, when the topic comes up in my courses, I simply open my old folder and dump the contents into the nearest circular file. And here we go again.

And I'm mighty glad I wrote them, because I now want to invoke that passage to recant an argument made later in the same article.

In that essay I reported Mary Leakey's discovery (at Laetoli, thirty miles south of Olduvai Gorge in Tanzania) of the oldest known hominid fossils—teeth and jaws 3.35 to 3.75 million years old. Mary Leakey suggested (and so far as I know, still believes) that these remains should be classified in our genus, *Homo.* I therefore argued that the conventional evolutionary sequence leading from small-brained but fully erect *Australopithecus* to larger-brained *Homo* might have to be reassessed, and that the australopithecines might represent a side branch of the human evolutionary tree.

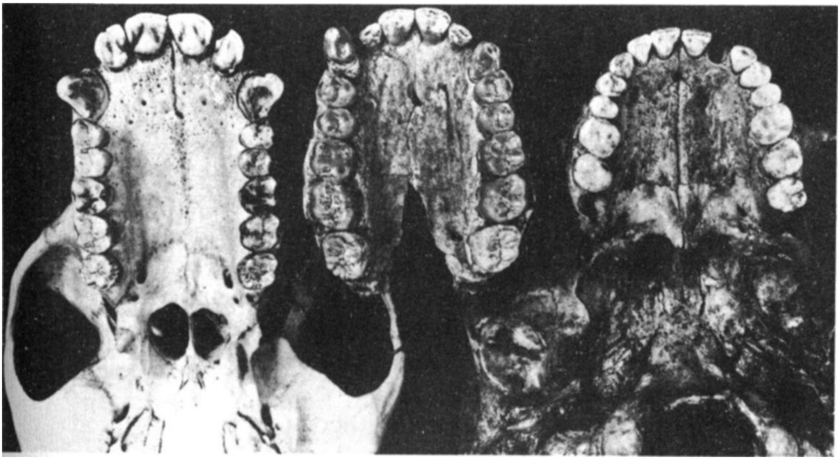
Early in 1979, newspapers blazed with reports of a new species—more ancient in time and more primitive in appearance than any other hominid fossil—*Australopithecus afarensis,* named by Don Johanson and Tim White. Could any two claims possibly be more different—Mary Leakey's argument that the oldest hominids belong to our own genus, *Homo,* and Johanson and White's decision to name a new species because the oldest hominids possess a set of apelike features shared by no other fossil hominid. Johanson and White must have discovered some new and fundamentally different bones. Not at all. Leakey and Johanson and White are arguing about the same bones. We are witnessing a debate about the interpretation of specimens, not a new discovery.

Johanson worked in the Afar region of Ethiopia from 1972 to 1977 and unearthed an outstanding series of hominid remains. The Afar specimens are 2.9 to 3.3 million years old. Premier among them is the skeleton of an australopithecine named Lucy. She is nearly 40 percent complete—much more than we have ever possessed for any individual from these early days of our history. (Most hominid fossils, even though they serve as a basis for endless speculation and elaborate storytelling, are fragments of jaws and scraps of skulls.)

Johanson and White argue that the Afar specimens and Mary Leakey's Laetoli fossils are identical in form and belong to the same species. They also point out that the Afar and Laetoli bones and teeth represent everything we know about hominids exceeding 2.5 million years in age—all the other African specimens are younger. Finally, they claim that the teeth and skull pieces of these old remains share a set of features absent in later fossils and reminiscent of apes. Thus, they assign the Laetoli and Afar remains to a new species, *A. afarensis.*

The debate is just beginning to warm up, but three opinions have already been vented. Some anthropologists, pointing to different features, regard the Afar and Laetoli specimens as members of our own genus, *Homo.* Others accept Johanson and White's conclusion that these older fossils are closer to the later south and east African *Aus-*

tralopitherus than to *Homo.* But they deny a difference sufficient to warrant a new species and prefer to include the Afar and Laetoli fossils within the species *A. africanus,* originally named for South African specimens in the 1920s. Still others agree with Johanson and White that the Afar and Laetoli fossils deserve a new name.



The palate of *Australopithecus afarensis* (center, compared with that of a modern chimpanzee (left) and a human (right).

COURTESY OF TIM WHITE AND THE CLEVELAND MUISEUM OF NATURAL HISTORY

As a rank anatomical amateur, my opinion is worth next to nothing. Yet I must say that if a picture is worth all the words of this essay (or only half of them if you follow the traditional equation of 1 for 1,000), the palate of the Afar hominid certainly says "ape" to me. (I must also confess that the designation of *A. afarensis* supports several of my favorite prejudices. Johanson and White emphasize that the Afar and Laetoli specimens span a million years but are virtually identical. I believe that most species do not alter much during the lengthy period of their success and that most evolutionary change accumulates during very rapid events of splitting from ancestral stocks—see essays 17 and 18. Moreover, since I depict human evolution as a bush rather than a ladder, the more species the merrier. Johanson and White do, however, accept far more gradualism than I would advocate for later human evolution.)

Amidst all this argument about skulls, teeth, and taxonomic placement, another and far more interesting feature of the Afar remains has not been disputed. Lucy's pelvis and leg bones clearly show that *A. afarensis* walked as erect as you or I. This fact has been prominently reported by the press, but in a very misleading way. The newspapers have conveyed, almost unanimously, the idea that previous orthodoxy had viewed the evolution of larger brains and upright postures as a gradual transition in tandem, perhaps with brains leading the way—from pea-brained quadrupeds to stooping half brains to fully erect, big-brained *Homo.* The *Xew York Times* writes (January 1979): "The evolution of bipedalism was thought to have been a gradual process involving intermediate forerunners of modern human beings that were stooped, shuffle-gaited 'ape-men,' creatures more intelligent than apes but not as intelligent as modern human beings." Absolutely false, at least for the past fifty years of our knowledge.

We have known since australopithecines were discovered in the 1920s that these hominids had relatively small brains and fully erect posture. *(A. afncanus* has a brain about one-third the volume of ours and a completely upright gait. A correction for its small body size does not remove the large discrepancy between its brain and ours.) This "anomaly" of small brain and upright posture has been a major issue in the literature for decades and wins a prominent place in all important texts.

Thus, the designation *of A. afarensis* does not establish the historical primacy of upright posture over large brains. But it does, in conjunction with two other ideas, suggest something very novel and exciting, something curiously missing from the press reports or buried amidst misinformation about the primacy of upright posture. *A. afarensis* is important because it teaches us that perfected upright gait had already been achieved nearly four million years ago. Lucy's pelvic structure indicates bipedal posture for the Afar remains, while the remarkable footprints just discovered at

Laetoli provide even more direct evidence. The later south and east African australopithecines do not extend back much further than two and a half million years. We have thus added nearly one and a half million years to the history of fully upright posture.

To explain why this addition is so important, I must break the narrative and move to the opposite end of biology—from fossils of whole animals to molecules. During the past fifteen years, students of molecular evolution have accumulated a storehouse of data on the amino acid sequences of similar enzymes and proteins in a wide variety of organisms. This information has generated a surprising result. If we take pairs of species with securely dated times of divergence from a common ancestor in the fossil record, we find that the number of amino acid differences correlates remarkably well with time since the split—the longer that two lineages have been separate, the more the molecular difference. This regularity has led to the establishment of a molecular clock to predict times of divergence for pairs of species without good fossil evidence of ancestry. To be sure, the clock does not beat with the regularity of an expensive watch—it has been called a "sloppy clock" by one of its leading supporters—but it has rarely gone completely haywire.

Darwinians were generally surprised by the clock's regularity because natural selection should work at markedly varying rates in different lineages at different times: very rapidly in complex forms adapting to rapidly changing environments, very slowly in stable, well-adapted populations. If natural selection is the primary cause of evolution in populations, then we should not expect a good correlation between genetic change and time unless rates of selection remain fairly constant—as they should not by the argument stated above. Darwinians have escaped this anomaly by arguing that irregularities in the rate of selection smooth out over long periods of time. Selection might be intense for a few generations and virtually absent for a time thereafter, but the net change averaged over long periods could still be regular. But Darwinians have also been forced to face the possibility that regularity of the molecular clock reflects an evolutionary process not mediated by natural selection, the random fixation of neutral mutations. (I must defer this "hot" topic to another time and more space.)

In any case, the measurement of amino acid differences between humans and living African great apes (gorillas and chimpanzees) led to the most surprising result of all. We are virtually identical for genes that have been studied, despite our pronounced morphological divergence. The average difference in amino acid sequences between humans and African apes is less than one percent (0.8 percent to be precise)—corresponding to a mere five million years since divergence from a common ancestor on the molecular clock. Allowing for the slop, Allan Wilson and Vincent Sarich, the Berkeley scientists who uncovered this anomaly, will accept six million years, but not much more. In short, if the clock is valid, *A. afarensis* is pushing very hard at the theoretical limit of hominid ancestry.

Until recently, anthropologists tended to dismiss the clock, arguing that hominids provided a genuine exception to an admitted rule. They based their skepticism about the molecular clock upon an animal called *Ramapithecus,* an African and Asian fossil known mainly from jaw fragments and ranging back to fourteen million years in age. Many anthropologists claimed that *Ramapithecus* could be placed on our side of the ape-human split—that, in other words, the divergence between hominids and apes occurred more than fourteen million years ago. But this view, based on a series of technical arguments about teeth and their proportions, has been weakening of late. Some of the strongest supporters of *Ramapithecus* as a hominid are now prepared to reassess it as an ape or as a creature near to the common ancestry of ape and human but still before the actual split. The molecular clock has been right too often to cast it aside for some tentative arguments about fragments of jaws. (I now expect to lose a $ 10 bet I made with Allan Wilson a few years back. He generously gave me seven million years as a maximum for the oldest ape-human common ancestor, but I held out for more. And while I'm not shelling out yet, I don't really expect to collect.*)

We may now put together three points to suggest a major reorientation in views about human evolution: the age and upright posture of *A. afarensis,* the ape-human split on the molecular clock, and the dethroning of *Ramapithecus* as a hominid.

We have never been able to get away from a brain-centered view of human evolution, although it has never represented more than a powerful cultural prejudice imposed upon nature. Early evolutionists argued that enlargement of the brain must have preceded any major alteration of our bodily frame. (See views of G.E. Smith in essay 10. Smith based his pro-Piltdown conviction upon an almost fanatical belief in cerebral primacy.) But *A. africanus,* upright and small brained, ended that conceit in the 1920s, as predicted by a number of astute evolutionists and philosophers, from Ernst Haeckel to Friedrich Engels. Nevertheless, "cerebral primacy," as I like to call it, still held on in altered form. Evolutionists granted the historical primacy of upright posture but conjectured that it arose at a leisurely pace and that the real discontinuity—the leap that made us fully human—occurred much later when, in an unprecedented burst of evolutionary speed, our brains tripled in size within a million years or so.

Consider the following, written ten years ago by a leading expert: "The great leap in cephalization of genus *Homo* took place within the past two million years, after some ten million years of preparatory evolution toward bipedalism, the tool-using hand, etc." Arthur Koestler has carried this view of a cerebral leap toward humanity to an unexcelled height of invalid speculation in his latest *book, Janus.* Our brain grew so fast, he argues, that the outer cerebral cortex, seat of smarts and rationality, lost control over emotive, animal centers deep within our brains. This primitive bestiality surfaces in war, murder, and other forms of mayhem.

"Jan., 1980. I just paid. Might as well start off the new decade right.

I believe that we must reassess fundamentally the relative importance we have assigned to upright posture and increase in brain size as determinants of human evolution. We have viewed upright posture as an easily accomplished, gradual trend and increase in brain size as a surprisingly rapid discontinuity—something special both in its evolutionary mode and the magnitude of its effect. I wish to suggest a diametrically opposite view. Upright posture is the surprise, the difficult event, the rapid and fundamental reconstruction of our anatomy. The subsequent enlargement of our brain is, in anatomical terms, a secondary epiphenomenon, an easy transformation embedded in a general pattern of human evolution.

Six million years ago at most, if the molecular clock runs true (and Wilson and Sarich would prefer five), we shared our last common ancestor with gorillas and chimps. Presumably, this creature walked primarily on all fours, although it may have moved about on two legs as well, as apes and many monkeys do today. Little more than a million years later, our ancestors were as bipedal as you or I. This, not later enlargement of the brain, was the great punctuation in human evolution.

Bipedalism is no easy accomplishment. It requires a fundamental reconstruction of our anatomy, particularly of the foot and pelvis. Moreover, it represents an anatomical reconstruction outside the general pattern of human evolution. As I argue in essay 9, through the agency of Mickey Mouse, humans are neotenic—we have evolved by retaining juvenile features of our ancestors. Our large brains, small jaws, and a host of other features, ranging from distribution of bodily hair to ventral pointing of the vaginal canal, are consequences of eternal youth. But upright posture is a different phenomenon. It cannot be achieved by the "easy" route of retaining a feature already present in juvenile stages. For a baby's legs are relatively small and weak, while bipedal posture demands enlargement and strengthening of the legs.

By the time we became upright as *A. afarensis,* the game was largely over, the major alteration of architecture accomplished, the trigger of future change already set. The later enlargement of our brain was anatomically easy. We read our larger brain out of the program of our own growth, by prolonging rapid rates of fetal growth to later times and preserving, as adults, the characteristic proportions of a juvenile primate skull. And we evolved this brain in concert with a host of other neotenic features, all part of a general pattern.

Yet I must end by pulling back and avoiding a fallacy of reasoning—the false equation between magnitude of effect and intensity of cause. As a pure problem in architectural reconstruction, upright posture is far-reaching and fundamental, an enlarged brain superficial and secondary. But the effect of our large brain has far outstripped the relative ease of its construction. Perhaps the most amazing thing of all is a general property of complex systems, our brain prominent among them—their capacity to translate merely quantitative changes in structure into wondrously different qualities of function.

It is now two in the morning and I'm finished. I think I'll walk over to the refrigerator and get a beer; then I'll go to sleep. Culture-bound creature that I am, the dream I will have in an hour or so when I'm supine astounds me ever so much more than the stroll I will now perform perpendicular to the floor.

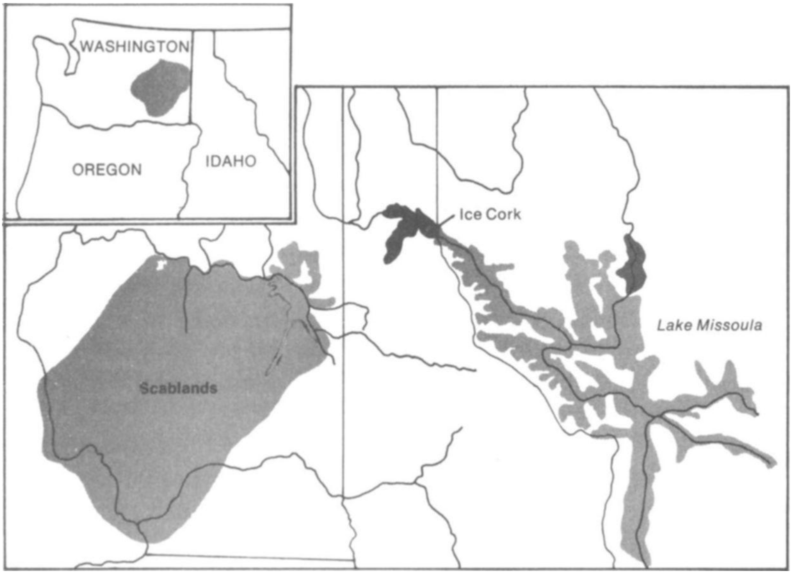
The Great Scablands Debate

THE INTRODUCTORY PARAGRAPHS of popular guidebooks usually tout prevailing orthodoxy in its purest form—dogma unadulterated by the "howevers" of professional writing. Consider the following from our National Park Service's auto tour of Arches National Park:

> The world and all it contains is in a continuous process of change. Most of the changes in our world are very tiny and so escape our notice. They are real, however, and over an immense span of time their combined effect is to bring about great change. If you stand at the base of a canyon wall and rub your hand on the sandstone, hundreds of grains of sand are dislodged. It seems like an insignificant change, but that's how the canyon was formed. Various forces have dislodged and carried away grains of sand. Sometimes the process is "very fast" (as when you rub the sandstone) but most of the time it is much slower. If you allow sufficient time, you can tear down a mountain or create a canyon—a few grains at a time.

As the primary lesson of geology, this pamphlet proclaims that big results arise as the accumulated effect of tiny changes. My hand rubbing the canyon wall is an adequate (if anything, overeffective) illustration of rates that carved the canyon itself. Time, geology's inexhaustible resource, performs all the miracles.

Yet, when the pamphlet turns to details, we encounter a different scenario for erosion in Arches. We learn that a balanced rock known as "Chip Off the Old Block" fell during the winter of 1975-76. Before and after photographs of the magnificent Skyline Arch receive the following commentary: "It remained thus for as long as man knew the arch, until, late in 1940, the block of stone fell, and Skyline was suddenly twice its former size." The arches form by sudden, intermittent collapse and toppling, not by imperceptible removal of sand grains. Yet gradualist orthodoxy is so entrenched that the authors of this pamphlet failed to note the inconsistency between their own factual account and the stated theory of their introduction. In other essays of this section, I argue that gradualism is a culturally conditioned prejudice, not a fact of nature, and I make a plea for pluralism in concepts of rate. Punctuational change is at



The channeled scablands of eastern Washington.

least as important as imperceptible accumulation. In this essay I tell a local, geologic story. But it conveys the same message—that dogmas play their worst role when they lead scientists to reject beforehand a counterclaim that could be tested in nature.

Flow basalts of volcanic origin blanket most of eastern Washington. These basalts are often covered by a thick layer of loess, a fine-grained, loosely packed sediment blown in by winds during the ice ages. In the area between Spokane and the Snake and Columbia rivers to the south and west, many spectacular, elongate, subparallel channelways are gouged through the loess and deeply into the hard basalt itself. These coulees, to use the local name, must have been conduits for glacial meltwaters, for they run down gradient from an area near the southern extent of the last glacier into the two major rivers of eastern Washington. The channeled scablands—as geologists designate the entire area—are puzzling as well as awesome, and for several reasons:

1. The channels connect across tall divides that once separated them. Since the channels are hundreds of feet deep, this extensive anastomosis indicates that a prodigious amount of water must once have flowed over the divide.
2. As another item favoring channels filled to the brim with water, the sides of the coulees contain many hanging valleys where tributaries enter the main channels. (A hanging valley is a tributary channel that enters a main channel high above the main channel's modern stream bed.)
3. The hard basalt of the coulees is deeply gouged and scoured. This pattern of erosion does not look like the work of gentle rivers in the gradualist mode.
4. The coulees often contain a number of high-standing hills composed of loess that has not been stripped away. These are arranged as if they were once islands in a gigantic braided stream.
5. The coulees contain discontinuous deposits of basaltic stream gravel, often composed of rock foreign to the local area.

Just after World War I, Chicago geologist J Harlen Bretz advanced an unorthodox hypothesis to account for this unusual topography (yes, that's J without a period, and don't ever let one slip in, for his wrath can be terrible). He argued that the channeled scablands had been formed all at once by a single, gigantic flood of glacial meltwater. This local catastrophe filled the coulees, cut through hundreds of feet of loess and basalt, and then receded in a matter of days. He ended his major work of 1923 with these words:

> Fully 3,000 square miles of the Columbia Plateau were swept by the glacial flood, and the loess and silt cover removed. More than 2,000 square miles of this area were left as bare, eroded rock-cut channel floors, now the scablands, and nearly 1,000 square miles carry gravel deposits derived from the eroded basalt. It *was* a debacle which swept the Columbia Plateau.

Bretz's hypothesis became a minor *cause cilebre* within geological circles. Bretz's stout and lonely defense of his catastrophic hypothesis won some grudging admiration, but virtually no support at first. The "establishment," as represented by the United States Geological Survey, closed ranks in opposition. They had nothing better to propose, and they did admit the peculiar character of scabland topography. But they held firm to the dogma that catastrophic causes must never be invoked so long as any gradualist alternative existed. Instead of testing Bretz's flood on its own merits, they rejected it on general principles.

On January 12, 1927, Bretz bearded the lion in its lair and presented his views at the Cosmos Club, in Washington, D.C., before an assembled group of scientists, many from the Geological Survey. The published discussion clearly indicates that a priori gradualism formed the basis for Bretz's glacial reception. I include typical comments from all detractors.

W. C. Alden admitted "it is not easy for one, like myself, who has never examined this plateau to supply offhand an alternative explanation of the phenomena." Nonetheless, undaunted, he continued: "The main difficulties seem to be: (1) The idea that all the channels must have been developed simultaneously in a very short time; and (2) the tremendous amount of water that he postulates. . . . The problem would be easier if less water was required and if longer time and repeated floods could be allotted to do the work."

James Gilluly, this century's chief apostle of geological gradualism, ended a long comment by noting "that the actual floods involved at any given time were of the order of magnitude of the present Columbia's or at most a few times as large, seems by no means excluded by any evidence as yet presented."

E. T. McKnight offered a gradualist alternative for the gravels: "This writer believes them to be the normal channel deposits of the Columbia during its eastward shift over the area in preglacial, glacial, and postglacial times."

G. R. Mansfield doubted that "so much work could be done on basalt in so short a time." He also proposed a calmer explanation: "The scablands seem to me better explained as the effects of persistent ponding and overflow of marginal glacial waters, which changed their position or their places of outlet from time to time through a somewhat protracted period."

Finally, O. E. Meinzer admitted that "the erosion features of the region are so large and bizarre that they defy description." They did not, however, defy gradualist explanation: "I believe the existing features can be explained by assuming normal stream work of the ancient Columbia River." Then, more baldly than most of his colleagues, he proclaimed his faith: "Before a theory that requires a seemingly impossible quantity of water is fully accepted, every effort should be made to account for the existing features without employing so violent an assumption."

The story has a happy ending, at least from my point of view, for Bretz was delivered from the lion's lair by later evidence. Bretz's hypothesis has prevailed, and virtually all geologists now believe that catastrophic floods cut the channeled scablands. Bretz had found no adequate source for his floodwaters. He knew that the glaciers had advanced as far as Spokane, but neither he nor anyone else could imagine a reasonable way to melt so much water so rapidly. Indeed, we still have no mechanism for such an episodic melting.

The solution came from another direction. Geologists found evidence for an enormous, ice-dammed glacial lake in western Montana. This lake emptied catastrophically when the glacier retreated and the dam broke. The spillway for its waters leads right into the channeled scablands.

Bretz had presented no really direct evidence for deep, surging water. Gouging might have proceeded sequentially, rather than all at once; anastomosis and hanging valleys might reflect filled coulees with gentle, rather than raging, flow. But when the first good aerial photographs of the scablands were taken, geologists noticed that several areas on the coulee floors are covered with giant stream bed ripples, up to 22 feet high and 425 feet long. Bretz, like an ant on a Yale bladderball, had been working on the wrong scale. He had been walking over the ripples for decades but had been too close to see them. They are, he wrote quite correctly, "difficult to identify at ground level under a cover of sagebrush." Observations can only be made at appropriate scales.

Hydraulic engineers can infer the character of flow from the size and shape of ripples on a stream bed. V. R. Baker estimates a maximum discharge of 752,000 cubic feet per second in the scabland flow channels. Such a flood could have moved 36-foot boulders.

I could end here with a cardboard version of the story much to my liking: Perceptive hero suppressed by blinded dogmatists stands firm, expresses his allegiance to fact over received opinion, and eventually prevails by patient persuasion and overwhelming documentation. The outline of this tale is surely valid: gradualist bias *did* lead to a rejection of Bretz's catastrophic hypothesis out of hand, and Bretz (apparently) was right. But, as I read through the original papers, I realized that this good guy-bad guy scenario must yield to a more complex version. Bretz's opponents were not benighted dogmatists. They did have a priori preferences, but they also had good reasons to doubt catastrophic flooding based on Bretz's original arguments. Moreover, Bretz's style of scientific inquiry virtually guaranteed that he would not triumph with his initial data.

Bretz proceeded in the classic tradition of strict empiricism. He felt that adventurous hypotheses could only be established by long and patient collecting of information in the field. He eschewed theoretical discussion and worried little about the valid conceptual problem that so bothered his adversaries: where could so much water come from so suddenly?

Bretz tried to establish his hypothesis by toting up evidence of erosion in the field, piece by patient piece. He seemed singularly uninterested in finding the missing item that would render his story coherent—a source for the water. For this attempt might involve speculation without direct evidence, and Bretz relied only upon fact. When Gilluly challenged him on the absence of a source for the water, Bretz simply replied: "I believe that my interpretation of channeled scabland should stand or fall on the scabland phenomena themselves."

But why should an opponent be converted by such an incomplete theory? Bretz believed that the southern end of the glacier had melted precipitously, but no scientist could imagine a way to melt ice so quickly. (Bretz tentatively suggested volcanic activity under the ice, but quickly abandoned the theory when Gilluly attacked.) Bretz stayed in the scablands, while the answer sat in western Montana. Glacial Lake Missoula had been in the literature since the 1880s, but Bretz did not make the connection—he was working in other ways. His opponents were right. We still do not know a way to melt so much ice so quickly. But the premise shared by all participants was wrong: the source of the water was water.

Events that "cannot happen" according to received wisdom rarely gain respectability by a simple accumulation of evidence for their occurrence; they require a mechanism to explain how they *can* happen. Early supporters of continental drift ran into the same difficulty that Bretz encountered. Their evidence of faunal and lithological similarities between continents now widely separated strikes us today as overwhelming, but it failed in their time because no reasonable force had been proposed for moving continents. The theory of plate tectonics has since provided a mechanism and established the idea of continental drift.

Moreover, Bretz's opponents did not rest their case entirely on the unorthodox character of Bretz's hypothesis. They also marshaled some specific facts on their side, and they were partly right. Bretz originally insisted upon a single flood, while his opponents cited much evidence to show that the scablands had not formed all at once. We now know that Lake Missoula formed and re-formed several times as the glacial margin fluctuated. In his latest work, Bretz called for eight separate episodes of catastrophic flooding. Bretz's opponents were wrong in inferring gradual change from the evidence of temporal spread: catastrophic episodes can be separated by long periods of quiescence. But Bretz was also wrong in attributing the formation of the scablands to a single flood.

I prefer heroes of flesh, blood, and fallibility, not of tinseled cardboard. Bretz is inscribed on my ledger because he stood against a firm, highly restrictive dogma that never had made any sense: the emperor had been naked for a century. Charles Lyell, the godfather of geological gradualism, had pulled a fast one in establishing the doctrine of imperceptible change. He had argued, quite rightly, that geologists must invoke the invariance (uniformity) of natural law through time in order to study the past scientifically. He then applied the same term—uniformity—to an empirical claim about rates of processes, arguing that change must be slow, steady, and gradual, and that big results can only arise as the accumulation of small changes.

But the uniformity of law does not preclude *natural* catastrophes, particularly on a local scale. Perhaps some invariant laws operate to produce infrequent episodes of sudden, profound change. Bretz may not have cared for this brand of philosophical waffling. He probably would brand it as vacuous nonsense preached by an urban desk man. But he had the independence and gumption to live by a grand old slogan from Horace, often espoused by science but not often followed: *Nullius addictusjurare in verba magistn,* "I am not bound to swear allegiance to the words of any master."

My tale ends with two happy postscripts. First, Bretz's hypothesis that channeled scabland reflects the action of catastrophic flooding has been fruitful far beyond Bretz's local area. Scablands have been found in association with other western lakes, most notably Lake Bonneville, the large ancestor of a little puddle in comparison—Great Salt Lake, Utah. Other applications have ranged about as far as they can go. Bretz has become the darling of planetary geologists who find in the channelways of Mars a set of features best interpreted by Bretz's style of catastrophic flooding.

Second, Bretz did not share the fate of Alfred Wegener, dead on the Greenland ice while his theory of continental drift lay in limbo. J Harlen Bretz presented his hypothesis sixty years ago, but he has lived to enjoy his vindication. He is now well into his nineties, feisty as ever and justly pleased with himself. In 1969, he published a forty-page paper summarizing a half century of controversy about the channeled scablands of eastern Washington. He closed with this statement:

> The International Association for Quaternary Research held its 1965 meeting in the United States. Among the many field excursions it organized was one in the northern Rockies and the Columbia Plateau in Washington. .. . The party . . . traversed the full length of the Grand Coulee, part of the Quincy basin and much of the Palouse Snake scabland divide, and the great flood gravel deposits in the Snake Canyon. The writer, unable to attend, received the next day a telegram of "greetings and salutations" which closed with the sentence, "We are now all catastrophists."

Postscript

I sent a copy of this article to Bretz after its publication in *Natural History.* He replied on October 14, 1978:

> Dear Mr. Gould,
>
> Your recent letter is most gratifying. Thank you for understanding.
>
> I have been surprised by the way my pioneer Scabland work has been applauded and further developed. I knew all along that I was right but the decades of doubt and challenge had produced an emotional lethargy, I think. Then the surprise following Victor Baker's field trip in June woke me up again. What! Had I become a semi-authority on extra-terrestrial processes and events?
>
> Physically incapacitated now (I am 96), I can only cheer the work of others in a field where I was a pathfinder. Again I thank you.
>
> J Harlen Bretz

In November 1979, at the annual meeting of the Geological Society of America, the Penrose Medal (the profession's premier award) was given to J Harlen Bretz.

An Early Start

POOH-BAH, THE Lord High Everything Else of Titipu, boasted a family pride so strong as to be "something inconceivable." "You will understand this," he said to Nanki-Poo in suggesting that a bribe would be both appropriate and expensive, "when I tell you that I can trace my ancestry back to a protoplasmal primordial atomic globule."

If human pride is nurtured by such vastly extended roots, then the end of 1977 was a bounteous time for self-esteem. Early in November, an announcement of the discovery of some fossil prokaryotes from South Africa pushed the antiquity of life back to 3.4 billion years. (Prokaryotes, including bacteria and blue green algae, form the kingdom Monera. Their cells contain no organelles—no nucleus, no mitochondria—and they are regarded as the simplest forms of life on earth.) Two weeks later, a research team from the University of Illinois announced that the so-called methane-producing bacteria are not closely related to other monerans after all, but form a separate kingdom of their own.

If true monerans were alive 3.4 billion years ago, then the common ancestor of monerans and these newly christened "methanogens" must be considerably more ancient. Since the oldest dated rocks, the Isua Supracrustals of West Greenland, are 3.8 billion years old, we are left with very little time between the development of suitable conditions for life on the earth's surface and the origin of life itself. Life is not a complex accident that required immense time to convert the vastly improbable into the nearly certain—to build laboriously, step by step, through a large chunk of time'': vastness, the most elaborate machinery on earth from the simple constituents of our original atmosphere. Instead, life, for all its intricacy, probably arose rapidly about as soon as it could; perhaps it was as inevitable as quartz or feldspar. (The earth is some 4'/2 billion years old, but it passed through a molten or near-molten stage some time after its formation and probably did not form a solid crust much before the deposition of the West Greenland sequence.) No wonder these stories hit the front page of the *New York Times,* and even inspired an editorial for Veterans' Day musings.

Twenty years ago, I spent a summer at the University of Colorado, fortifying myself for the transition from high school to college. Amidst the various joys of snowcapped peaks and sore asses from trying to "set a trot," I well remember the highlight of my stay—George Wald's lecture on the "Origin of Life." He presented with infectious charm and enthusiasm the perspective that developed in the early 1950s and reigned as an orthodoxy until very recently.

In Wald's view, the spontaneous origin of life could be considered as a virtually inevitable consequence of the earth's atmosphere and crust, and of its favorable size and position in the solar system. Still, he argued, life is so staggeringly complex that its origin from simple chemicals must have consumed an immense amount of time—probably more time than its entire subsequent evolution from DNA molecule to advanced beetles (or whatever you choose to place atop the subjective ladder). Thousands of steps, each requiring the one before, each improbable in itself. Only the immensity of time guaranteed the result, for time converts the improbable to the inevitable—give me a million years and I'll flip a hundred heads in a row more than once. Wald wrote in 1954: "Time is in fact the hero of the plot. The time with which we have to deal is the order of two billion years. . . . Given so much time, the 'impossible' becomes possible, the possible probable, and the probable virtually certain. One has only to wait: time itself performs the miracles."

This orthodox view congealed without the benefit of any direct data from paleontology to test it, for the paucity of fossils before the great Cambrian "explosion" 600 million years ago is, perhaps, the outstanding fact and frustration of my profession. In fact, the first unambiguous evidence of Precambrian life appeared in the same year that Wald theorized about its origin. Harvard paleobotanist Elso Barghoorn and Wisconsin geologist S. A. Tyler described a series of prokaryotic organisms from cherts of the Gunflint Formation, rocks nearly two billion years old from the northern shore of Lake Superior. Still, the gap between the Gunflint and the earth's origin spanned 2'/2 billion years, more than enough time for Wald's slow and steady construction.

But our knowledge of life continued its trek backward. Laminated carbonate deposits, called stromatolites, had been known for some time from rocks of the Bulawayan Series, 2.6 to 2.8 billion years old, in Southern Rhodesia. The laminations resemble patterns formed by modern blue green algal mats that trap and bind sediment. The organic interpretation of stromatolites won many converts after Barghoorn and Tyler's Gunflint discoveries removed the odor of heresy from belief in Precambrian fossils. Then, ten years ago in 1967, Barghoorn and J. W. Schopf reported "algalike" and "bacteriumlike" organisms from the Fig Tree Series of South Africa. Now the orthodox idea of slow construction spanning most of the earth's history began to crumble, for the Fig Tree rocks, based on dates available in 1967, seemed to be more than 3.1 billion years old. Schopf and Barghoorn dignified their discoveries with formal Latin names, but their own characterizations—algalike and bacteriumlike—reflected their doubts. In fact, Schopf later decided that the balance of evidence stood against the biological nature of these structures.

The recent announcement of 3.4-billion-year-old life is not a startlingly new discovery, but a satisfactory culmination of a decade's debate about the status of life in the Fig

Tree. The new evidence, gathered by Andrew H. Knoll and Barghoorn, also comes from cherts of the Fig Tree Series. But now the evidence is close to conclusive; moreover, recent dates indicate a greater age of 3.4 billion years for the series. In fact, the Fig Tree cherts may be the oldest appropriate rocks on earth for the discovery of ancient life. Older Greenland rocks have been too altered by heat and pressure to preserve organic remains. Knoll tells me that some unstudied cherts in Rhodesia may range back to 3.6 billion years, but eager scientists will have to await a political denouement before their arcane concerns attract sympathy or ensure safety. Still, the notion that life has been found in the oldest rocks that could contain evidence of it forces us, I think, to abandon the view of life's slow, steady, and improbable development. Life arose rapidly, perhaps as soon as the earth cooled down sufficiently to support it.

The new fossils from the Fig Tree Series are far more convincing than the previous discoveries. "In younger rocks [they] would without hesitation be called algal microfossils," Knoll and Barghoorn claim. This interpretation rests upon five arguments:

1. The new structures are within the size range of modern prokaryotes. The earlier structures described by Schopf and Barghoorn were disturbingly large; Schopf later rejected them as biological, primarily on the basis of their large size. The new fossils, averaging 2.5 micrometers in diameter (a micrometer is a millionth of a meter), have a mean volume only 0.2 percent as large as the earlier structures now considered inorganic.

2. Populations of modern prokaryotes have a characteristic distribution of size. They can be arranged in a typical bell-shaped curve, with the average diameter most frequent and a continual decrease in number towards larger or smaller sizes. Thus, prokaryotic populations not only have a diagnostic average size (point 1 above), they also have a characteristic pattern of variation about this average. The new microfossils form a beautiful bell-shaped distribution with limited spread (range from 1 to 4 micrometers). The previous, larger structures exhibited much greater variation and no strong mean.

3. The new .structures are "variously elongated, flattened, wrinkled, or folded" in a manner strikingly similar to Gunflint and later Precambrian prokaryotes. Such shapes are characteristic of postmortem degradation in modern prokaryotes. The larger, earlier structures were distressingly spherical; spheres, as a standard configuration of minimal surface area, can be easily produced by a host of inorganic processes—consider bubbles.

4. Most convincingly, about one quarter of the new microfossils have been found in various stages of cell division. Lest such a proportion caught *in flagrante delicto* sems unreasonably high, I point out that prokaryotes can divide every twenty minutes or so and take several minutes to complete the process. A single cell might well spend one-fourth of its life making two daughters.

5. These four arguments based on morphology are persuasive enough for me, but Knoll and Barghoorn add some biochemical evidence as well. Atoms of a single element often exist in several alternate forms of different weight. These forms, called isotopes, have the same number of protons but different numbers of neutrons. Some isotopes are radioactive and break down spontaneously to other elements; others are stable and persist unchanged throughout geologic time. Carbon has two major stable isotopes, C^{12} with 6 protons and 6 neutrons, and C^{13} with 6 protons and 7 neutrons. When organisms fix carbon in photosynthesis, they use preferentially the lighter isotope C^{12}. Hence, the C^{12}/C^{13} ratio of carbon fixed by photosynthesis is higher than the ratio in inorganic carbon (in a diamond, for example). Moreover, since both isotopes are stable, their ratio will not alter through time. The C^{12}/C^{13} ratios for Fig Tree carbon are too high for an inorganic origin; they are in the range for fixation by photosynthesis. This, in itself, would not establish the case for life in the Fig Tree; light carbon can be fixed preferentially in other ways. But combined with the evidence of size, distribution, shape, and cellular division, this additional support from biochemistry completes a convincing case.

If prokaryotes were well established 3.4 billion years ago, how much further back shall we seek the origin of life? I have already pointed out that no suitable (or at least accessible) older rocks are known on earth, so for now we can proceed no further from the direct evidence of fossils. We turn instead to the second front-page item, the claim of Carl Woese and his associates that methanogens are not bacteria at all, but may represent a new kingdom of prokaryotic life, distinct from the Monera (bacteria and blue green algae). Their report has been widely distorted, most notably in the *New York Times* editorial of November 11, 1977. The *Times* proclaimed that the great dichotomy of plants and animals had finally been broken: "Every child learns about things being vegetable or animal—a division as universal as the partition of mammals into male and female. Yet... [we now have] a 'third kingdom' of life on earth, organisms that are neither animal nor vegetable, but of another category altogether." But biologists abandoned "the great dichotomy" long ago, and no one now tries to cram all single-celled creatures into the two great groups traditionally recognized for complex life. Most popular these days is a system of five kingdoms: plants, animals, fungi, protists (single-celled eukaryotes, including amoebas and paramecia, with nucleus, mitochondria, and other organelles), and the prokaryotic monerans. If methanogens are promoted, they will form a sixth kingdom, joining the monerans in a superkingdom, Prokaryota. Most biologists regard the division between prokaryotes and eukaryotes, not between plants and animals, as the fundamental partition of life.

Woese's research group (see Fox, *et ai,* 1977 in the bibliography) isolated a common RNA from ten methanogens and from three monerans for comparison (DNA makes RNA, and RNA serves as the template upon which proteins are synthesized). A single strand of RNA, like DNA, consists of a sequence of nucleotides. Any one of four nucleotides can occupy each position, and each group of three nucleotides specifies an amino acid; proteins are built of amino acids arranged in folded chains. This, in a compressed phrase, is the "genetic code." Biochemists can now "sequence" RNA, that is, they can read the entire sequence of nucleotides in order down the RNA strand.

The prokaryotes (methanogens, bacteria, and blue-green algae) must have had a common ancestor at some time near the origin of life. Thus, all prokaryotes had the same RNA sequence at one point in their past; any current differences arose by divergence from this common ancestral sequence, after the trunk of the prokaryotic tree split up into its several branches. If molecular evolution proceeded at a constant rale, then the extent of current difference between any two forms would directly record the amount of time since their lineages split from a common ancestor—that is, the last time they shared the same RNA sequence. Perhaps, for example, a different nucleotide in the two forms at 10 percent of all common positions would indicate a time of divergence a billion years ago; 20 percent, two billion years, and so on.

Woese and his group measured the RNA differences for all pairs of species among the ten methanogens and three monerans and used the results to construct an evolutionary tree. This tree contains two major limbs—all the methanogens on one, all the monerans on the other. They chose their three monerans to represent the greatest differences within the group—enteric (gut) bacteria versus free-living blue-green algae, for example. Nonetheless, each moneran is more similar to all other monerans than any moneran is to any methanogen.

The simplest interpretation of these results holds that methanogens and monerans are separate evolutionary groups, with a common ancestry preceding the appearance of either. (Previously, methanogens had been classified among the bacteria; in fact, they had not been recognized as a coherent entity at all, but had been regarded as a set of independent evolutionary events—convergent evolution for the ability to make methane). This interpretation underlies Woese's claim that methanogens are separate from monerans and should be recognized as a sixth kingdom. Since good monerans had already evolved by Pig Tree times, 3.4 billion or more years ago, the common ancestry of methanogens and monerans must have been even earlier, thus pushing the origin of life even further back toward the beginning of the earth itself.

This simple interpretation, as Woese and his group realize, is not the only possible reading of their results. We may propose two other perfectly plausible hypotheses: (1) The three monerans that they used may not represent the entire group very well. Perhaps the RNA sequences of other monerans will differ as much from the first three as all the methanogens do. We would then have to include the methanogens with all monerans in a single grand group. (2) The assumption of nearly constant evolutionary rates may not hold. Perhaps the methanogens split off from one branch of monerans long after the main groups of monerans had branched from their common ancestor. These early methanogens may then have evolved at a rate far in excess of that followed by moneran groups in diverging from each other. In this case, the great difference in RNA sequence between any methanogen and any moneran would only record a rapid evolutionary rate for early methanogens, not a common ancestry with monerans before the monerans themselves split into subgroups. The gross amount of biochemical difference will accurately record time of divergence only if evolution proceeds at reasonably constant biochemical rates.

But one other observation makes Woese's hypothesis attractive and inspires my own strong rooting for it. The methanogens are anaerobic; they die in the presence of oxygen. Hence, they are confined today to unusual environments: muds at the bottom of ponds depleted of oxygen or deep hot springs in Yellowstone Park, for example. (The methanogens grow by oxidizing hydrogen and reducing carbon dioxide to methane—hence their name.) Now, amidst all the disagreement that afflicts the study of our early earth and its atmosphere, one point has gained general assent: our original atmosphere was devoid of oxygen and rich in carbon dioxide, the very conditions under which methanogens thrive and for which the earth's original life might have evolved. Could modern methanogens be remnants of the earth's first biota, originally evolved to match its general condition, but now restricted by the spread of oxygen to a few marginal environments? We believe that most free oxygen in our atmosphere is the product of organic photosynthesis. The Fig Tree organisms were already indulging in photosynthesis. Thus, the golden age of methanogens may have passed long before the advent of Fig Tree monerans. If this reverie be confirmed, then life must have originated long before Fig Tree times.

In short, we now have direct evidence of life in the oldest rocks that could contain it. And, by reasonably strong inference, we have reason to believe that a major radiation of methanogens predated these photosynthesizing monerans. Life probably arose about as soon as the earth became cool enough to support it.

Two closing thoughts, admittedly reflecting my personal prejudices: First, as a strong adherent to exobiology, that great subject without a subject matter (only theology may exceed us in this), I am delighted by the thought that life may be more intrinsic to planets of our size, position, and composition than we had ever dared to imagine. I feel even more certain that we are not alone, and I hope that more effort will be directed toward the search for other civilizations by radio-telescope. The difficulties are legion, but a positive result would be the most stupendous discovery in human history.

Secondly, I am led to wonder why the old, discredited orthodoxy of gradual origin ever gained such strong and general assent. Why did it seem so reasonable? Certainly not because any direct evidence supported it.

I am, as several other essays emphasize, an advocate of the position that science is not an objective, truth-directed machine, but a quintessentially human activity, affected by passions, hopes, and cultural biases. Cultural traditions of thought strongly influence scientific theories, often directing lines of speculation, especially (as in this case) when virtually no data exist to constrain either imagination or prejudice. In my own work (see essays 17 and 18), I have been impressed by the powerful and unfortunate influence that gradualism has exerted on paleontology via the old motto *natura nonfacitsaltum* ("nature does not make leaps").

Gradualism, the idea that all change must be smooth, slow, and steady, was never read from the rocks. It represented a common cultural bias, in part a response of nineteenth-century liberalism to a world in revolution. But it continues to color our supposedly objective reading of life's history.

In the light of gradualistic presuppositions, what other interpretation could have been placed upon the origin of life? It is an enormous step from the constituents of our original atmosphere to a DNA molecule. Therefore, the transition must have progressed laboriously through multitudes of intervening steps, one at a time, over billions of years.

But the history of life, as I read it, is a series of stable states, punctuated at rare intervals by major events that occur with great rapidity and help to establish the next stable era. Prokaryotes ruled the earth for three billion years until the Cambrian explosion, when most major designs of multicellular life appeared within ten million years. Some 375 million years later, about half the families of invertebrates became extinct within a few million years. The earth's history may be modelled as a series of occasional pulses, driving recalcitrant systems from one stable state to the next.

Physicists tell us that the elements may have formed during the first few minutes of the big bang; billions of subsequent years have only reshuffled the products of this cataclysmic creation. Life did not arise with such speed, but I suspect that it originated in a tiny fraction of its subsequent duration. But the reshuffling and subsequent evolution of DNA have not simply recycled the original products; they have produced wonders.

Might We Fit Inside a Sponge's Cell

I SPENT DECEMBER 31, 1979 reading through a stack of New York Sunday papers for the last weekend of the decade. Prominently featured, as always in the doldrums of such artificial transition, were lists of predictions about "ins" and "outs" across the boundary: what will the eighties reject that the seventies treasured? what, despised during the seventies, will the eighties rediscover?

This surfeit of contemporary speculation drove my mind back to the last transition between centuries and to a consideration of biological ins and outs at this broader scale. The hottest subject of nineteenth-century biology did suffer a pronounced eclipse in the twentieth. Yet I happen to maintain a strong fondness for it. I also believe that new methods will revive it as a major concern for the remaining decades of our century.

Darwin's revolution led a generation of natural historians to view the reconstruction of life's tree as their most important evolutionary task. As ambitious men embarked upon a bold new course, they did not focus narrowly upon little twiglets (the relation of lions to tigers), or even upon ordinary branches (the link between cockles and mussels); they sought to root the trunk itself and to identify its major limbs: how are plants and animals related? from what source did the vertebrates spring?

In their mistaken view, these naturalists also possessed a method that could extract the answers they sought from the spotty data at their disposal. For, under Haeckel's "biogenetic law"—ontogeny recapitulates phylogeny—an animal climbs its own family tree during its embryological development. The simple observation of embryos should reveal a parade of adult ancestors in proper order. (Nothing is ever quite so uncomplicated, of course. The recapitulationists knew that some embryonic stages represented immediate adaptations, not ancestral reminiscences; they also understood that stages could be mixed up, even inverted, by unequal rates of development among different organs. Yet they believed that such "superficial" modifications could always be recognized and subtracted, leaving the ancestral parade intact.) E.G. Conklin, who later became an opponent of "phylogenizing," recalled the beguiling appeal of Haeckel's law:

> Here was a method which promised to reveal more important secrets of the past than would the unearthing of all the buried monuments of antiquity—in fact nothing less than a complete genealogical tree of all the diversified forms of life which inhabit the earth.

But the turn of the century also heralded the collapse of recapitulation. It died primarily because Mendelian genetics (rediscovered in 1900) rendered its premises untenable. (The "parade of adults" required that evolution proceed only by an addition of new stages to the end of ancestral ontogenies. But if new features are controlled by genes, and these genes must be present from the very moment of conception, then why shouldn't new features be expressed at any stage of embryonic development or later growth?) But its luster had faded long before. The assumption that ancestral reminiscences could always be distinguished from recent embryonic adaptations had not been sustained. Too many stages were missing, too many others discombobulated. The application of Haeckel's law produced endless, unresolvable, fruitless argument, not an unambiguous tree of life. Some tree builders wanted to derive vertebrates from echinoderms, others from annelid worms, still others from horseshoe crabs. E.B. Wilson, apostle of the "exact," experimental method that would supplant speculative phylogenizing, complained in 1894:

> It is a ground of reproach to morphologists that their science should be burdened with such a mass of phylogenetic speculations and hypotheses, many of them mutually exclusive, in the absence of any well-defined standard of value by which to estimate their relative probability. The truth is that the search . . . has too often led to a wild speculation unworthy of the name of science; and it would be small wonder if the modern student, especially after a training in the methods of more exact sciences, should regard the whole phylogenetic aspect of morphology as a kind of speculative pedantry unworthy of serious attention.

Phylogenizing fell from general favor, but you can't keep an intrinsically exciting subject down. (I speak of high-level phylogenizing—the trunk and limbs. For twigs and small branches, where evidence is more adequate, work has always proceeded apace, with more assurance and less excitement.) We didn't need "Roots" to remind us that genealogy exerts a strange fascination over people. If uncovering the traces of a distant great-grandparent in a small overseas village fills us with satisfaction, then probing further back to an African ape, a reptile, a fish, that still-unknown ancestor of vertebrates, a single-celled forebear, even to the origin of life itself, can be positively awesome. Unfortunately, one might even say perversely, the further back we go, the more fascinated we become and the less we know. In this column, I will discuss one classic issue in phylogenizing as an example of the joys and frustrations of a subject that will not go away: the origin of multicellularity in animals.

Ideally, we might hold out for a simple, empirical resolution of the issue. Might we not hope to find a sequence of fossils so perfectly intermediate between a protist (single-celled ancestor) and a metazoan (multicelled descendant) that all doubt would be erased? We may effectively write off such a hope: the transition occurred in unfossilizable, soft-bodied creatures long before the inception of an adequate fossil record during the Cambrian explosion, some 600 million years ago. The first metazoan fossils do not surpass the most primitive modern metazoans in their similarity to protists. We must turn to living organisms, hoping that some still preserve appropriate marks of ancestry.

There is no mystery to the method of genealogical reconstruction. It is based on the analysis of similarities between postulated relatives. "Similarity," unfortunately, is no simple concept. It arises for two fundamentally different reasons. The construction of evolutionary trees requires that the two be rigorously separated, for one indicates genealogy while the other simply misleads us. Two organisms may maintain the same feature because both inherited it from a common ancestor. These are *homologous* similarities, and they indicate "propinquity of descent," to use Darwin's words. Forelimbs of people, porpoises, bats and horses provide the classic example of homology in most textbooks. They look different, and do different things, but are built of the same bones. No engineer, starting from scratch each time, would have built such disparate structures from the same parts. Therefore, the parts existed before the particular set of structures now housing them: they were, in short, inherited from a common ancestor.

Two organisms may also share a feature in common as a result of separate but similar evolutionary change in independent lineages. These are *analogous* similarities; they are the bugbear of genealogists because they confound our naive expectation that things looking alike should be closely related. The wings of birds, bats and butterflies adorn most texts as a standard example of analogy. No common ancestor of any pair had wings.

Our difficulties in identifying the trunks and limbs of life's tree do not record muddled thinking about methods. All major naturalists, from Haeckel on (and even before) stated their procedure correctly: separate homologous from analogous similarity, discard analogies, and build genealogy from homology alone. Haeckel's law was a procedure, unfortunately incorrect, for the recognition of homology. The goal is, and has been, clear enough.

In a broad sense, we know how to identify homology. Analogy has its limits. It may build striking external, functional similarity in two unrelated lineages, but it does not modify thousands of complex and independent parts in the same way. At a certain level of precision, similarities must be homologous. Unfortunately, we rarely have enough information to be confident that this required level has been attained. When we compare primitive metazoans with different protists as potential relatives, we often work with only a few features held in common for any contrast—too few to be sure about homology. Moreover, small genetic changes often have profound effects upon external, adult form. Therefore, a similarity that looks too uncanny and complex to arise more than once may actually record a simple and repeatable change. Most importantly, we aren't even comparing the right organisms, but only pale reflections of them. The transition from protist to metazoan occurred more than 600 million years ago. All true ancestors and original descendants disappeared eons ago. We can only hope that their essential, identifying features have been retained in some modern forms. Yet, if retained, they have surely been modified and overlain with a plethora of specialized adaptations. How can we separate original structure from later modification from new adaptation? No one has ever found an unfailing guide.

Only two scenarios have been favored for the origin of metazoans from protists: in the first (amalgamation) a group of protistan cells came together, began to live as a colony, evolved a division of labor and function among cells and regions, and finally formed an integrated structure; in the second (division), cellular partitions formed within a single protistan cell. (A third potential scenario, repeated failure of daughter cells to separate following cell division, has few takers these days.)

At the very outset of our inquiry, we come up against the problem of homology. What about multicellularity itself? Did it arise only once? Have we explained its occurrence in all animals once we decide how it arose in the most primitive? Or did it evolve several times? In other words, is the multicellularity of various animal lineages homologous or analogous?

The metazoan group usually regarded as most primitive, the sponges, clearly arose by the first scenario of amalgamation. In fact, modern sponges are little more than loosely knit federations of flagellated protists. In some species, cells can even be disaggregated by passing the sponge through a fine silk cloth. The cells then move independently, reaggregate into small clumps, differentiate and regenerate an entire new sponge in its original form. If all animals arose from sponges, then multicellularity is homologous throughout our kingdom, and it arose by amalgamation.

But most biologists regard sponges as an evolutionary dead end without subsequent descendants. Multicellularity is, after all, a prime candidate for frequent, independent evolution. It displays the two primary features of analogous similarity: it is reasonably simple to accomplish, and it is both highly adaptive and the only potential path to the benefits it confers. Single cells, ostrich eggs notwithstanding, cannot become very large. The earth's physical environment contains scores of habitats available only to creatures beyond the size limit of a single cell. (Consider only the stability that arises from being large enough to enter a realm where gravity overshadows the forces that act upon surfaces. Since the surface/volume ratio declines with growth, increasing size is the surest path to this realm.)

Not only has multicellularity evolved separately in the three great higher kingdoms of life (plants, animals, and fungi), but it probably arose several times in each kingdom. Most biologists agree that all origins within plants and fungi occurred by amalgamation—these organisms are the descendants of protistan colonies. Sponges also arose by amalgamation. May we then close the issue and state that multicellularity, although analogous both across and within kingdoms, evolved in the same basic way each time? Modern protists include colonial forms that display both regular arrangement of cells and incipient differentiation. Remember the *Volvox* colonies of high school biology labs? (Actually, I must confess that I don't. I attended a public high school in New York just before Sputnik went up. We had no lab at all, though it arrived in a flash just as I left.) Some volvoxes form colonies with a definite number of cells arranged in a regular manner. The cells may differ in size, and reproductive function may be confined to those at one end. Is it such a big step to a sponge?

Only among animals may we make a good case for another scenario. Did some animals, ourselves included, arise by division? This question cannot be answered until we resolve one of the oldest riddles in zoology: the status of the phylum Cnidaria (corals and their allies, but also including the beautiful, translucent Ctenophora, or comb-jellies). Almost everyone agrees that the Cnidaria arose by amalgamation. The dilemma resides in their relationship with other animal phyla. Almost all possible schemes have their supporters: cnidarians as descendants of sponges and ancestors of nothing else; cnidarians as a separate branch of the animal kingdom without descendants; cnidarians as the ancestors of all "higher" animal phyla (the classical view of the nineteenth century); cnidarians as degenerate descendants of a higher phylum. If either of the last two schemes can ever be established, then our issue is settled—all animals arose by amalgamation, probably twice (sponges and everything else). But if the "higher" animal phyla are not closely related to cnidarians, if they represent a third, separate evolution of multicellularity in the animal kingdom, then the scenario of division must be seriously considered.

Supporters of a separate origin for the higher animals generally cite the Platyhelminthes (flatworms) as a potentially ancestral stock. Earl Hanson, a biologist at Wesleyan University, has been a leading crusader, both for a platyhelminth origin of higher animals and for the scenario of division. If his iconoclastic view prevails, then the higher animals, including humans of course, are probably the only multicellular products of division rather than amalgamation.

Hanson has pursued his case by studying the similarities between a group of protists known as ciliates (including the familiar *Paramecium),* and the "simplest" of flatworms, the Acoela (named for their failure to develop a body cavity). Many ciliates maintain large numbers of nuclei within their single cell. If cellular partitions arose between the nuclei, would the resulting creature be enough like an acoelous flatworm to justify a claim for homology?

Hanson documents an extensive set of similarities between the multinucleate ciliates and the acoeles. Acoeles are tiny marine flatworms. Some can swim, and a few live in water up to 250 meters in depth; but most crawl along the sea bottom in shallow water, living under rocks or in sand and mud. They are similar in size to the multinucleate ciliates. (It is not true that all metazoans are larger than all protists. The ciliates range in length from 1/100 to 3 millimeters, while some acoeles are less than 1 millimeter in length.) The internal similarities of ciliates and acoeles reside primarily in their shared simplicity; for acoeles, unlike conventional metazoans, lack both a body cavity and the organs associated with it. They have no permanent digestive, excretory, or respiratory system. Like the ciliate protists, they form temporary food vacuoles and perform digestion within them. Both ciliates and acoeles divide their bodies roughly into inner and outer layers. Ciliates maintain an ectoplasm (outer layer) and endoplasm (inner layer), and concentrate their nuclei in the endoplasm. Acoeles devote an inner region to digestion and reproduction, and an outer region to locomotion, protection, and capture of food.

The two groups also display some outstanding differences. Acoeles build a nerve net and reproductive organs that can become quite complex. Some have penises, for example, and impregnate each other hypodermically by penetrating through the body wall. They undergo embryonic development after fertilization. Ciliates,„by contrast, have no organized nervous system. They divide by fission and have no embryology, although they do indulge in sex via a process called conjugation. (In conjugation, two ciliates come together and exchange genetic material. They then separate and each divides later to form two daughters. Sex and reproduction, combined in nearly all metazoa, are separate processes in ciliates.) Most prominently, of course, acoeles are cellularized, ciliates are not.

These differences should not debar a hypothesis of close genealogicalyelationship. After all, as I argued previously, contemporary ciliates and acoeles are more than half a billion years beyond their potential common ancestor. Neither represents a transitional form in the origin of multicellularity. The debate centers instead on the similarities, and on the oldest and most basic issue of all: are the similarities homologous or analogous?

Hanson argues for homology, claiming that acoele simplicity is an ancestral condition within the platyhelminths—and that similarities between ciliates and acoeles, largely a result of this simplicity, do record genealogical connection. His detractors reply that the simplicity of acoeles is a secondary result of their "regressive" evolution from more complex platyhelminths, a consequence of pronounced reduction in body size within acoeles. Larger turbellarians (the platyhelminth group including acoeles) have intestines and excretory organs. If acoele simplicity is a derived condition *within* the turbellarians, then it cannot reflect direct inheritance from a ciliate stock.

Unfortunately, the similarities that Hanson cites are of the sort that always produce unresolvable wrangling about homology vs. analogy. They are neither precise, nor numerous enough to guarantee homology. Many are based upon the *absence* of complexity in acoeles, and evolutionary loss is easy and repeatable, whereas separate development of precise and intricate structures may be unlikely. Moreover, acoele simplicity is a predictable result of their small body size—it may represent a functional convergence upon ciliate design by a group that secondarily entered their range of body size, not a connection by descent. Again, we invoke the principle of surfaces and volumes. Many physiological functions, including breathing, digestion, and excretion, must proceed through surfaces and serve the entire body's volume. Large animals have such a low ratio of external surface to internal volume that they must evolve internal organs to provide more surface. (Functionally, lungs are little more than bags of surface for exchange of gases, while intestines are sheets of surface for the passage of digested food.) But small animals maintain such a high ratio of external surface to internal volume that they often can breathe, feed, and excrete through the external surface alone. The smallest representatives of many phyla more complex than platyhelminths also lose internal organs. *Caecum,* for example, the smallest snail, has lost its internal respiratory system entirely and takes in oxygen through its external surface.

Other similarities, cited by Hanson, may be homologous, but so widespread among other creatures that they merely illustrate the broader affinity of all protists with all metazoans, not any specific pathway of descent. Meaningful homologies must be confined to characters that are both shared by descent *and* derived. (Derived characters evolve uniquely in the common ancestor of two groups that share them; they are marks of genealogy. A shared primitive character, on the other hand, cannot specify descent. The presence of DNA in both ciliates and acoeles tells us nothing about their affinity because all protists and metazoans have DNA.) Thus, Hanson mentions "complete ciliation" as a "permanent character significantly held in common by ciliates and acoeles." But cilia, although homologous, are a shared primitive character; many other groups, including cnidarians, have them. The *completeness* of ciliation, on the other hand, represents an "easy" evolutionary event that may only be analogous in ciliates and acoeles. The external surface sets a limit to the maximal number of cilia that may be affixed. Small animals, with high surface/volume ratios, may indulge in ciliary locomotion; large animals cannot insert enough cilia on their relatively declining surface to propel their mass. The complete ciliation of acoeles may reflect a secondary, adaptive response to their small size. The tiny snail *Caecum* also moves by cilia; all its larger relatives use muscular contraction for locomotion.

Hanson is, of course, well aware that he cannot prove his intriguing hypothesis with the classical evidence of morphology and function. "The best we can say," he concludes, "is that many suggestive similarities are present [between ciliates and acoeles], but no rigorously definable homologies." Is there another method that might resolve the issue, or are we permanently condemned to unresolvable wrangling? Homology might be established with confidence if we could generate a new set of characters sufficiently numerous, comparable, and complex—for analogy cannot be the explanation of detailed, part-by-part similarity in thousands of independent items. The laws of mathematical probability will not allow it.

Fortunately, we now have a potential source of such information—the DNA sequence of comparable proteins. All protists and metazoans share many homologous proteins. Each protein is built of a long chain of amino acids; each amino acid is coded by a sequence of three nucleotides in DNA. Thus, the DNA code for each protein may contain hundreds of thousands of nucleotides in a definite order.

Evolution proceeds by substitution of nucleotides. After two groups split from a common ancestor, their nucleotide sequences begin to accumulate changes. The number of changes seems to be at least roughly proportional to the amount of time since the split. Thus, overall similarity in nucleotide sequence for homologous proteins may measure the extent of genealogical separation. A nucleotide sequence is a homologizer's dream—for it represents thousands of potentially independent characters. Each nucleotide position is a site of possible change.

Techniques are just now becoming available for the routine sequencing of nucleotides. Within ten years, I believe, we will be able to take homologous proteins from all the ciliate and metazoan groups at issue, sequence them, measure the similarities between each pair of organisms and obtain greater insight (perhaps even resolution) for this old genealogical mystery. If acoeles are most similar to protist groups that might achieve multicellularity by evolving cell membranes within their bodies, then Hanson will be vindicated. But if they are closest to protists that can reach multicellularity by integration within a colony, then the classical view will prevail, and all metazoa will emerge as the products of amalgamation.

The study of genealogy has been unfairly eclipsed in our century by the analysis of adaptation, but it cannot lose its power to fascinate. Simply consider what Hanson's scenario implies about our relationship with other multicellular organisms. Few zoologists doubt that all higher animals achieved their multicellular status by whatever method the flatworms followed. If acoeles evolved by the cellularization of a ciliate, then our multicellular body is the homolog of a single protistan cell. If sponges, cnidarians, plants and fungi arose by amalgamation, then their bodies are the homologs of a protistan colony. Since each ciliate cell is the homolog of an individual cell in any protistan colony, we must conclude—and I do mean this literally—that the entire human body is the homolog of a single cell in a sponge, coral, or plant.

The curious paths of homology go further back. The protistan cell itself may have evolved from a symbiosis of several simpler prokaryotic (bacterial or blue green algal) cells. Mitochondria and chloroplasts seem to be the homologs of entire prokaryotic cells. Thus, each cell of any protist, and each cell in any metazoan body, may be, by genealogy, an integrated colony of prokaryotes. Shall we then view ourselves both as a congeries of bacterial colonies and as the homolog of a single cell in a sponge or onion skin? Think upon it next time you swallow a carrot or slice a mushroom.

Were Dinosaurs Dumb?

WHEN MUHAMMAD ALI flunked his army intelligence test, he quipped (with a wit that belied his performance on the exam): "I only said I was the greatest; I never said I was the smartest." In our metaphors and fairy tales, size and power are almost always balanced by a want of intelligence. Cunning is the refuge of the little guy. Think of Br'er Rabbit and Br'er Bear; David smiting Goliath with a slingshot; Jack chopping down the beanstalk. Slow wit is the tragic flaw of a giant.

The discovery of dinosaurs in the nineteenth century provided, or so it appeared, a quintessential case for the negative correlation of size and smarts. With their pea brains and giant bodies, dinosaurs became a symbol of lumbering stupidity. Their extinction seemed only to confirm their flawed design.

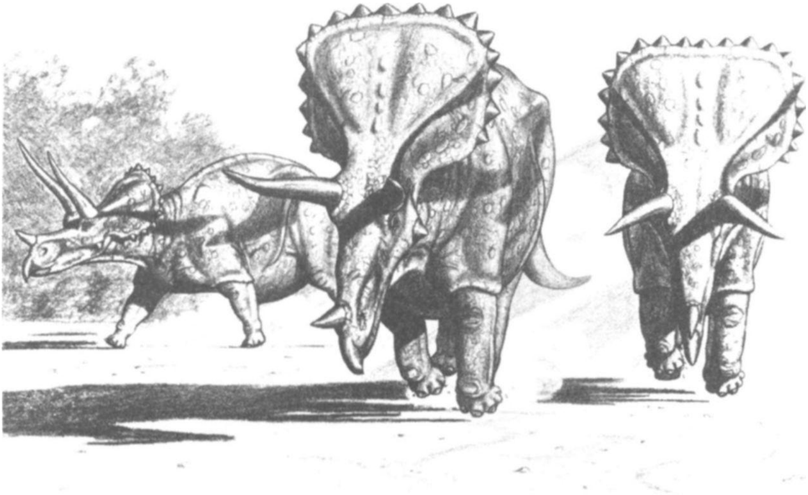
Dinosaurs were not even granted the usual solace of a giant—great physical prowess. God maintained a discreet silence about the brains of behemoth, but he certainly marveled at its strength: "Lo, now, his strength is in his loins, and his force is in the navel of his belly. He moveth his tail like a cedar. . . . His bones are as strong pieces of brass; his bones are like bars of iron (Job 40:16-18]." Dinosaurs, on the other hand, have usually been reconstructed as slow and clumsy. In the standard illustration, *Brontosaurus* wades in a murky pond because he cannot hold up his own weight on land.

Popularizations for grade school curricula provide a good illustration of prevailing orthodoxy. I still have my third grade copy (1948 edition) of Bertha Morris *Parker's Animals of Yesterday,* stolen, I am forced to suppose, from P.S. 26, Queens (sorry Mrs. McInerney). In it, boy (teleported back to the Jurassic) meets brontosaur:

> It is huge, and you can tell from the size of its head that it must be stupid. . . . This giant animal moves about very slowly as it eats. No wonder it moves slowly! Its huge feet are very heavy, and its great tail is not easy to pull around. You are not surprised that the thunder lizard likes to stay in the water so that the water will help it hold up its huge body. . . . Giant dinosaurs were once the lords of the earth. Why did they disappear? You can probably guess part of the answer—their bodies were too large for their brains. If their bodies had been smaller, and their brains larger, they might have lived on.

Dinosaurs have been making a strong comeback of late, in this age of "I'm OK, you're OK." Most paleontologists are now willing to view them as energetic, active, and capable animals. The *Brontosaurus* that wallowed in its pond a generation ago is now running on land, while pairs of males have been seen twining their necks about each other in elaborate sexual combat for access to females (much like the neck wrestling of giraffes). Modern anatomical reconstructions indicate strength and agility, and many paleontologists now believe that dinosaurs were warmblooded (see essay 26).

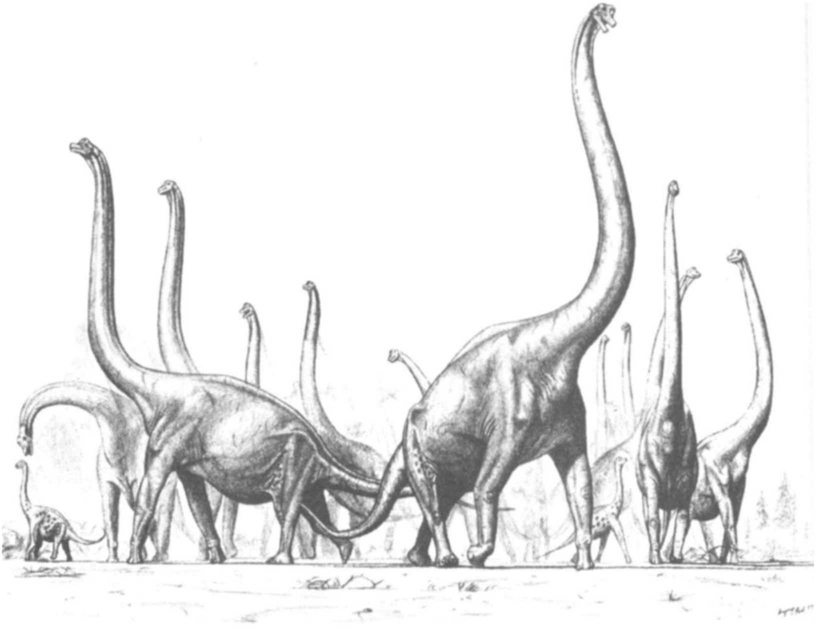
The idea of warmblooded dinosaurs has captured the public imagination and received a torrent of press coverage. Yet another vindication of dinosaurian capability has received very little attention, although I regard it as equally significant. I refer to the issue of stupidity and its correlation with size. The revisionist interpretation, which I support in this column, does not enshrine dinosaurs as paragons of intellect, but it does maintain that they were not



Triceratops GREGORY S. PAUL

small brained after all. They had the "right-sized" brains for reptiles of their body size.

I don't wish to deny that the flattened, minuscule head of largebodied *Stegosaurus* houses little brain from our subjective, top-heavy perspective, but I do wish to assert that we should not expect more of the beast. First of all, large animals have relatively smaller brains than related, small animals. The correlation of brain size with body size among kindred animals (all reptiles, all mammals, for example) is remarkably regular. As we move from small to large animals, from mice to elephants or small lizards to Komodo dragons, brain size increases, but not so fast as body size. In other words, bodies grow faster than brains, and large animals have low ratios of brain weight to body weight. In fact, brains grow only about two-thirds as fast as bodies. Since we have no reason to believe that large animals are consistently stupider than their smaller relatives, we must conclude that large animals require relatively less brain to do as well as smaller animals. If we do not recognize this relationship, we are likely to underestimate the mental



Brachiosaurus **GREGORY S. PAUL**

Brachiosaurus CRECORY S. PAUL

power of very large animals, dinosaurs in particular.

Second, the relationship between brain and body size is not identical in all groups of vertebrates. All share the same rate of relative decrease in brain size, but small mammals have much larger brains than small reptiles of the same body weight. This discrepancy is maintained at all larger body weights, since brain size increases at the same rate in both groups—two-thirds as fast as body size.

Put these two facts together—all large animals have relatively small brains, and reptiles have much smaller brains than mammals at any common body weight—and what should we expect from a normal, large reptile? The answer, of course, is a brain of very modest size. No living reptile even approaches a middle-sized dinosaur in bulk, so we have no modern standard to serve as a model for dinosaurs.

Fortunately, our imperfect fossil record has, for once, not severely disappointed us in providing data about fossil brains. Superbly preserved skulls have been found for many species of dinosaurs, and cranial capacities can be measured. (Since brains do not fill craniums in reptiles, some creative, although not unreasonable, manipulation must be applied to estimate brain size from the hole within a skull.) With these data, we have a clear test for the conventional hypothesis of dinosaurian stupidity. We should agree, at the outset, that a reptilian standard is the only proper one—it is surely irrelevant that dinosaurs had smaller brains than people or whales. We have abundant data on the relationship of brain and body size in modern reptiles. Since we know that brains increase two-thirds as fast as bodies as we move from small to large living species, we can extrapolate this rate to dinosaurian sizes and ask whether dinosaur brains match what we would expect of living reptiles if they grew so large.

Harry Jerison studied the brain sizes of ten dinosaurs and found that they fell right on the extrapolated reptilian curve. Dinosaurs did not have small brains; they maintained just the right-sized brains for reptiles of their dimensions. So much for Ms. Parker's explanation of their demise.

Jerison made no attempt to distinguish among various kinds of dinosaurs; ten species distributed over six major groups scarcely provide a proper basis for comparison. Recently, James A. Hopson of the University of Chicago gathered more data and made a remarkable and satisfying discovery.

Hopson needed a common scale for all dinosaurs. He therefore compared each dinosaur brain with the average reptilian brain we would expect at its body weight. If the dinosaur falls on the standard reptilian curve, its brain receives a value of 1 .C (called an encephalization quotient, or EQ,—the ratio of actual brain to expected brain for a standard reptile of the same body weight). Dinosaurs lying above the curve (more brain than expected in a standard reptile of the same body weight) receive values in excess of 1.0, while those below the curve measure less than 1.0.

Hopson found that the major groups of dinosaurs can be ranked by increasing values of average EQ. This ranking corresponds perfectly with inferred speed, agility and behavioral complexity in feeding (or avoiding the prospect of becoming a meal). The giant sauropods, *Brontosaurus* and its allies, have the lowest EOJs—0.20 to 0.35. They must have moved fairly slowly and without great maneuverability. They probably escaped predation by virtue of their bulk alone, much as elephants do today. The armored ankylosaurs and stegosaurs come next with EOJs of 0.52 to 0.56. These animals, with their heavy armor, probably relied largely upon passive defense, but the clubbed tail of ankylosaurs and the spiked tail of stegosaurs imply some active fighting and increased behavioral complexity.

The ceratopsians rank next at about 0.7 to 0-9. Hopson remarks: "The larger ceratopsians, with their great horned heads, relied on active defensive strategies and presumably required somewhat greater agility than the tail-weaponed forms, both in fending off predators and in intraspecific combat bouts. The smaller ceratopsians, lacking true horns, would have relied on sensory acuity and speed to escape from predators." The ornithopods (duckbills and their allies) were the brainiest herbivores, with EOJs from 0.85 to 1.5. They relied upon "acute senses and relatively fast speeds" to elude carnivores. Flight seems to require more acuity and agility than standing defense. Among ceratopsians, small, hornless, and presumably fleeing *Protoceratops* had a higher EQ_than great three-horned *Tnceratops.*

Carnivores have higher EOJs than herbivores, as in modern vertebrates. Catching a rapidly moving or stoutly fighting prey demands a good deal more upstairs than plucking the right kind of plant. The giant theropods *(Tyrannosaurus* and its allies) vary from 1.0 to nearly 2.0. Atop the heap, quite appropriately at its small size, rests the little coelurosaur *Stenonychosaurus* with an EQ_ well above 5.0. Its actively moving quarry, small mammals and birds perhaps, probably posed a greater challenge in discovery and capture than *Tnceratops* afforded *Tyrannosaurus.*

I do not wish to make a naive claim that brain size equals intelligence or, in this case, behavioral range and agility (I don't know what intelligence means in humans, much less in a group of extinct reptiles). Variation in brain size within a species has precious little to do with brain power (humans do equally well with 900 or 2,500 cubic centimeters of brain). But comparison across species, when the differences are large, seems reasonable. I do not regard it as irrelevant to our achievements that we so greatly exceed koala bears —much as I love them—in EQ. The sensible ordering among dinosaurs also indicates that even so coarse a measure as brain size counts for something.

If behavioral complexity is one consequence of mental power, then we might expect to uncover among dinosaurs some signs of social behavior that demand coordination, cohesiveness, and recognition. Indeed we do, and it cannot be accidental that these signs were overlooked when dinosaurs labored under the burden of a falsely imposed obtuseness. Multiple trackways have been uncovered, with evidence for more than twenty animals traveling together in parallel movement. Did some dinosaurs live in herds? At the Davenport Ranch sauropod trackway, small footprints lie in the center and larger ones at the periphery. Could it be that some dinosaurs traveled much as some advanced herbivorous mammals do today, with large adults at the borders sheltering juveniles in the center?

In addition, the very structures that seemed most bizarre and useless to older paleontologists—the elaborate crests of hadrosaurs, the frills and horns of ceratopsians, and the nine inches of solid bone above the brain of *Pachycephalosaurus*—now appear to gain a coordinated explanation as devices for sexual display and combat. Pachycephalosaurs may have engaged in head-butting contests much as mountain sheep do today. The crests of some hadrosaurs are well designed as resonating chambers; did they engage in bellowing matches? The ceratopsian horn and frill may have acted as sword and shield in the battle for mates. Since such behavior is not only intrinsically complex, but also implies an elaborate social system, we would scarcely expect to find it in a group of animals barely muddling through at a moronic level.

But the best illustration of dinosaurian capability may well be the fact most often cited against them—their demise. Extinction, for most people, Carries many of the connotations attributed to sex not so long ago—a rather disreputable business, frequent in occurrence, but not to anyone's credit, and certainly not to be discussed in proper circles. But, like sex, extinction is an ineluctable part of life. It is the ultimate fate of all species, not the lot of unfortunate and ill-designed creatures. It is no sign of failure.

The remarkable thing about dinosaurs is not that they became extinct, but that they dominated the earth for so long. Dinosaurs held sway for 100 million years while mammals, all the while, lived as small animals in the interstices of their world. After 70 million years on top, we mammals have an excellent track record and good prospects for the future, but we have yet to display the staying power of dinosaurs.

People, on this criterion, are scarcely worth mentioning —5 million years perhaps since *Australopithecus,* a mere 50,000 for our own species, *Homo sapiens.* Try the ultimate test within our system of values: Do you know anyone who would wager a substantial sum, even at favorable odds, on the proposition that *Homo sapiens* will last longer than *Brontosaurus?*

Nature's Odd Couples

From Nature's chain whatever link you strike,
Tenth, or ten thousandth, breaks the chain alike.
Alexander Pope,
An Essay on Man (1733)

POPE'S COUPLET EXPRESSES a common, if exaggerated, concept of connection among organisms in an ecosystem. But ecosystems are not so precariously balanced that the extirpation of one species must act like the first domino in that colorful metaphor of the cold war. Indeed, it could not be, for extinction is the common fate of all species—and they cannot all take their ecosystems with them. Species often have as much dependence upon each other as Longfellow's "Ships that pass in the night." New York City might even survive without its dogs (I'm not so sure about the cockroaches, but I'd chance it).

Shorter chains of dependence are more common. Odd couplings between dissimilar organisms form a stock in trade for popularizers of natural history. An alga and a fungus make lichen; photosynthetic microorganisms live in the tissue of reef-building corals. Natural selection is opportunistic; it fashions organisms for their current environments and cannot anticipate the future. One species often evolves an unbreakable dependency upon another species; in an inconstant world, this fruitful tie may seal its fate.

I wrote my doctoral dissertation on the fossil land snails of Bermuda. Along the shores, I would often encounter large hermit crabs incongruously stuffed—big claw protruding—into the small shell of a neritid snail (nerites include the familiar "bleeding tooth"). Why, I wondered, didn't these crabs trade their cramped quarters for more commodious lodgings? After all, hermit crabs are exceeded only by modern executives in their frequency of entry into the real estate market. Then, one day, I saw a hermit crab with proper accommodations—a shell of the "whelk" *Cittarium pica,* a large snail and major food item throughout the West Indies. But the *Cittarium* shell was a fossil, washed out of an ancient sand dune to which it had been carried 120,000 years before by an ancestor of its current occupant. I watched carefully during the ensuing months. Most hermits had squeezed into nerites, but a few inhabited whelk shells and the shells were always fossils.

I began to put the story together, only to find that I had been scooped in 1907 by Addison E. Verrill, master taxonomist, Yale professor, protege of Louis Agassiz, and diligent recorder of Bermuda's natural history. Verrill searched the records of Bermudian history for references to living whelks and found that they had been abundant during the first years of human habitation. Captain John Smith, for example, recorded the fate of one crew member during the great famine of 1614-15: "One amongst the rest hid himself in the woods, and lived only on Wilkes and Land Crabs, fat and lusty, many months." Another crew member stated that they made cement for the seams of their vessels by mixing lime from burned whelk shells with turtle oil. Verrill's last record of living *Cittarium* came from kitchen middens of British soldiers stationed on Bermuda during the war of 1812. None, he reported, had been seen in recent times, "nor could I learn that any had been taken within the memory of the oldest inhabitants." No observations during the past seventy years have revised Verrill's conclusion that *Cittarium* is extinct in Bermuda.

As I read Verrill's account, the plight of *Cenobita dwgenes* (proper name of the large hermit crab) struck me with that anthropocentric twinge of pain often invested, perhaps improperly, in other creatures. For I realized that nature had condemned *Cenobita* to slow elimination on Bermuda. The neritid shells are too small; only juvenile and very young adult crabs fit inside them—and very badly at that. No other modern snail seems to suit them and a successful adult life requires the discovery and possession (often through conquest) of a most precious and dwindling commodity—a *Cittanum* shell. But *Cittarium,* to borrow the jargon of recent years, has become a "nonrenewable resource" on Bermuda, and crabs are still recycling the shells of previous centuries. These shells are thick and strong, but they cannot resist the waves and rocks forever—and the supply constantly diminishes. A few "new" shells tumble down from the fossil dunes each year—a precious legacy from ancestral crabs that carried them up the hills ages ago—but these cannot meet the demand. *Cenobita* seems destined to fulfill the pessimistic vision of many futuristic films and scenarios: depleted survivors fighting to the death for a last morsel. The scientist who named this large hermit chose well. Diogenes the Cynic lit his lantern and searched the streets of Athens for an honest man; none could he find. *C. dwgenes* will perish looking for a decent shell.

This poignant story of *Cenobita* emerged from deep storage in my mind when I heard a strikingly similar tale recently. Crabs and snails forged an evolutionary interdependence in the first story. A more unlikely combination —seeds and dodos—provides the second, but this one has a happy ending.

William Buckland, a leading catastrophist among nineteenth-century geologists, summarized the history of life on a large chart, folded several times to fit in the pages of his popular work *Geology and Mineralogy Considered With Reference to Natural Theology.* The chart depicts victims of mass extinctions grouped by the time of their extirpation. The great animals are crowded together: ichthyosaurs, dinosaurs, ammonites, and pterosaurs in one cluster; mammoths, woolly rhinos, and giant cave bears in another. At the far right, representing modern animals, the dodo stands alone, the first recorded extinction of our era. The dodo, a giant flightless pigeon (twenty-five pounds or more in weight), lived in fair abundance on the island of Mauritius. Within 200 years of its discovery in the fifteenth century, it had been wiped out—by men who prized its tasty eggs and by the hogs that early sailors had transported to Mauritius. No living dodos have been seen since 1681.

In August, 1977, Stanley A. Temple, a wildlife ecologist at the University of Wisconsin, reported the following remarkable story (but see postscript for a subsequent challenge). He, and others before him, had noted that a large tree, *Calvana major,* seemed to be near the verge of extinction on Mauritius. In 1973, he could find only thirteen "old, overmature, and dying trees" in the remnant native forests. Experienced Mauritian foresters estimated the trees' ages at more than 300 years. These trees produce well-formed, apparently fertile seeds each year, but none germinate and no young plants are known. Attempts to induce germination in the controlled and favorable climate of a nursery have failed. Yet *Calvaria* was once common on Mauritius; old forestry records indicate that it had been lumbered extensively.

Calvaria's large fruits, about two inches in diameter, consist of a seed enclosed in a hard pit nearly half an inch thick. This pit is surrounded by a layer of pulpy, succulent material covered by a thin outer skin. Temple concluded that *Calvaria* seeds fail to germinate because the thick pit "mechanically resists the expansion of the embryo within." How, then, did it germinate in previous centuries?

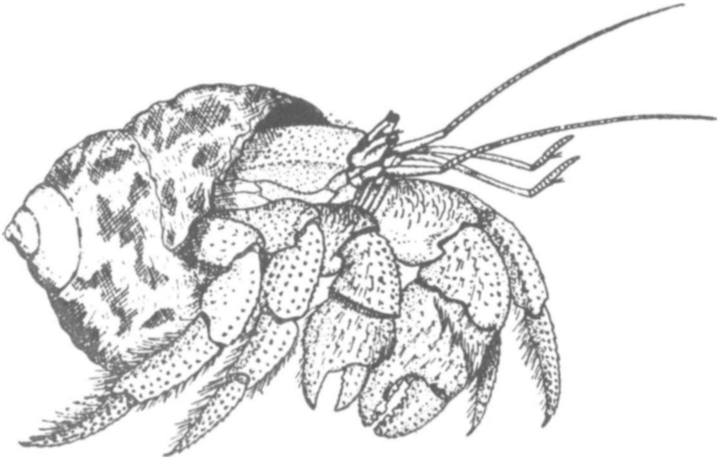
Temple put two facts together. Early explorers reported that the dodo fed on fruits and seeds of large forest trees; in fact, fossil *Calvaria* pits have been found among skeletal remains of the dodo. The dodo had a strong gizzard filled with large stones that could crush tough bits of food. Secondly, the age of surviving *Calvaria* trees matches the demise of the dodo. None has sprouted since the dodo disappeared almost 300 years ago.

Temple therefore argues that *Calvaria* evolved its unusually thick pit as an adaptation to resist destruction by crushing in a dodo's gizzard. But, in so doing, they became dependent upon dodos for their own reproduction. Tit for tat. A pit thick enough to survive in a dodo's gizzard is a pit too thick for an embryo to burst by its own resources. Thus, the gizzard that once threatened the seed had become its necessary accomplice. The thick pit must be abraded and scratched before it can germinate.

Several small animals eat the fruit of *Calvaria* today, but they merely nibble away the succulent middle and leave the internal pit untouched. The dodo was big enough to swallow the fruit whole. After consuming the middle, dodos would have abraded the pit in their gizzards before regurgitating it or passing it in their feces. Temple cites many analogous cases of greatly increased germination rates for seeds after passage through the digestive tracts of various animals.

Temple then tried to estimate the crushing force of a dodo's gizzard by making a plot of body weight versus force generated by the gizzard in several modern birds. Extrapolating the curve up to a dodo's size, he estimates that *Calvaria* pits were thick enough to resist crushing; in fact, the thickest pits could not be crushed until they had been reduced nearly 30 percent by abrasion. Dodos might well have regurgitated the pits or passed them along before subjecting them to such an extended treatment. Temple took turkeys—the closest modern analogue to dodos—and force-fed them *Calvaria* pits, one at a time. Seven of seventeen pits were crushed by the turkey's gizzard, but the other ten were regurgitated or passed in feces after considerable abrasion. Temple planted these seeds and three of them germinated. He writes: "These may well have been the first *Calvaria* seeds to germinate in more than 300 years." *Calvaria* can probably be saved from the brink of extinction by the propagation of artificially abraded seeds. For once, an astute observation, combined with imaginative thought and experiment, may lead to preservation rather than destruction.

I wrote this essay to begin the fifth year of my regular column in Natural History magazine. I said to myself at the beginning that I would depart from a long tradition of popular writing in natural history. I would not tell the fascinating tales of nature merely for their own sake. I would tie any particular story to a general principle of evolutionary theory: pandas and sea turtles to imperfection as the proof of evolution, magnetic bacteria to principles of scaling, mites that eat their mother from inside to Fisher's theory of sex ratio. But this column has no message beyond the evident homily that things are connected to other things in our complex world—and that local disruptions have wider consequences. I have only recounted these two, related stories because they touched me—one bitterly, the other with sweetness.



Coenobita diogenes in the shell of *Cittanum.* Drawn from life by A. Verrill in 1900.

Postscript

Some stories in natural history are too beautiful and complex to win general acceptance. Temple's report received immediate publicity in the popular press *(New York Times* and other major newspapers, followed two months later by my article). A year later (March 30, 1979), Dr. Owadally of the Mauritian Forestry Service raised some important doubts in a technical comment published in the professional journal *Science* (where Temple's original article had appeared). I reproduce below, verbatim, both Owadally's comment and Temple's response:

> I do not dispute that coevolution between plant and animal exists and that the germination of some seeds may be assisted by their passing through the gut of animals. However, that "mutualism" of the famous dodo and *Calvaria major* (tambalacoque) is an example *(1)* of coevolution is untenable for the following reasons.
>
> 1) *Calvaria major* grows in the upland rain forest of Mauritius with a rainfall of 2500 to 3800 mm per annum. The dodo according to Dutch sources roamed over the northern plains and the eastern hills in the Grand Port area—that is, in a drier forest—where the Dutch established their first settlement. Thus it is highly improbable that the dodo and the tambalacoque occurred in the same ecological niche. Indeed, extensive excavations in the uplands for reservoirs, drainage canals, and the like have failed to reveal any dodo remains.
>
> 2) Some writers have mentioned the small woody seeds found in Mare aux Songes and the possibility that their germination was assisted by the dodo or other birds. But we now know that these seeds are not tambalacoque but belong to another species of lowland tree recently identified as *Sideroxylon longifolium.*
>
> 3) The Forestry Service has for some years been studying and effecting the germination of tambalacoque seeds without avian intervention *(2).* The germination rate is low but not more so than that of many other indigenous species which have, of recent decades, showed a marked deterioration in reproduc-

tion. This deterioration is due to various factors too complex to be discussed in this comment. The main factors have been the depredations caused by monkeys and the invasion by exotic plants.

4) A survey of the climax rain forest of the uplands made in 1941 by Vaughan and Wiehe *(3)* showed that there was quite a significant population of young tambalacoque plants certainly less than 75 to 100 years old. The dodo became extinct around 1675!

5) The manner in which the tambalacoque seed germinates was described by Hill *(4),* who demonstrated how the embryo is able to emerge from the hard woody endocarp. This is effected by the swollen embryo breaking off the bottom half of the seed along a well-defined fracture zone.

It is necessary to dispel the tambalacoque-dodo "myth" and recognize the efforts of the Forestry Service of Mauritius to propagate this magnificent tree of the upland plateau.

A. W. OWADALLY

Forestry Service, Curepipe, Mauritius

References and Notes

1. S. Temple, *Science* 197, 885 (1977).
2. Young *Calvaria major* plants that are 9 months old or more can be seen at the Forest Nursery in Curepipe.
3. R. E. Vaughan and P. O. Wiehe, / *Ecol.* 19, 127 (1941).
4. A. W. Hill, *Ann. Bot.* **5,** 587 (1941).

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The plant-animal mutualism that may have existed between the dodo and *Calvaria major* became impossible to prove experimentally after the dodo's extinction. What I pointed out *(1)* was the possibility that such a relation may have occurred, thus providing an explanation for the extraordinarily poor germination rate in *Caharia.* I acknowledge the potential for error in historical reconstructions.

I disagree, however, with the conclusion of Owadally

(2) that the dodo and *Calvaria* were geographically separated. There have been virtually no bones of dodos or any other animals found in the uplands of Mauritius not because the animals were never there, but because the island's topography does not cause alluvial deposits there. Catchment basins in certain lowland areas accumulated many bones of animals that were washed into these areas from the surrounding uplands. Accounts of early explorers, summarized by Hachisuka *(3,* p. 85), definitely refer to dodos occurring in the uplands, and Hachisuka makes a point of clarifying the misconception that dodos were strictly coastal birds. Early forestry records from Mauritius (•/) indicate that *Calvaria* was found in the lowlands as well as on the upland plateau. Although native forests only occur in the uplands today, one of the surviving *Calvaria* trees is located at an elevation of only 150 m. Thus, the dodo and *Calvaria* may have been sympatric, making a mutualistic relation possible.

Taxonomic authorities on sapotaceous plants of the Indian Ocean region recognize seeds of *Calvaria major,* as well as the smaller seeds of *Sideroxylon longifolium,* from alluvial deposits of the Mare aux Songes marsh *(5),* but this has little relevance to the question of mutualism. Mutualistic species will not necessarily be fossilized together.

The Mauritius Forestry Service has only recently succeeded in propagating *Calvaria* seeds, and the unmentioned reason for their recent success strengthens the case for mutualism. Success was achieved when the seeds were mechanically abraded before planting *(6).* A dodo's digestive tract merely abraded the endocarp naturally the same way the staff of the Mauritius Forestry Service does artificially before the seeds are planted.

The reference Owadally cites *(7)* is equivocal about the age of the surviving *Calvaria* trees because there is no easy way to accurately date them. Coincidently, Wiehe, the coauthor of the paper Owadally cites, was also my source of the estimated age of over 300 years for the surviving trees. I agree that there were more trees surviving in the 1930's than today, which further suppports the notion that *Calvaria major* is a declining species and may have been so since 1681.

I erred in not citing Hill *(8).* However, Hill does not describe how and under what conditions he induced a seed to germinate. Without these details, his description is of little relevance to the question of mutualism.

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References and Notes

1. S.A. Temple, *Science* 197, 885 (1977).
2 A. W. Owadally, *ibid.* 203, 1363 (1979).
3. M. Hachisuka, *The Dodo and Kindred Birds* (Witherby, London, 1953).
4. N. R. Brouard, *A History of the Woods and Forests of Maimtius* (Government Printer, Mauritius, 1963).
5. F. Friedmann, personal communication.
6. A. M. Gardner, personal communication.
7. R. E. Vaughan and P. O. Wiehe,/ *Ecol.* 19, 127 (1941).
8. A. W. Hill, *Ann. Bot.* **5,** 587 (1941).

I think that Temple has responded adequately (even triumphantly) to Owadally's first three points. As a paleontologist, I can certainly affirm his arguments about the rarity of upland fossils. Our fossil record of upland faunas is exceedingly spotty; the specimens we do possess are generally found in lowland deposits, well worn and washed in from higher ground. Owadally was certainly remiss in not mentioning (point 3) that the Forestry Service abrades its *Calvaria* seeds before they germinate; for the necessity of abrasion lies at the heart of Temple's hypothesis. But Temple was equally remiss in not citing the local Mauritian efforts, which, apparently, predate his own discovery.

Owadally's fourth point, however, represents the potential disproof of Temple's claim. If "quite a significant population" of *Calvaria* trees were less than 100 years old in 1941, then dodos cannot have assisted their germination. Temple denies that so young an age has been demonstrated, and I certainly have no additional insight that can resolve this crucial question.

This exchange highlights a disturbing issue in the transmission of news about science to the public. Many sources cited Temple's original story. I did not find a single mention of the subsequent doubts. Most "good" stories turn out to be false, or at least overextended, but debunking doesn't match the fascination of a clever hypothesis. Most of the "classic" stories of natural history are wrong, but nothing is so resistant to expurgation as textbook dogma.

The debate between Owadally and Temple is too close to call at the moment. I'm rooting for Temple, but if Owadally's fourth point is correct, then the dodo hypothesis will become, in Thomas Henry Huxley's inimitable words, "a beautiful theory, killed by a nasty, ugly little fact."

Sticking Up for Marsupials

I AM ANNOYED that the rapacious ways of my own species have irrevocably prevented me from seeing the dodo in action, for a pigeon as large as a turkey must have been something else, and stuffed, moldy specimens just don't carry conviction. We who revel in nature's diversity and feel instructed by every animal tend to brand *Homo sapiens* as the greatest catastrophe since the Cretaceous extinction. Yet I would argue that the rise of the Isthmus of Panama a mere two to three million years ago must rank as the most devastating biological tragedy of recent times.

South America had been an island continent throughout the Tertiary period (for seventy million years before the onset of continental glaciation). Like Australia, it housed a unique suite of mammals. But Australia was a backwater compared with the range and variety of South American forms. Many survived the onslaught of North American species after the isthmus rose. Some spread and prospered: the opossum moved as far as Canada; the armadillo is still making its way north.

Despite the success of a few, extirpation of the most dramatically different South American forms must be ranked as the dominant effect of contact between mammals of the two continents. Two entire orders perished (we group all modern mammals into about twenty-five orders). Think how our zoos would have been enriched with a liberal sprinkling of notoungulates, a large and diverse group of plant-eating mammals, ranging from rhino-sized *Toxodon,* first exhumed by Charles Darwin on shore leave from the *Beagle,* to rabbit and rodent analogues among the typotheres and hegetotheres. Consider the litopterns with their two subgroups—the large, long-necked camel-like macrauchenids and the most remarkable group of all, the horse-like proterotheres. (Proterotheres even repeated some of the evolutionary trends followed by true horses: three-toed *Diadiaphorus* preceded *Thoatherium,* a single-toed species that outdid Man 'O War by reducing its vestigial side toes to a degree never matched by modern horses.) They are all gone forever, victims in large part of faunal disruptions set in motion by the rising isthmus. (Several notoungulates and litopterns survived well into the glacial epoch. They may even have received their *coup de grace* from early human hunters. Still, I do not doubt that many would still be with us if South America had remained an island.)

The native predators of these South American herbivores also disappeared completely. The modern carnivores of South America, the jaguars and their allies, are all North American interlopers. The indigenous carnivores, believe it or not, were all marsupials (although some flesh-eating niches were occupied by the phororhacids, a remarkable group of giant birds, now also extinct). The marsupial carnivores, although not as diverse as placental carnivores in northern continents, formed an impresive array, from fairly small animals to bear-sized species. One lineage evolved in uncanny parallel with the saber-toothed cats of North America. The marsupial *Thylacosmilus* developed long, stabbing upper canines and a protecting flange of bone on the lower jaw—just like *Smilodon* of the La Brea tar pits.

Although it is not commonly bruited about, marsupials are not doing badly in South America today. North America may only boast the so-called Virginia opossum (actually a South American migrant), but opossums in South America are a rich and varied group of some sixty-five species. In addition, the caenolestids, pouchless "opossum rats," form a separate group with no close affinity to true opossums.

But the third great group of South American marsupials, the carnivorous borhyaenids, were completely wiped out and replaced by northern cats.

The traditional view—though I dedicate this essay to opposing it—attributes the extirpation of carnivorous marsupials to the general inferiority of pouched versus placental mammals. (All living mammals except marsupials and the egg-laying platypus and echidna are placentals.) The argument seems hard to beat. Marsupials flourished only on the isolated island continents of Australia and South America where large placental carnivores never gained a foothold. The early Tertiary marsupials of North America soon disappeared as placentals diversified; South American marsupials took a beating when the Central American corridor opened for placental immigration.

These arguments of biogeography and geological history gain apparent support from the conventional idea that marsupials are anatomically and physiologically inferior to placentals. The very terms of our taxonomy reinforce this prejudice. All mammals are divided into three parts: the egg-laying monotremes are called Prototheria, or premammals; placentals win the prize as Eutheria, or true mammals; the poor marsupials lie in limbo as Metatheria, or middle mammals—not all quite there.

The argument for structural inferiority rests largely upon differing modes of reproduction in marsupials versus placentals, bolstered by the usual smug assumption that different from us is worse. Placentals, as we know and experience, develop as embryos in intimate connection with a mother's body and blood supply. With some exceptions, they are born as reasonably complete and capable creatures. Marsupial fetuses never developed the essential trick that permits extensive development within a mother's body. Our bodies have an uncanny ability to recognize and reject foreign tissues, an essential protection against disease, but a currently intractable barrier to medical procedures ranging from skin grafts to heart transplants. Despite all the homilies about mother love, and the presence of 50 percent maternal genes in offspring, an embryo is still foreign tissue. The maternal immune system must be masked to prevent rejection. Placental fetuses have "learned" to do this; marsupials have not.

Marsupial gestation is very short—twelve to thirteen days in the common oppossum, followed by sixty to seventy days of further development in the external pouch. Moreover, internal development does not proceed in intimate connection with the mother, but shielded from her. Two-thirds of gestation occurs within the "shell membrane," a maternal organ that prevents the incursion of lymphocytes, the "soldiers" of the immune system. A few days of placental contact follow, usually via the yolk sac. During this time, the mother mobilizes her immune system, and the embryo is born (or, more accurately, expelled) soon after.

The marsupial neonate is a tiny creature, equivalent in development to a rather early placental embryo. Its head and forelimbs are precociously developed, but the hind limbs are often little more than undifferentiated buds. It must then undertake a hazardous journey, slowly pulling itself along through the relatively great distance to mother's nipples and pouch (we can now understand the necessity of well-developed forelimbs). Our embryonic life within a placental womb sounds altogether easier and unconditionally better.

What challenge can then be offered to these biogeographical and structural accounts of marsupial inferiority? My colleague John A. W. Kirsch has recently marshaled the arguments. Citing work of P. Parker, Kirsch contends that marsupial reproduction follows a different adaptive mode, not an inferior path. True, marsupials never evolved a mechanism to turn off the maternal immune system and permit a completed development within the womb. But early birth may be an equally adaptive strategy. Maternal rejection need not represent a failure of design or lost evolutionary opportunity; it may reflect an ancient and perfectly adequate approach to the rigors of survival. Parker's argument goes right back to Darwin's central contention that individuals struggle to maximize their own reproductive success, that is, to increase the representation of their own genes in future generations. Several highly divergent, but equally successful, strategies can be followed in (unconscious) pursuit of this goal. Placentals invest a great deal of time and energy in offspring before their birth. This commitment does increase the chance of an offspring's success, but the placental mother also takes a risk: if she should lose her litter, she has irrevocably expended a large portion of her life's reproductive effort for no evolutionary gain. The marsupial mother pays a much higher toll in neonatal death, but her reproductive cost is small. Gestation has been very short and she may breed again in the same season. Moreover, the tiny neonate has not placed a great drain upon her energetic resources, and has subjected her to little danger in a quick and easy birth.

Turning to biogeography, Kirsch challenges the usual assumption that Australia and South America were refugia for inferior beasts that couldn't hang on in the placental world of the Northern Hemisphere. He views their southern diversity as a reflection of success in their ancestral homeland, not as a feeble effort in peripheral territory. His argument relies upon M. A. Archer's claim for close genealogical relationship between borhyaenids (South American marsupial carnivores) and thylacines (marsupial carnivores of the Australian region). Taxonomists have previously regarded these two groups as an example of evolutionary convergence—separate development of similar adaptations (as in the marsupial and placental saber-tooths, mentioned previously). In fact, taxonomists have viewed the Australian and South American radiation of marsupials as completely independent events, following the separate invasion of both continents by primitive marsupials pushed out from northern lands. But if borhyaenids and thylacines are closely related, then the southern continents must have exchanged some of their products, probably via Antarctica. (In our new geology of drifting continents, southern hemisphere lands were much closer together when mammals rose to prominence, following the dinosaurs' demise.) A more parsimonious view imagines an Australian center of origin for marsupials and a dispersal to South America following the evolution of thylacinids, rather than two separate marsupial invasions of South America—borhyaenid ancestors from Australia, and all the others from North America. Although the simplest explanations are not always true in our wondrously complex world, Kirsch's arguments do cast considerable doubt on the usual assumption that marsupial homelands are refugia, not centers of origin.

Yet I must confess that this structural and biogeographical defense of marsupials falters badly before one cardinal fact, prominently featured above: the Isthmus of Panama rose, placental carnivores invaded, marsupial carnivores quickly perished, and the placentals took over. Does this not speak for clear competitive superiority of North American placental carnivores? I could sneak around this unpleasant fact by ingenious conjecture, but I prefer to admit it. How then can I continue to defend marsupial equality?

Although the borhyaenids lost big, I find no scrap of evidence to attribute defeat to their status as marsupials. I prefer an ecological argument predicting hard times for any indigenous group of South American carnivores, marsupial or placental. The real victims happened to be marsupials, but this taxonomic fact may be incidental to a fate sealed for other reasons.

R. Bakker has been studying the history of mammalian carnivores throughout the Tertiary. Integrating some new ideas with conventional wisdom, he finds that the northern placental carnivores experienced two kinds of evolutionary "tests." Twice, they suffered short periods of mass extinction, and new groups, perhaps with greater adaptive flexibility, took over. During times of continuity, high diversity of both predators and prey engendered intense competition and strong evolutionary trends for improvement in feeding (quick ingestion and efficient slicing) and locomotion (high acceleration in ambush predators, endurance in long-distance hunters). South American and Australian carnivores were tested in neither way. They suffered no mass extinctions, and the original incumbents persisted. Diversity never approached northern levels, and competition remained less intense. Bakker reports that their levels of morphological specialization for running and feeding lie far below those of northern carnivores living at the same time.

H. J. Jerison's studies of brain size provide an impressive confirmation. On northern continents, placental predators and prey evolved successively larger brains throughout the Tertiary. In South America, both marsupial carnivores and their placental prey quickly plateaued at about 50 percent of brain weight for average modern mammals of the same body sizes. Anatomical status as marsupial or placental seems to make no difference; a relative history of evolutionary challenge may be crucial. If, by happenstance, northern carnivores had been marsupials and southern carnivores placentals, I suspect that the outcome of isthmian exchange would still have been a rout for South America. North American faunas were continually tested in the fiery furnaces of mass destruction and intense competition. The South American carnivores were never strongly challenged. When the Isthmus of Panama rose, they were weighed in the evolutionary balance for the first time. Like Daniel's king, they were found wanting.

Our Allotted Lifetimes

J. P. MORGAN, MEETING with Henry Ford in E. L. Doctorow's *Ragtime,* praises the assembly line as a faithful translation of nature's wisdom:

> Has it occurred to you that your assembly line is not merely a stroke of industrial genius but a projection of organic truth? After all, the interchangeability of parts is a rule of nature. . . . All mammals reproduce in the same way and share the same designs of self-nourishment, with digestive and circulatory systems that are recognizably the same, and they enjoy the same senses. .. . Shared design is what allows taxonomists to classify mammals as mammals.

An imperious tycoon should not be met with equivocation; nonetheless, I can only reply "yes, and no" to Morgan's pronouncement. Morgan was wrong if he thought that large mammals are geometric replicas of smaller relatives. Elephants have relatively smaller brains and thicker legs than mice, and these differences record a general rule of mammalian design, not the idiosyncracies of particular animals.

But Morgan was right in arguing that large animals are essentially similar to small members of their group. The similarity, however, does not reside in a constant shape. The basic laws of geometry dictate that animals must change their shape in order to work the same way at different sizes. Galileo himself established the classic example in 1638: the strength of an animal's leg is a function of its cross-sectional area (length **X** length); the weight that legs must support varies as the animal's volume (length **X** length **X** length). If mammals did not increase the relative thickness of their legs as they got larger, they would soon collapse (since body weight would increase so much faster than the supporting strength of limbs). To remain the same in function, animals must change their form.

The study of these changes in form is called "scaling theory." Scaling theory has uncovered a striking regularity of changing shape over the 25-millionfold range of mammalian weight from shrew to blue whale. If we plot brain weight versus body weight for all mammals on the so-called mouse-to-elephant (or shrew-to-whale) curve, very few species deviate far from a single line expressing the general rule: brain weight increases only two-thirds as fast as body weight as we move from small to large mammals. (We share with bottle-nosed dolphins the honor of greatest upward deviance from the curve.)

We can often predict these regularities from the basic physics of objects. The heart, for example, is a pump. Since all mammalian hearts work in essentially the same way, small hearts must pump considerably faster than large ones (imagine how much faster you could work a finger-sized, toy bellows than the giant model that fuels a blacksmith's forge or an old-fashioned organ). On the mouse-to-elephant curve for mammals, the length of a heartbeat increases between one-fourth and one-third as fast as body weight as we move from small to large mammals. The generality of this conclusion has recently been affirmed in an interesting study by J. E. Carrel and R. D. Heathcote on the scaling of heart rate in spiders. They used a cool laser beam to illuminate the hearts of resting spiders and drew a crab spider-to-tarantula curve for eighteen species spanning nearly a thousandfold range of body weight. Again, scaling is regular with heart rate increasing four-tenths as fast as body weight (.409 times as fast, to be exact).

We may extend this conclusion for hearts to a general statement about the pace of life in small versus large animals. Small animals tick through life far more rapidly than large animals—their hearts work more quickly, they breathe more frequently, their pulse beats much faster. Most importantly, metabolic rate, the so-called fire of life, increases only three-fourths as fast as body weight in mammals. To keep themselves going, large mammals do not need to generate as much heat per unit of body weight as small animals. Tiny shrews move frenetically, eating nearly all their waking lives to keep their metabolic fire burning at the maximal rate among mammals; blue whales glide majestically, their hearts beating the slowest rhythm among active, warm-blooded creatures.

The scaling of lifetime among mammals suggests an intriguing synthesis of these disparate data. We have all had enough experience with mammalian pets of various sizes to understand that small mammals tend to live for a shorter lime than large ones. In fact, mammalian lifetime scales at about the same rate as heartbeat and breath time—between one-fourth and one-third as fast as body weight as we move from small to large animals. *(Homo sapiens* emerges from this analysis as a very peculiar animal. We live far longer than a mammal of our body size should. In essay 9, I argue that humans evolved by an evolutionary process called "neoteny"—the preservation in adults of shapes and growth rates that characterize juvenile stages of ancestral primates. I also believe that neoteny is responsible for our elevated longevity. Compared with other mammals, all stages of human life arrive "too late." We are born as helpless embryos after a long gestation; we mature late after an extended childhood; we die, if fortune be kind, at ages otherwise reached by warmblooded animals only at the very largest sizes.)

Usually, we pity the pet mouse or gerbil that lived its full span of a year or two at most. How brief its life, while we endure for the better part of a century. As the main theme of this essay, I want to argue that such pity is misplaced (our personal grief, of course, is quite another matter; with this, science does not deal). Morgan was right in *Ragtime*—small and large mammals are essentially similar. Their lifetimes are scaled to their life's pace, and all endure for approximately the same amount of biological time. Small mammals tick fast, burn rapidly, and live for a short time; large mammals live long at a stately pace. Measured by their own internal clocks, mammals of different sizes tend to live for the same amount of time.

We are prevented from grasping this important and comforting concept by a deeply ingrained habit of Western thought. We are trained from earliest memory to regard absolute Newtonian time as the single valid measuring stick in a rational and objective world. We impose our kitchen clock, ticking equably, upon all things. We marvel at the quickness of a mouse, express boredom at the torpor of a hippopotamus. Yet each is living at the appropriate pace of its own biological clock.

I do not wish to deny the importance of absolute, astronomical time to organisms (see essay 31). Animals must measure it to lead successful lives. Deer must know when to regrow their antlers, birds when to migrate. Animals track the day-night cycle with their circadian rhythms; jet lag is the price we pay for moving much faster than nature intended.

But absolute time is not the appropriate measuring stick for all biological phenomena. Consider the magnificent song of the humpback whale. E. O. Wilson has described the awesome effect of these vocalizations: "The notes are eerie yet beautiful to the human ear. Deep basso groans and almost inaudibly high soprano squeaks alternate with repetitive squeals that suddenly rise or fall in pitch." We do not know the function of these songs. Perhaps they enable whales to find each other and to stay together during their annual transoceanic migrations. Perhaps they are the mating songs of courting males.

Each whale has its own characteristic song; the highly complex patterns are repeated over and over again with great faithfulness. No scientific fact that I have learned in the last decade struck me with more force than Roger S.

Payne's report that the length of some songs may extend for more than half an hour. I have never been able to memorize the five-minute first *Kyrie* of the B-minor Mass (and not for want of trying); how could a whale sing for thirty minutes and then repeat itself accurately? Of what possible use is a thirty-minute repeat cycle—far too long for a human to recognize; we would never grasp it as a single song (without Payne's recording machinery and much study after the fact). But then I remembered the whale's metabolic rate, the enormously slow pace of its life compared with ours. What do we know about a whale's perception of thirty minutes? A humpback may scale the world to its own metabolic rate; its half-hour song may be our minute waltz. From any point of view, the song is spectacular; it is the most elaborate single display so far discovered in any animal. I merely urge the whale's point of view as an appropriate perspective.

We can provide some numerical precision to support the claim that all mammals, on average, live for the same amount of biological time. In a method developed by W. R. Stahl, B. Giinther, and E. Guerra in the late 1950s and early 1960s, we search the mouse-to-elephant equations for biological properties that scale at the same rate against body weight. For example, Giinther and Guerra give the following equations for mammalian breath time and heartbeat time versus body weight.

$$\text{breath time} = .0000470\ \text{body}^{028}$$

$$\text{heartbeat time} = .0000119\ \text{body}^{0\text{-}28}$$

(Nonmathematical readers need not be overwhelmed by the formalism. The equations simply state that both breath time and heartbeat time increase about .28 times as fast as body weight as we move from small to large mammals.) If we divide the two equations, body weight cancels out because it is raised to the same power in both.

$$\frac{\text{breath time}}{\text{heartbeat time}} \qquad \frac{.0000470\ \text{JaedV\^{}**}}{.0000119\ \text{Jbedy*\^{}}} = 4.0$$

This states that the ratio of breath time to heartbeat time is 4.0 in mammals of any body size. In other words, all mammals, whatever their size, breathe once for each four heartbeats. Small mammals breathe and beat their hearts faster than large mammals, but both breath and heart slow up at the same relative rate as mammals get larger.

Lifetime also scales at the same rate as body weight (.28 times as fast as we move from small to large mammals). This means that the ratio of both breath time and heartbeat time to lifetime is also constant over the entire range of mammalian size. When we perform a calculation similar to the one above, we find that all mammals, regardless of their size, tend to breathe about 200 million times during their lives (their hearts, therefore, beat about 800 million times). Small mammals breathe fast, but live for a short time. Measured by the internal clocks of their own hearts or the rhythm of their own breathing, all mammals live the same time. (Astute readers, after counting their breaths or taking their pulses, may have calculated that they should have died long ago. But *Homo sapiens* is a markedly deviant mammal in more ways than braininess alone. We live about three times as long as mammals of our body size "should," but we breathe at the "right" rale and thus live to breathe about three times as often as an average mammal of our body size. I regard this excess of living as a happy consequence of neoteny.)

The mayfly lives but a day as an adult. It may, for all I know, experience that day as we live a lifetime. Yet all is not relative in our world, and such a short glimpse of it guarantees distortion in interpreting events ticking on longer scales. In a brilliant metaphor, the pre-Darwinian evolutionist Robert Chambers wrote in 1844 of a mayfly watching the metamorphosis of a tadpole into a frog:

> Suppose that an ephemeron [a mayfly], hovering over a pool for its one April day of life, were capable of observing the fry of the frog in the waters below. In its aged afternoon, having seen no change upon them for such a long time, it would be little qualified to conceive that the external branchiae [gills] of these creatures were to decay, and be replaced by internal lungs, that

feet were to be developed, the tail erased, and the animal then to become a denizen of the land.

Human consciousness arose but a minute before midnight on the geologic clock. Yet we mayflies try to bend an ancient world to our purposes, ignorant perhaps of the messages buried in its long history. Let us hope that we are still in the early morning of our April day.

Natural Attraction: Bacteria, the Birds and the Bees

THE FAMOUS WORDS "blessed art thou among women" were uttered by the angel Gabriel as he announced to Mary that she would conceive by the Holy Spirit. In medieval and Renaissance painting, Gabriel bears the wings of a bird, often elaborately spread and adorned. While visiting Florence last year, I became fascinated by the "comparative anatomy" of Gabriel's wings as depicted by the great painters of Italy. The faces of Mary and Gabriel are so beautiful, their gestures often so expressive. Yet the wings, as painted by Fra Angelico or by Martini, seem stiff and lifeless, despite the beauty of their intricate feathering.

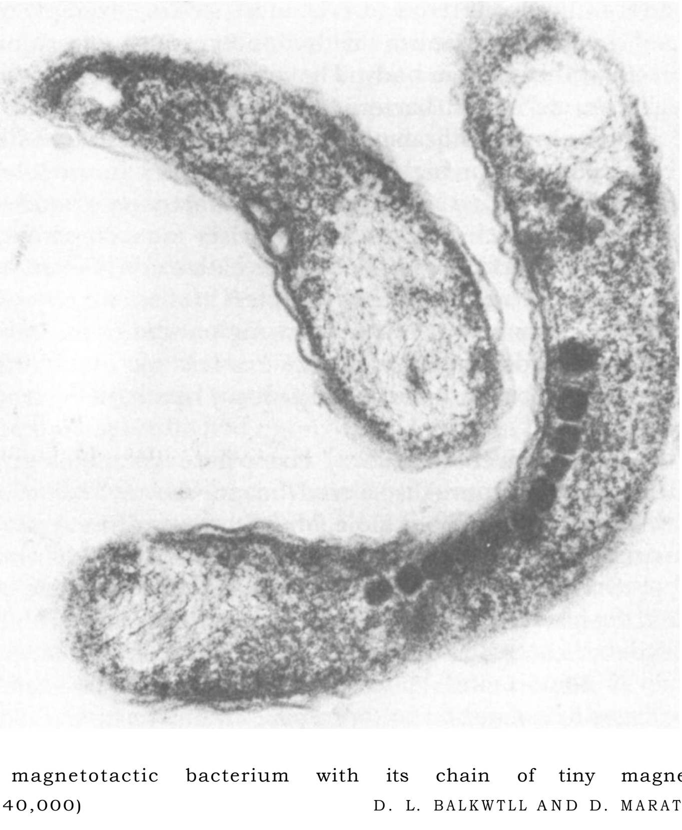
But then I saw Leonardo's version. Gabriel's wings are so supple and graceful that I scarcely cared to study his face or note the impact he had upon Mary. And then I recognized the source of the difference. Leonardo, who studied birds and understood the aerodynamics of wings, had painted a working machine on Gabriel's back. His wings are both beautiful and efficient. They have not only the right orientation and camber, but the correct arrangement of feathers as well. Had he been just a bit lighter, Gabriel might have flown without divine guidance. In contrast, the other Gabriels bear flimsy and awkward ornaments that could never work. I was reminded that aesthetic and functional beauty often go hand in hand (or rather arm in arm in this case).

In the standard examples of nature's beauty—the cheetah running, the gazelle escaping, the eagle soaring, the tuna coursing, and even the snake slithering or the inchworm inching—what we perceive as graceful form also represents an excellent solution to a problem in physics. When we wish to illustrate the concept of adaptation in evolutionary biology, we often try to show that organisms unconsciously "know" physics—that they have evolved remarkably efficient machines for eating and moving. When Mary asked Gabriel how she could possibly conceive, "seeing I know not a man," the angel replied: "For with God nothing shall be impossible." Many things are impossible for nature. But what nature can do, she often does surpassingly well. Good design is usually expressed by correspondence between an organism's form and an engineer's blueprint.

I recently encountered an even more striking example of good design: an organism that builds an exquisite machine directly within its own body. The machine is a magnet; the organism, a "lowly" bacterium. When Gabriel departed, Mary went to visit Elizabeth, who had also conceived with a bit of help from on high. Elizabeth's babe (the future John the Baptist) "leaped in her womb" and Mary pronounced the *Magnificat,* including the line (later set so incomparably by Bach) *et exaltavit humilu*—"and he hath exalted them of low degree." The tiny bacteria, simplest in structure among organisms, inhabitants of the first rung on traditional (and fallacious) ladders of life, illustrate in a few microns all the wonder and beauty that some organisms require meters to express.

In 1975, University of New Hampshire microbiologist Richard P. Blakemore discovered "magnetotactic" bacteria in sediments near Woods Hole, Massachusetts. (Just as geotactic organisms orient toward gravitational fields and phototactic creatures toward light, magnetotactic bacteria align themselves and swim in preferred directions within magnetic fields.) Blakemore then spent a year at the University of Illinois with microbiologist Ralph Wolfe and managed to isolate and culture a pure strain of magnetotactic bacteria. Blakemore and Wolfe then turned to an expert on the physics of magnetism, Richard B. Frankel of the National Magnet Laboratory at M.I.T. (I thank Dr. Frankel for his patient and lucid explanation of their work.)

Frankel and his colleagues found that each bacterium builds within its body a magnet made of twenty or so opaque, roughly cubic particles, measuring about 500 angstroms on a side (an angstrom is one ten-millionth of a millimeter). These particles are made primarily of the magnetic material Fe_3O_4, called magnetite, or lodestone. Frankel then calculated the total magnetic moment per bacterium and found that each contained enough magnetite to orient itself in the earth's magnetic field against the disturbing influence of Brownian motion. (Particles small enough to be unaffected by the gravitational fields that stabilize us



A magnetotactic bacterium with its chain of tiny magnets (X 40,000) D. L. BALKWTLL AND D. MARATEA or by the surface forces that affect objects of intermediate size are buffeted in a random manner by thermal energy of the medium in which they lie suspended. The "play" of dust particles in sunlight provides a standard illustration of Brownian motion.)

The magnetotactic bacteria have built a remarkable machine, using virtually the only configuration that could work as a compass within their tiny bodies. Frankel explains why the magnetite must be arranged as particles and why the particles must be about 500 angstroms on a side. To work as an efficient compass, magnetite must be present as so-called single domain particles, that is, as bits with a single magnetic moment, containing opposite north- and south-seeking ends. The bacteria contain a chain of such particles, oriented with their magnetic moments north pole to the next south pole along the row—"like the elephants head to tail in a circus finale," as Frankel states. In this way, the entire chain of particles operates as a single magnetic dipole with north- and south-seeking ends.

If the particles were a bit smaller (less than 400 angstroms on a side), they would be "superparamagnetic"—a big word indicating that thermal energy at room temperature would cause internal reorientation of the particle's magnetic moment. On the other hand, if particles were greater than 1,000 angstroms on a side, separate magnetic domains pointing in different directions would form *within* the particle. This "competition" would reduce or cancel the particle's overall magnetic moment. Thus, Frankel concludes, "the bacteria have solved an interesting problem in physics by producing particles of magnetite of just the right size for a compass, of dimension 500 angstroms."

But evolutionary biology is preeminently the science of "why," and we must ask what such a small creature could possibly do with a magnet. Since a bacterium's cruising range is probably a few inches for the few minutes of its existence, I find it hard to believe that oriented motion in a north or south direction can play any role in its repertoire of adaptive traits. But what preferred direction of motion might make a difference? Frankel suggests, quite plausibly in my view, that an ability to move *down* might be crucial for such a bacterium—for down is the direction of sediments in aquatic environments, and down might lead to a region of preferred oxygen pressure. In this instance, "them of low degree" might wish to debase themselves even further.

But how does a bacterium know which way is down? With the smug prejudices of our enormous selves, we might think the question inane for its obvious answer: all they have to do is stop whatever they are doing and fall. Not at all. We fall because gravity affects us. Gravity—the standard example of a "weak force" in physics—influences us only because we are large. We live in a world of competing forces, and the relative strength of these forces depends primarily upon the size of objects affected by them. For familiar creatures of macroscopic dimensions, the ratio of surface area to volume is crucial. This ratio decreases continually as an organism grows, since areas increase as length squared and volumes as length cubed. Small creatures, insects for example, live in a world dominated by forces acting on their surfaces. Some can walk on water or hang upside down from a ceiling because surface tension is so strong and the gravitational force that might pull them down so weak. Gravitation works on volumes (or, to be more precise, upon masses that are proportional to volumes in a constant gravitational field). Gravitation rules us with our low ratio of surface to volume. But it troubles an insect very little—and a bacterium not at all.

The world of a bacterium is so unlike our own that we must abandon all our certainties about the way things are and start from scratch. Next time you see *Fantastic Voyage* on the tube, take your eyes off Raquel Welch and the predaceous white blood corpuscle long enough to ponder how the miniaturized adventurers would really fare as microscopic objects within a human body (they behave just like regular folks in the film). They would, first of all, be subject to shocks of the Brownian motion, thus making the film something of a random blur. Also, as Isaac Asimov pointed out to me, their ship could not run on its propeller, since blood is too viscous at such a scale. It should have, he said, a flagellum—like a bacterium.

D'Arcy Thompson, premier student of scaling since Galileo, urged us to set aside our prejudices if we would understand the world of a bacterium. In his masterpiece, *Growth and Form* (published in 1942 but still in print), he ends his chapter "On Magnitude" in his incomparable prose:

> Life has a range of magnitude narrow indeed compared to that with which physical science deals; but it is wide enough to include three such discrepant conditions as those in which a man, an insect and a bacillus have their being and play their several roles. Man is ruled by gravitation, and rests on mother earth. A water-beetle finds the surface of a pool a matter of life and death, a perilous entanglement or an indispensable support. In a third world, where the bacillus lives, gravitation is forgotten, and the viscosity of the liquid, the resistance defined by Stokes's law, the molecular shocks of the Brownian movement, doubtless also the electric charges of the ionized medium, make up the physical environment and have their potent and immediate influence upon the organism. The predominant factors are no longer those of our scale; we have come to the edge of a world of which we have no experience, and where all our preconceptions must be recast.

So how does a bacterium know which way is down? We use magnets for horizontal orientation so exclusively that we often forget (in fact, I suspect many of us do not know) that the earth's magnetic field also has a vertical component, its strength depending upon latitude. (We damp out the vertical deflection in building compasses because it doesn't interest us. As large creatures ruled by gravitation, we know which way is down. Only at our scale could folly be personified as not knowing "which way is up.") A compass needle follows the earth's lines of force. At the equator, these lines are horizontal to the surface. Toward the poles, they dip more and more strongly *into* the earth. At the magnetic pole itself, the needle points straight down. At my latitude in Boston, the vertical component is actually stronger than the horizontal. A bacterium, swimming north as a free compass needle, also swims down at Woods Hole.

This putative function for a bacterial compass is pure speculation at the moment. But if these bacteria use their magnets primarily to swim down (rather than to find each other, or to do Lord knows what, if anything, in their unfamiliar world), then we can make some testable predictions. Members of the same species, living in natural populations adapted to life at the equator, will probably not make magnets, for here a compass needle has no vertical component. In the Southern Hemisphere, magnetotactic bacteria should display reversed polarity and swim in the direction of their south-seeking pole.

Magnetite has also been reported as a component of several larger organisms, all of which perform remarkable feats of horizontal orientation—the conventional use of a compass for familiar creatures of our scale. Chitons, eight-plated relatives of clams and snails, live primarily on rocks near sea level in tropical regions. They scrape food from the rocks with a long file called a radula—and the tips of the radular teeth are made of magnetite. Many chitons make substantial excursions from a living site, but "home" back to the precise spot thereafter. The idea that they might use their magnetite as an orienting compass suggests itself, but the evidence so far offers no support. It is not even clear that chitons have enough magnetite to perceive the earth's field, and Frankel tells me that their particles are mostly above the single domain limit.

Some bees have magnetite in their abdomens, and we know that they are affected by the earth's magnetic field (see article by J. L. Gould, no relation, J. L. Kirschvink, and K. S. Defeyes in bibliography). Bees do their famous dance on the vertical surface of their honeycomb by converting the orientation of their flight to food in relation to the sun into an angle danced with respect to gravity. If the comb is turned so that bees must dance on a horizontal surface, where they cannot express direction in gravitational terms, they become disoriented at first. Finally, after several weeks, they align their dances to the magnetic compass. Moreover, a swarm of bees, placed into an empty hive without cues for orientation, build their comb in the magnetic direction it occupied in their parental hive. Pigeons, certainly no duffers at homing, build a structure made of magnetite between their brain and skull. This magnetite exists as single domains and can therefore function as a magnet (see C. Walcott *el al.* in bibliography).

The world is full of signals that we don't perceive. Tiny creatures live in a different world of unfamiliar forces. Many animals of our scale greatly exceed our range of perception for sensations familiar to us. Bats avoid obstacles by bouncing sound off them at frequencies that I cannot hear, although some people can. Many insects see into the ultraviolet and follow the "invisible" nectar guides of flowers to sources of food for them and pollen that they will carry to the next flower for fertilization (plants build these orienting color streaks for their own advantages, not to convenience the insects).

What an imperceptive lot we are. Surrounded by so much, so fascinating and so real, that we do not see (hear, smell, touch, taste) in nature, yet so gullible and so seduced by claims for novel power that we mistake the tricks of mediocre magicians for glimpses of a psychic world beyond our ken. The paranormal may be a fantasy; it is certainly a haven for charlatans. But "parahuman" powers of perception lie all about us in birds, bees, and bacteria. And we can use the instruments of science to sense and understand what we cannot directly perceive.

Bully for Brontosaurus

QUESTION: What do Catherine the Great, Attila the Hun, and Bozo the Clown have in common? Answer: They all have the same middle name.

Question: What do San Marino, Tannu Tuva, and Monaco have in common? Answer: They all realized that they could print pretty pieces of perforated paper, call them stamps, and sell them at remarkable prices to philatelists throughout the world. (Did these items ever bear any relationship to postage or utility? Does anyone own a canceled stamp from Tannu Tuva?) Some differences, however, must be admitted. Although San Marino (a tiny principality within Italy) and Tannu Tuva (a former state adjacent to Mongolia but now annexed to the Soviet Union) may rely on stamps for a significant fraction of their GNP, Monaco, as we all know, has another considerable source of outside income—the casino of Monte Carlo (nurtured by all the hype and elegance of the Grimaldis—Prince Rainier, Grace Kelly, and all that).

So completely do we identify Monaco with Monte Carlo that we can scarcely imagine any other activity, particularly something productive, taking place in this little land of fantasy and fractured finances.

Nonetheless, people are born, work, and die in Monaco. And this tiny nation boasts, among other amenities, a fine station for oceanographic research. This combination of science and hosteln makes Monad) an excellent plate for large professional meetings. In 1913, Monaco hosted the International Zoological Congress, the largest of all meetings within my clan. This 1913 gathering adopted the important Article 79, or "plenary powers decision," stating that "when stability of nomenclature is threatened in an individual case, the strict application of the Code may under specified conditions be suspended by the International Commission on Zoological Nomenclature."

Now I will not blame any reader for puzzlement over the last paragraph. The topic—rules for giving scientific names to organisms—is easy enough to infer. But why should we be concerned with such legalistic arcana? Bear with me. We shall detour around the coils of *Boa constrictor,* meet the International Code of Zoological Nomenclature head-on, and finally arrive at a hot issue now generating much passion and acrimony at the heart of our greatest contemporary fad. You may deny all concern for rules of taxonomy, our last domain of active Latin (now that Catholicism has embraced the vernacular), but millions of Americans are now het up about the proper name of *Brontosaurus,* the canonical dinosaur. And you can't grasp the name of the beast without engaging the beastly rules of naming.

Nonprofessionals often bridle at the complex Latin titles used by naturalists as official designations for organisms. Latin is a historical legacy from the foundation of modern taxonomy in the mid-eighteenth century—a precomputer age when Romespeak was the only language shared by scientists throughout the world. The names may seem cumbersome, now that most of us pass our youthful years before a television set, rather than declaiming *hic-haec-hoc* and *amo-amas-amat.* But the principle remains sound. Effective communication demands that organisms have official names, uniformly recognized in all countries, while a world of changing concepts and increasing knowledge requires that rules of naming foster maximal stability and minimal disruption.

New species are discovered every day; old names must often change as we correct past errors and add new information. If every change of concept demanded a redesignalion of all names and a reordering of all categories, natural history would devolve into chaos. Our communications would fail as species, the basic units of all our discourse, would have no recognized labels. All past literature would be a tangle of changing designations, and we could not read without a concordance longer than the twenty volumes of the *Oxford English Dictionary.*

The rules for naming animals are codified in the *International Code of Zoological Nomenclature,* as adopted and continually revised by the International Union of Biological Sciences (plant people have a different code based on similar principles). The latest edition (1985), bound in bright red, runs to 338 pages. I will not attempt to summarize the contents, but only state the primary goal: to promote maximal stability as new knowledge demands revision.

Consider the most prevalent problem demanding a solution in the service of stability: When a single species has been given two or more names, how do we decide which to validate and which to reject? This common situation can arise for several reasons: Two scientists, each unaware of the other's work, may name the same animal; or a single scientist, mistaking a variable species for two or more separate entities, may give more than one name to members of the same species. A simple and commonsensical approach might attempt to resolve all such disputes with a principle of priority—let the oldest name prevail. In practice, such "obvious" solutions rarely work. The history of taxonomy since Linnaeus has featured three sequential approaches to this classic problem.

1. *Appropriateness.* Modern nomenclature dates from the publication, in 1758, of the tenth edition of Linnaeus's *Systema Naturae.* In principle, Linnaeus endorsed the rule of priority. In practice, he and most of his immediate successors commonly changed names for reasons, often idiosyncratic, of supposed "appropriateness." If the literal Latin of an original name ceased to be an accurate descriptor, new names were often devised. (For example, a species originally named *floridensis* to denote a restricted geographic domain might be renamed *americanus* if it later spread throughout the country.)

Some unscrupulous taxonomists used appropriateness as a thinly veiled tactic to place their own stamp upon species by raiding rather than by scientific effort. A profession supposedly dedicated to expanding knowledge about things began to founder into a quagmire of arguments about names. In the light of such human foibles, appropriateness could not work as a primary criterion for taxonomic names.

2. *Priority.* The near anarchy of appropriateness provoked a chorus of demands for reform and codification. The British Association for the Advancement of Science finally appointed a committee to formulate a set of official rules for nomenclature. The Strickland Committee, obedient to the age-old principle that

periods of permissiveness lead to stretches of law 'n' order (before the cycle swings round again), reported in 1842 with a "strict construction" that must have brought joy to all Robert Borks of the day. Priority in publication shall be absolutely and uncompromisingly enforced. No ifs, ands, buts, quibbles, or exceptions.

This decision may have ended the anarchy of capricious change, but it introduced another impediment, perhaps even worse, based on the exaltation of incompetence. When new species are introduced by respected scientists, in widely read publications with clear descriptions and good illustrations, people take notice and the names pass into general use. But when Ignatz Doofus publishes a new name with a crummy drawing and a few lines of telegraphic and muddled description in the *Proceedings of the Philomathematical Society of Pfennighalhpfennig* (circulation 533), it passes into well-deserved oblivion. Unfortunately, under the Strickland Code of strict priority, Herr Doofus's name, if published first, becomes the official moniker of the species—so long as Doofus didn't break any rule in writing his report. The competence and usefulness of his work have no bearing on the decision. The resulting situation is perversely curious. What other field defines its major activity by the work of the least skilled? As Charles Michener, our greatest taxonomist of bees, once wrote: "In other sciences the work of incompetents is merely ignored; in taxonomy, because of priority, it is preserved."

If the Sterling/Doofus ratio were high, priority might pose few problems in practice. Unfortunately, the domain of Doofuses forms a veritable army, issuing cannonade after cannonade of publications filled with new names destined for oblivion but technically constituted in correct form. Since every profession has its petty legalists, its boosters of tidiness and procedure over content, natural history sank into a mire of unproductive pedantry that, in Ernst Mayr's words, "deflected taxonomists from biological research into bibliographic archeology." Legions of technocrats delighted in searching obscure and forgotten publications for an earlier name that could displace some long-accepted and stable usage. Acrimonious arguments proliferated, for Doofus's inadequate descriptions rarely permitted an unambiguous identification of his earlier name with any well-defined species. Thus, a rule introduced to establish stability against capricious change for appropriateness sowed even greater disruption by forcing the abandonment of accepted names for forgotten predecessors.

3. *Plenary Powers.* The abuses of Herr Doofus and his ilk induced a virtual rebellion among natural historians. A poll of Scandinavian zoologists, taken in 1911, yielded 2 in favor and 120 opposed to strict priority. All intelligent administrators know that the key to a humane and successful bureaucracy lies in creative use of the word *ordinarily.* Strict rules of procedure are ordinarily inviolable—unless a damned good reason for disobedience arises, and then flexibility permits humane and rational exceptions. The Plenary Powers Rule, adopted in Monaco in 1913 to stem the revolt against strict priority, is a codification of the estimable principle of *ordinarily.* It provided, as quoted early in this essay, that the first designation shall prevail, unless a later name has been so widely accepted that its suppression in favor of a forgotten predecessor would sow confusion and instability.

Such exceptions to strict priority cannot be asserted by individuals but must be officially granted by the International Commission of Zoological Nomenclature, acting under its plenary powers. The procedure is somewhat cumbersome and demands a certain investment of time and paperwork, but the plenary powers rule has served us well and has finally achieved stability by locating the fulcrum between strict priority and proper exception. To suppress an earlier name under the plenary powers, a taxonomist must submit a formal application and justification to the International Commission (a body of some thirty professional zoologists). The commission then publishes the case, invites commentary from taxonomists throughout the world, considers the initial appeal with all elicited support and rebuttal, and makes a decision by majority vote.

The system has worked well, as two cases may illustrate. The protozoan species *Tetrahymena pyriforme* has long been a staple for biological research, particularly on the physiology of single-celled organisms. John Corliss counted more than 1,500 papers published over a 27-year span—all using this name. However, at least ten technically valid names, entirely forgotten and unused, predate the first publication of *Tetrahymena.* No purpose would be served by resurrecting any of these earlier designations and suppressing the universally accepted *Tetrahymena.* Corliss's petition to the commission was accepted without protest, and *Tetrahymena* has been officially accepted under the plenary powers.

One of my favorite names recently had a much closer brush with official extinction. The generic names of many animals are the same as their common designation: the gorilla is *Gorilla;* the rat, *Rattus.* But I know only one case of a vernacular name identical with both generic *and* specific parts of the technical Latin. The boa constrictor is (but almost wasn't) *Boa constrictor,* and it would be a damned shame if we lost this lovely consonance. Nevertheless, in 1976, *Boa constrictor* barely survived one of the closest contests ever brought before the commission, as thirteen members voted to suppress this grand name in favor of *Boa canina,* while fifteen noble nays stood firm and saved the day. The details are numerous and not relevant to this essay. Briefly, in the founding document of 1758, Linnaeus placed nine species in his genus *Boa,* including *canina* and *constrictor.* As later zoologists divided Linnaeus's overly broad concept *ol Boa* into several genera, a key question inevitably arose: Which of Linnaeus's original species should become the "type" (or name bearer) for the restricted version of *Boa,* and which should be assigned to other genera? Many professional herpetologists had accepted *canina* as the best name bearer (and assigned *constrictor* to another genus); but a world of both technical and common usage, from textbooks to zoo labels to horror films, recognized *Boa constrictor.* The commission narrowly opted, in a tight squeeze (sorry, I couldn't resist that one), for the name we all know and love. Ernst Mayr, in casting his decisive vote, cited the virtue of stability in validating common usage—the basis for the plenary powers decision in the first place:

> I think here is clearly a case where stability is best served by following usage in the general zoological literature. I have asked numerous zoologists "what species does the genus *Boa* call to your mind?" and they all said immediately *"constrictor.* "... Making *constrictor* the type of *Boa* will remove all ambiguity from the literature.

These debates often strike nonprofessionals as a bit ridiculous—a sign, perhaps, that taxonomy is more wordplay than science. After all, science studies the external world (through the dark glass of our prejudices and perceptions to be sure). Questions of first publication versus common usage raise no issues about the animals "out there," and only concern human conventions for naming. But this is the point, not the problem. These are debates about names, not things—and the arbitrary criteria of human decision-making, not boundaries imposed by the external world, apply to our resolutions. The aim of these debates (although not always, alas, the outcome) is to cut through the verbiage, reach a stable and practical decision, and move on to the world of things.

Which leads—did you think that I had forgotten my opening paragraph?—back to philately. The United States government, jumping on the greatest bandwagon since the hula hoop, recently issued four striking stamps bearing pictures of dinosaurs—and labeled *Tyrannosaurus, Stegosaurus, Pteranodon,* and *Brontosaurus.*

Thrusting itself, with all the zeal of a convert, into the heart of commercial hype, the U.S. Post Office seems committed to shedding its image for stodginess in one fell, crass swoop. Its small brochure, announcing October as "national stamp collecting month," manages to sponsor a contest, establish a tie-in both with T-shirts and a videocassette for *The Land Before Time,* and offer a dinosaur "discovery kit" (a $9.95 value for just $3.95; "Valid while supplies last. Better hurry!"). You will, in this context, probably not be surprised to learn that the stamps were officially launched on October 1, 1989, in Orlando, Florida, at Disney World.

Amidst this maelstrom of marketing, the Post Office also engendered quite a brouhaha about the supposed subject of one stamp—a debate given such prominence in the press that much of the public (at least judging from my voluminous mail) now thinks that an issue of great scientific importance has been raised to the detriment and shame of an institution otherwise making a worthy step to modernity. (We must leave this question for another time, but I confess great uneasiness about such approbation. I appreciate the argument that T-shirts and videos heighten awareness and expose aspects of science to millions of kids otherwise unreached. I understand why many will accept the forceful spigot of hype, accompanied by the watering-down of content—all in the interest of extending contact. But the argument works only if, having made contact, we can then woo these kids to a deeper intellectual interest and commitment. Unfortunately, we are often all too ready to compromise. We hear the blandishments: Dumb it down; hype it up. But go too far and you cannot turn back; you lose your own soul by dripping degrees. The space for wooing disappears down the maw of commercialism. Too many wise people, from Shakespeare to my grandmother, have said that dignity is the only bit of our being that cannot be put up for sale.)

This growing controversy even reached the august editorial pages of the *New York Times* (October 11, 1989), and their description serves as a fine epitome of the supposed mess:

> The Postal Service has taken heavy flak for mislabeling its new 25-cent dinosaur stamp, a drawing of a pair of dinosaurs captioned *"Brontosaurus."* Furious purists point out that the "brontosaurus" is now properly called "apatosaurus." They accuse the stamp's authors of fostering scientific illiteracy, and want the stamps recalled.

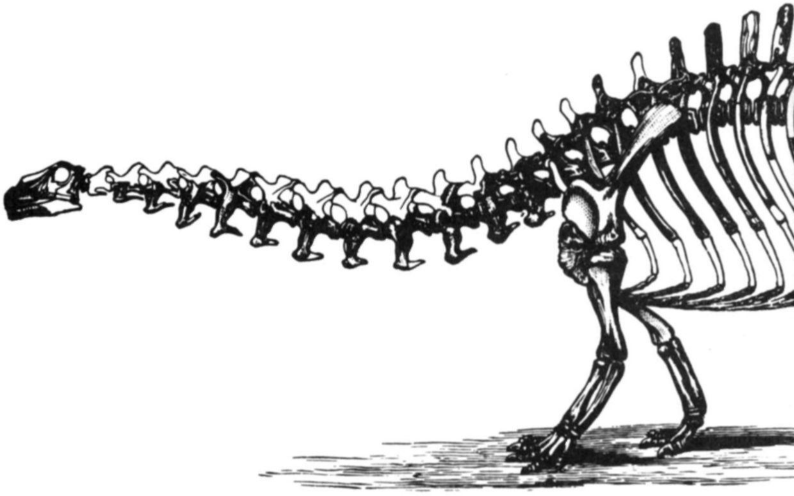
Brontosaurus versus *Apatosaurus.* Which is right? How important is this issue? How does it rank amidst a host of other controversies surrounding this and other dinosaurs: What head belongs on this dinosaur (whether it be called *Brontosaurus* or *Apatosaurus);* were these large dinosaurs warm-blooded; why did they become extinct? The press often does a good job of reporting basic facts of a dispute, but fails miserably in supplying the context that would allow a judgment about importance. I have tried, in the first part of this essay, to supply the necessary context for grasping *Brontosaurus* versus *Apatosaurus.* I regret to report, and shall now document, that the issue could hardly be more trivial—for the dispute is only about names, not about things. The empirical question was settled to everyone's satisfaction in 1903. To understand the argument about names, we must know the rules of taxonomy and something about the history of debate on the principle of priority. But the exposure of context for *Brontosaurus* versus *Apatosaurus* does provide an interesting story in itself and does raise important issues about the public presentation of science—and thus do I hope to snatch victory (or at least interest) from the jaws of defeat (or triviality).

Brontosaurus versus *Apatosaurus* is a direct legacy of the most celebrated feud in the history of vertebrate paleontology—Cope versus Marsh. As E. D. Cope and O. C. Marsh vied for the glory of finding spectacular dinosaurs and mammals in the American West, they fell into a pattern of rush and superficiality born of their intense competition and mutual dislike. Both wanted to bag as many names as possible, so they published too quickly, often with inadequate descriptions, careless study, and poor illustrations. In this unseemly rush, they frequently gave names to fragmentary material that could not be well characterized and sometimes described the same creature twice by failing to make proper distinctions among the fragments. (For a good history of this issue, see D. S. Berman and J. S. Mcintosh, 1978. These authors point out that both Cope and Marsh often described and officially named a species when only a few bones had been excavated and most of the skeleton remained in the ground.)

In 1877, in a typically rushed note, O. C. Marsh named and described *Apatosaurus ajax* in two paragraphs without illustrations ("Notice of New Dinosaurian Reptiles from the Jurassic Formation," *American Journal of Science,* 1877). Although he noted that this "gigantic dinosaur ... is represented in the Yale Museum by a nearly complete skeleton in excellent preservation," Marsh described only the vertebral column. In 1879, he published another page of information and presented the first sketchy illustrations—of pelvis, shoulder blade, and a few vertebrae ("Principal Characters of American Jurassic Dinosaurs, Part II," *American Journal of Science,* 1879). He also took this opportunity to pour some vitriol upon Mr. Cope, claiming that Cope had misnamed and misdescribed several forms in his haste. "Conclusions based on such work," Marsh asserts, "will naturally be received with distrust by anatomists."

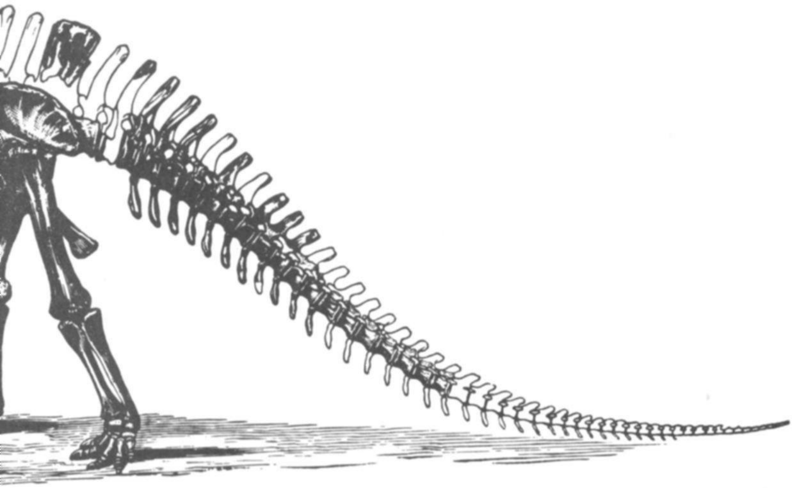
In another 1879 -article, Marsh introduced the genus *Brontosaurus,* with two paragraphs (even shorter than those initially devoted to *Apatosaurus),* no illustrations, andjust a few comments on the pelvis and vertebrae. He did estimate the length of his new beast at seventy to eighty feet, in comparison with some fifty feet Cor *Apatosaurus* ("Notice of New Jurassic Reptiles," *American Journal of Science,* 1879).

Marsh considered *Apatosaurus* and *Brontosaurus* as distinct but



Marsh's famous illustration of the complete skeleton of *Brontosaurus.* FROM THE SIXTEENTH ANNUAL REPORT OF THE U.S. GEOLOGICAL SURVEY, 1895. NEC. NO. 328654. COURTESY DEPARTMENT OF LIBRARY SERVICES, AMERICAN MUSEUM OF NATURAL HISTORY.

closely related genera within the larger family of sauropod dinosaurs. *Brontosaurus* soon became everyone's typical sauropod—indeed *the* canonical herbivorous dinosaur of popular consciousness, from the Sinclair logo to Walt Disney's *Fantasia*— for a simple and obvious reason. Marsh's *Brontosaurus* skeleton, from the most famous of all dinosaur localities at Como Bluff Quarry 10, Wyoming, remains to this day "one of the most complete sauropod skeletons ever found" (quoted from Berman and Mcintosh, cited previously). Marsh mounted the skeleton at Yale and often published his spectacular reconstruction of the entire animal. *(Apatosaurus,* meanwhile, remained a pelvis and some vertebrae.) In his great summary work, *The Dinosaurs of North America,* Marsh wrote (1896): "The best-known genus of the Atlantosauridae is *Brontosaurus,* described by the writer in 1879, the type specimen being a nearly entire skeleton, by far the most complete of any of the Sauropoda yet discovered." *Brontosaurus* also became the source of the old stereotype, now so strongly challenged, of slow, stupid, lumbering dinosaurs. Marsh wrote in



1883, when presenting his full reconstruction of *Brontosaurus* for the first time:

> A careful estimate of the size of *Brontosaurus,* as here restored, shows that when living the animal must have weighed more than twenty tons. The very small head and brain, and slender neural cord, indicate a stupid, slow-moving reptile. The beast was wholly without offensive or defensive weapons, or dermal armature. In habits, *Brontosaurus* was more or less amphibious, and its food was probably aquatic plants or other succulent vegetation.

In 1903, Flmer Riggs of the Field Museum in Chicago restudied Marsh's sauropods. Paleontologists had realized by then that Marsh had been overgenerous in his designation of species (a "splitter" in our jargon), and that many of his names would have to be consolidated. When Riggs restudied *Apatosaurus* and *Brontosaurus,* he recognized them as two versions of the same creature, with *Apatosaurus* as a more juvenile specimen. No big deal; it happens all-the time. Riggs rolled the two genera into one in a single paragraph:

> The genus *Brontosaurus* was based chiefly upon the structure of the scapula and the presence of five vertebrae in the sacrum. After examining the type specimens of these genera, and making a careful study of the unusually well-preserved specimen described in this paper, the writer is convinced that the Apatosaur specimen is merely a young animal of the form represented in the adult by the Brontosaur specimen. . . . In view of these facts the two genera may be regarded as synonymous. As the term *"Apatosaurus"* has priority, *"Brontosaurus"* will be regarded as a synonym.

In 1903, ten years before the plenary powers decision, strict priority ruled in zoological nomenclature. Thus, Riggs had no choice but to sink the later name, *Brontosaurus,* once he had decided that Marsh's earlier name, *Apatosaurus,* represented the same animal. But then I rather doubt that Riggs would have gone to bat for *Brontosaurus* even if he could have submitted a case on its behalf. After all, *Brontosaurus* was not yet an icon of pop culture in 1903—no Sinclair logo, no Alley-Oop, no *Fantasia,* no *Land Before Time.* Neither name had captured public or scientific fancy, and Riggs probably didn't lament the demise of *Brontosaurus.*

No one has ever seriously challenged Riggs's conclusion, and professionals have always accepted his synonymy. But Publication 82 of the "Geological Series of the Field Columbian Museum" for 1903—the reference for Riggs's article—never gained much popular currency. The name *Brontosaurus,* still affixed to skeletons in museums thoughout the world, still perpetuated in countless popular and semi-technical books about nature, never lost its luster, despite its technical limbo. Anyone could have applied to the commission for suppression of *Apatosaurus* under the plenary powers in recognition of the widespread popularity and stability of *Brontosaurus.* I suspect that such an application would have succeeded. But no one bothered, and a good name remains in limbo. (I also wish that someone had fought for suppression of the unattractive and inappropriate name *Hyracotherium* in favor of the lovely but later *Eohippus,* also coined by Marsh. But again, no one did.)

I'm afraid there's not much more to this story—not nearly the issue hyped by your newspapers as the Great Stamp Flap. No argument of fact arises at all, just a question of names, settled in

1903, but never transferred to a general culture that continues to learn and favor the technically invalid name *Brontosaurus.* But the story does illustrate something troubling about the presentation of science in popular media. The world of *USA Today* is a realm of instant fact and no analysis. Hundreds of bits come at us in pieces never lasting more than a few seconds—for the dumb-downers tell us that average Americans can't assimilate anything more complex or pay attention to anything longer.

This oddly "democratic" procedure makes all bits equal—the cat who fell off a roof in Topeka (and lived) gets the same space as the Soviet withdrawal from Afghanistan. Equality is a magnificent system for human rights and morality in general, but not for the evaluation of information. We are bombarded with too much in our inordinately complex world; if we cannot sort the trivial from the profound, we are lost in terminal overload. The criteria for sorting must involve context and theory—the larger perspective that a good education provides.

In the current dinosaur craze without context, all bits are mined for their superficial news value as items in themselves—a lamentable tendency abetted by the "trivial pursuit" one-upmanship that confers status on people who know (and flaunt) the most bits. (If you play this dangerous game in real life, remember that ignorance of context is the surest mark of a phony. If you approach me in wild lament, claiming that our postal service has mocked the deepest truth of paleontology, I will know that you have only skimmed the surface of my field.)

Consider the four items mentioned earlier in this essay. They are often presented in *USA Today* style as equal factoids. But with a context to sort the trivial from the profound, we may recognize some as statements about words, others as entries to the most general questions we can ask about the history of life. *Apatosaurus* versus *Brontosaurus* is a legalistic quibble about words and rules of naming. Leave the Post Office alone. They take enough flak (much justified of course) as it is. The proper head for *Apatosaurus* is an interesting empirical issue, but of little moment beyond the sauropods. Marsh found no skull associated with either his *Apatosaurus* or his *Brontosaurus* skeleton. He guessed wrong and mounted the head of another sauropod genus called *Camarosaurus. Apatosaurus* actually bore a head much more like that of the different genus *Diplodocus.* The head issue *(Camarosaurus-**like*** versus *Diplodorus-**Vike)*** and the name issue *(Apatosaurus* versus *Brontosaurus)* are entirely separate questions, although the press has confused and conflated them.

The question of warm-bloodedness (quite unresolved at the moment) is more general still, as it affects our basic concepts of dinosaur physiology and efficiency. The issue of extinction is the broadest of all—for basic patterns of life's history are set by differential survival of groups through episodes of mass dying. We are here today, arguing about empty issues like *Apatosaurus* versus *Brontosaurus,* because mammals got through the great Cretaceous extinction, while dinosaurs did not.

I hate to be a shill for the Post Office, but I think that they made the right decision this time. Responding to the great *Apatosaurus* flap, Postal Bulletin Number 21744 proclaimed: "Although now recognized by the scientific community as *Apatosaurus,* the name *Brontosaurus* was used for the stamp because it is more familiar to the general population. Similarly, the term "dinosaur" has been used generically to describe all the animals, even though the *Pteranodon* was a flying reptile." Touche and right on; no one bitched about *Pteranodon,* and that's a real error.

The Post Office has been more right than the complainers, for Uncle Sam has worked in the spirit of the plenary powers rule. Names fixed in popular usage may be validated even if older designations have technical priority. But now . . . Oh Lord, why didn't I see it before! Now I suddenly grasp the secret thread behind this overt debate! It's a plot, a dastardly plot sponsored by the apatophiles—that covert society long dedicated to gaining support for Marsh's original name against a potential appeal to the plenary powers. They never had a prayer before. Whatever noise they made, whatever assassinations they attempted, they could never get anyone to pay attention, never disturb the tranquillity and general acceptance of *Brontosaurus.* But now that the Post Office has officially adopted *Brontosaurus,* they have found their opening. Now enough people know about *Apatosaurus* for the first time. Now an appeal to the plenary powers would not lead to the validation of *Brontosaurus,* for *Apatosaurus* has gained precious currency. They have won; we brontophiles have been defeated.

Apatosaurus means "deceptive lizard"; *Brontosaurus* means "thunder lizard"—a far, far better name (but appropriateness, alas, as we have seen, counts for nothing). They have deceived us; we brontophiles have been outmaneuvered. Oh well, graciousness in defeat before all (every bit as important as dignity, if not an aspect thereof). I retreat, not with a bang of thunder, but with a whimper of hope that rectification may someday arise from the ashes of my stamp album.

Of Kiwi Eggs and the Liberty Bell

LIKE OZYMANDIAS, once king of kings but now two legs of a broken statue in Percy Shelley's desert, the great facade of Union Station in Washington, D.C., stands forlorn (but ready to front for a bevy of yuppie emporia now under construction), while Amtrak now operates from a dingy outpost at the side.* Six statues, portraying the greatest of human arts and inventions, grace its parapet. Electricity holds a bar of lightning; his inscription proclaims: "Carrier of light and power. Devourer of time and space. . . . Greatest servant of man. . . . Thou hast put all things under his feet."

Yet I will cast my vote for the Polynesian double canoe, constructed entirely with stone adzes, as the greatest invention for devouring time and space in all human history. These vessels provided sufficient stability for long sea voyages. The Polynesian people, without compass or sextant, but with unparalleled understanding of stars, waves, and currents, navigated these canoes to colonize the greatest emptiness of our earth, the "Polynesian triangle," stretching from New Zealand to Hawaii to Easter Island at its vertices. Polynesians sailed forth into the open Pacific more than a thousand years before Western navigators dared to leave

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*Il is so good and pleasant, in our world of woe and destruction, to report some good news for a change. Union Station has since reopened with a triumphant and vibrant remodeling that fully respects the spirit and architecture of the original. Trains now depart from the heart of this great station, and a renaissance of rational public transportation, with elements of grand style at the termini, may not be a pipe dream.

the coastline of Africa and make a beeline across open water from the Guinea coast to the Cape of Good Hope.

New Zealand, southwestern outpost of Polynesian migrations, is so isolated that not a single mammal (other than bats and seals with their obvious means of transport) managed to intrude. New Zealand was a world of birds, dominated by several species (thirteen to twenty-two by various taxonomic reckonings) of large, flightless moas. Only *Aepyornis,* the extinct elephant bird of Madagascar, ever surpassed the largest moa, *Dinomis maximus,* in weight. Ornithologist Dean Amadon estimated the average weight of/), *maximus* at 520 pounds (although some recent revisions nearly double this bulk), compared with about 220 pounds for ostriches, the largest living birds.

We must cast aside the myths of noble non-Westerners living in ecological harmony with their potential quarries. The ancestors of New Zealand's Maori people based a culture on hunting moas, but soon made short work of them, both by direct removal and by burning of habitat to clear areas for agriculture. Who could resist a 500-pound chicken?

Only one species of New Zealand ratite has survived. (Ratites are a closely related group of flightless ground birds, including moas, African ostriches, South American rheas, and Australian-New Guinean emus and cassowaries. Flying birds have a keeled breastbone, providing sufficient area for attachment of massive flight muscles. The breastbones of ratites lack a keel, and their name honors that most venerable of unkeeled vessels, the raft, or *ratis* in Latin.) We know this curious creature more as an icon on tins of shoe polish or as the moniker for New Zealand's human inhabitants—the kiwi, only hen-sized, but related most closely to moas among birds.

Three species of kiwis inhabit New Zealand today, all members of the genus *Apteryx* (literally, wingless). Kiwis lack an external tail, and their vestigial wings are entirely hidden beneath a curious plumage—shaggy, more like fur than feathers, and similar in structure to the juvenile down of most other birds. (Maori artisans used kiwi feathers to make the beautiful cloaks once worn by chiefs; but the small, secretive, and widely ranging nocturnal kiwis managed to escape the fate of their larger moa relatives.)

The furry bodies, with even contours unbroken by tail or wings, are mounted on stout legs—giving the impression of a double blob (small head and larger body) on sticks. Kiwis eat seeds, berries, and other parts of plants, but they favor earthworms. Their long, thin bills probe the soil continually, suggesting the oddly reversed perspective of a stick leading a blind man. This stick, however, is richly endowed as a sensory device, particularly as an organ of smell. The bill, uniquely among birds, bears long external nostrils, while the olfactory bulb of kiwi brains is second largest among birds relative to size of the forebrain. A peculiar creature indeed.

But the greatest of kiwi oddities centers upon reproduction. Females are larger than males. They lay one to three eggs and may incubate them for a while, but they leave the nest soon thereafter, relegating to males the primary task of incubation, a long seventy to eighty-four days. Males sit athwart the egg, body at a slight angle and bill stretched out along the ground. Females may return occasionally with food, but males must usually fend for

An amazing and famous photo of a female kiwi one day before laying its enormous egg. COURTESY OF THE OTOROHANCA ZOOLOGICAL SOCIETY, NEW ZEALAND.

themselves, covering both eggs and nest entrance with debris and going forth to forage once or twice on most nights.

The kiwi egg is a wonder to behold, and the subject of this essay. It is, by far, the largest of all bird eggs relative to body size. The three species of kiwis just about span the range of domestic poultry: the largest about the size of Rhode Island Reds; the smallest similar to bantams—say five pounds as a rough average (pretty meaningless, given the diversity of species, but setting the general domain). The eggs range to 25 percent of the female's body weight—quite a feat when you consider that she often lays two, and sometimes three, in a clutch, spacing them about thirty-three days apart. A famous X-ray photo of kiwi and egg taken at the kiwi sanctuary of Otorohanga, New Zealand, tells the tale more dramatically than any words I could produce. The egg is so large that females must waddle, legs spread far apart, for several days before laying, as the egg passes down the oviduct toward the cloaca. The incubation patch of male kiwis extends from the top of the chest all the way down to the cloaca—in other words, they need almost all their body to cover the egg.

A study of the general relationship between egg size and body size among birds shows that average birds of kiwi dimensions lay eggs weighing from 55 to 100 grams (as do domestic hens). Eggs of the brown kiwi weigh between 400 and 435 grams (about a pound). Put another way, an egg of this size would be expected from a twenty-eight-pound bird, but brown kiwis are about six times as small.

The obvious question, of course, is why? Evolutionary biologists have a traditional approach to riddles of this sort. They seek some benefit for the feature in question, then argue that natural selection has worked to build these advantages into the animal's way of life. The greatest triumphs of this method center upon odd structures that seem to make no sense or (like the kiwi egg) appear, prima facie, to be out of proportion and probably harmful. After all, anyone can see that a bird's wing (although not a kiwi's) is well designed for flight, so reference to natural selection teaches you little about adaptation that you didn't already know. Thus, the test cases of textbooks are apparently harmful structures that, on closer examination, confer crucial benefits upon organisms in their Darwinian struggle for reproductive success.

This general strategy of research suggests that if you can find out what a structure is good for, you will possess the major ingredient for understanding why it is so big, so colorful, so peculiarly shaped. Kiwi eggs should illustrate this basic method. They seem to be too big, but if we can discover how their large size benefits kiwis, we shall understand why natural selection favored large eggs. Readers who have followed my essays for some time will realize that I wouldn't be writing about this subject if I didn't think that this style of Darwinian reasoning embodied a crucial flaw.

The flaw lies not with the claim of utility. I regard it as proved that kiwis benefit from the unusually large size of their eggs—and for the most obvious reason. Large eggs yield large and well-developed chicks that can fend for themselves with a minimum of parental care after hatching. Kiwi eggs are not only large; they are also the most nutritious of all bird eggs for a reason beyond their maximal bulk: they contain a higher percentage of yolk than any other egg. Brian Reid and G. R. Williams report that kiwi eggs may contain 61 percent yolk and 39 percent albumin (or white). By comparison, eggs of other so-called precocial species (with downy young hatching in an active, advanced, and open-eyed state) contain 35 to 45 percent yolk, while eggs of altricial species (with helpless, blind, and naked hatchlings) carry only 13 to 28 percent yolk.

The lifestyle of kiwi hatchlings demonstrates the benefits of their large, yolky eggs. Kiwis are born fully feathered and usually receive no food from their parents. Before hatching, they consume the unused portion of their massive yolk reserve and do not feed (but live off these egg-based supplies) for their first seventy-two to eighty-four hours alfresco. Newly hatched brown kiwi chicks are often unable to stand because their abdomens are so distended with this reserve of yolk. They rest on the ground, legs splayed out to the side, and only take a first few clumsy steps when they are some sixty hours old. A chick does not leave its burrow until the fifth to ninth day when, accompanied by father, it sallies forth to feed sparingly.

Kiwis thus spend their first two weeks largely living off the yolk supply that their immense egg has provided. After ten to fourteen days, the kiwi chick may weigh one-third less than at hatching—a fasting marked by absorption of ingested yolk from the egg. Brian Reid studied a thick that died a few hours after hatching. Almost half its weight consisted of food reserves—112 grams of yolk and 43 grams of body fat in a 319-gram hatchling. Another chick, killed outside its burrow five to six days after hatching, weighed 281 grams and still held almost 54 grams of enclosed yolk.

I am satisfied that kiwis do very well by and with their large eggs. But can we conclude that the outsized egg was built by natural selection in the light of these benefits? This assumption—the easy slide from current function to reason for origin—is, to my mind, the most serious and widespread fallacy of my profession, for this false inference supports hundreds of conventional tales about pathways of evolution. I like to identify this error of reasoning with a phrase that ought to become a motto: *Current utility may not be equated with historical origin,* or, when you demonstrate that something works well, you have not solved the problem of how, when, or why it arose.

I propose a simple reason for labeling an automatic inference from current utility to historical origin as fallacious: Good function has an alternative interpretation. A structure now useful may have been built by natural selection for its current purpose (I do not deny that the inference often holds), but the structure may also have developed for another reason (or for no particular functional reason at all) and then been co-opted for its present use. The giraffe's neck either got long in order to feed on succulent leaves atop acacia trees or it elongated for a different reason (perhaps unrelated to any adaptation of feeding), and giraffes then discovered that, by virtue of their new height, they could reach some delicious morsels. The simple good fit of form to function—long neck to top leaves—permits, in itself, no conclusion about why giraffes developed long necks. Since Voltaire understood the foibles of human reason so well, he allowed the venerable Dr. Pangloss to illustrate this fallacy in a solemn pronouncement:

> Things cannot be other than they are. . . . Everything is made for the best purpose. Our noses were made to carry spectacles, so we have spectacles. Legs were clearly intended for breeches, and we wear them.

This error of sliding loo easily between current use and historical origin is by no means a problem for Darwinian biologists alone, although our faults have been most prominent and unexamined. This procedure of false inference pervades all fields that try to infer history from our present world. My favorite current example is a particularly ludicrous interpretation of the so-called anthropic principle in cosmology. Many physicists have pointed out—and I fully accept their analysis—that life on earth fits intricately with physical laws regulating the universe, in the sense that were various laws even slightly different, molecules of the proper composition and planets with the right properties could never have arisen—and we would not be here. From this analysis, a few thinkers have drawn the wildly invalid inference that human evolution is therefore prefigured in the ancient design of the cosmos—that the universe, in Freeman Dyson's words, must have known we were coming. But the current fit of human life to physical laws permits no conclusion about the reasons and mechanisms of our origin. Since we are here, we have to fit; we wouldn't be here if we didn't—though something else would, probably proclaiming, with all the hubris that a diproton might muster, that the cosmos must have been created with its later appearance in mind. (Diprotons are a prominent candidate for the highest bit of chemistry in another conceivable universe.)

But back to kiwi eggs. Most literature has fallen into the fallacy of equating current use with historical origin, and has defined the problem as explaining why the kiwi's egg should have been actively enlarged from an ancestor with an egg more suited to the expectations of its body size. Yet University of Arizona biologist William A. Calder III, author of several excellent studies on kiwi energetics (see 1978, 1979, and 1984 in the bibliography), has proposed an opposite interpretation that strikes me as much more likely (though I think he has missed two or three good arguments for its support, and I shall try to supply them here).

The alternative interpretation holds that kiwis are phyletic dwarfs, evolved from a lineage of much larger birds. Since these large ancestors laid big eggs appropriate to their body size, kiwis just never (or only slightly) reduced the size of their eggs as their bodies decreased greatly in bulk. In other words, kiwi eggs never became unusually large; kiwi bodies got small—and these state-merits are not equivalent, just as we know that an obese man is not short for his weight, despite the old jest.

(Such a hypothesis is not anti-adaptationist in the sense that maintenance of a large egg as size decreases—and in the face of energetic and biochemical costs imposed by such a whopping contribution to the next generation—may well require a direct boost from natural selection to prevent an otherwise advantageous decrease more in keeping with life at Colonel Sanders's favorite size. Still, there is a world of difference between retaining something you already have, and first developed for other reasons [in this case simple appropriateness for large body size], and actively evolving such a unique and cumbersome structure for some special benefit.)

Calder's interpretation might seem forced or farfetched but for the outstanding fact of taxonomy and biogeography cited as the introduction to this essay. Moas are the closest cousins of kiwis, and most moas were very large birds. "Is the kiwi perhaps a shrunken moa?" Calder asks. Unfortunately, all moa fossils lie in rocks of a geological yesterday, and kiwi fossils are entirely unknown—so we have no direct evidence about the size of ancestral kiwis. Still, I believe that all the inferential data support Calder's alternative hypothesis for the great size of kiwi eggs—a "structural" or "historical" explanation if you will, not a conventional account based on natural selection for immediate advantages.

Although the best argument for viewing kiwis as much smaller than their ancestors must be the large size of their closest moa cousins, Calder has also developed a quirky and intriguing speculation to support the dwarfed status of kiwis. (I hasten to point out that neither of these arguments amounts to more than a reasonable conjecture. All evidence can be interpreted in other ways. Both moas and kiwis, for example, might have evolved from a kiwi-sized common ancestor, with moas enlarging later. Still, since the kiwi is the smallest of all ratites—a runt among ostriches, rheas, emus, and cassowaries—its decrease seems more probable than moa increase. But we will not know until we have direct evidence of fossil ancestry.)

Calder notes that in many respects, some rather curious, kiwis have adopted forms and lifestyles generally associated with mammals, not birds. Kiwis, for example, are unique among birds in retaining ovaries on both sides (the right ovary degenerates in all other birds)—and eggs alternate between sides, as in mammals. The seventy- to eighty-four-day incubation period matches the eighty-day pregnancy expected for a mammal of kiwi body size, not the forty-four days predicted for birds of this weight. Calder continues: "When one adds to this list, the kiwi's burrow habit, its furlike body feathers, and its nocturnal foraging highly dependent on its sense of smell, the evidence for convergence seems overpowering." Of course, this conjunction of traits could be fortuitous and each might mean something quite unmammalian to a kiwi, but the argument does gain strength when we remember that no terrestrial mammals reached New Zealand, and that the success of many introduced species indicates a hospitable environment for any creature that could exploit a mammalian way of life.

You will be wondering what these similarities with mammals could possibly mean for my key claim that kiwis are probably descendants of much larger birds. After all, mammals are superior, noble, and large. But they aren't. The original and quintessential mammalian way of life (still exploited by a majority of species) is secretive, furtive, nocturnal, smell-oriented in a nonvisual world—and, above all, small. Remember that for two-thirds of their geological history, all mammals were little creatures living in the interstices of a world ruled by dinosaurs. If a large bird converged upon a basically mammalian lifestyle in the absence of "proper" inhabitants as a result of geographic isolation, *decrease* in size would probably be a first and best step.

Perhaps I have convinced you that kiwis probably decreased in size during their evolution. But why should this dwarfing help to explain their large eggs? Why didn't egg size just keep pace with body size as kiwis scaled down? We now come to the strong evidence of the case.

The study of changes in form and proportion as organisms increase or decrease in size is called allometry. It has been a popular and fruitful subject in evolutionary research since Julian Huxley's pioneering work of the 1920s. One of Huxley's own classic studies *(Journal of the Linnaean Society of London,* 1927) bore the title: "On the Relation between Egg-weight and Body-weight in Birds." Huxley found that if you plot one point for each species on the hummingbird-to-moa curve for egg weight versus body weight, relative egg size decreases in an even and predictable way. The eggs of large birds, he found, are absolutely larger, but relatively smaller in proportion to body weight, than those of small birds.

Huxley's work has since been extended several times with more voluminous and consistent data. In the two best studies that I know, Samuel Brody (in his masterful compendium, *Bioenergetics and Growth,* 1945) calculated a slope of 0.73, while H. Rahn, C. V. Paganelli, and A. Ar (1975), with even more data from some 800 species, derived a similar value of 0.67. This means that as birds increase in body weight, egg weight enlarges only about two-thirds as fast. Conversely, as birds decrease in size, egg weight diminishes more slowly—so little birds have relatively heavy eggs.

This promising datum will not, however, explain the kiwi's outsized egg, for the two-thirds slope represents the general standard for all birds. Kiwi eggs are huge compared with the *expected* egg weight for a bird of kiwi body weight along this standard curve.

But the literature of allomelry has also yielded a generality that will, I think, explain the kiwi's massive egg. The two-thirds slope of the egg weight/body weight curve represents a type of allometry technically called interspecific scaling—that is, you plot one point for each species in a related group of organisms and attempt to establish the characteristic change of proportion along a gradient of increasing size. (These curves are popularly called mouse-to-elephant for relationships among mammals—hence my designation hummingbird-to-moa for birds.) Allometricians have established hundreds of interspecific curves for birds and mammals.

Another kind of allometry is called intraspecific scaling. Here you plot one point for each individual among adults of varying body weights within a single species—the Tom Thumb-to-Manute Bol curve for human males, if you will. Since the similarity of these technical terms—interspecific and intraspecific—is so confusing, I shall call them, instead, among-species (for mouse-to-elephant) and within-species (for Thumb-to-Bol).

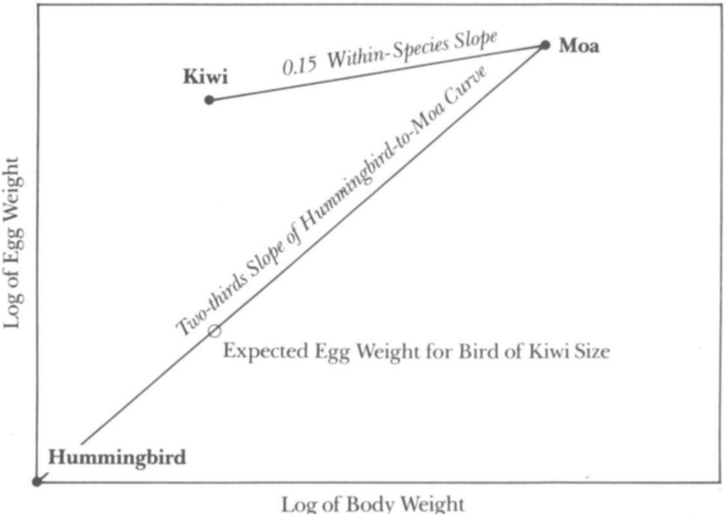
As an important generality in allometric studies, within-species curves usually have a substantially lower slope than among-species curves for the same property. For example (and in our best-studied case), the mouse-to-elephant curve for brain weight versus body weight in mammals has a slope of about two-thirds (as does the egg weight/body weight curve for birds). But the within-species curve from small to large adults of a single species, while varying from one group to another, almost always has a much lower slope in the range of 0.2 to 0.4. In other words, while brains increase about two-thirds as fast as bodies among species (implying that large mammals have relatively small brains), brains only increase about one-fifth to two-fifths as fast as bodies when we move from small to large adults within a single mammalian species.

Such a regularity, if it applied to egg weight as well, could resolve the kiwi paradox—if kiwis evolved from larger ancestors. Suppose that kiwi forebears start at moa size. By the hummingbird-to-moa among-species standard, egg size should decrease along the two-thirds slope. But suppose that natural selection is operating to favor small adults within a population. If the within-species curve for egg weight had a slope much lower than two-thirds, then size decrease by continued selection of small adults might produce a new species with outsized eggs well above the two-thirds slope, and therefore well above the expected weight for a bird of this reduced size. (Quantitative arguments like this are always easier to grasp by picture than by words—and a glance at the accompanying graph should resolve any confusion.)

But what is the expected within-species relationship for egg weight? Is the shape of the curve low, as for brain weight, thus affirming my conjecture? I reached for my well-worn copy of Brody's unparalleled compendium and found that for adults of domestic fowl, egg weight increases not two-thirds as fast, but only 15 percent as fast as body weight! (Brody uses this fact to argue that small hens are usually better than large, so long as egg production remains the same—for egg size diminishes very little with a large decrease in body mass, and the small loss in egg volume is more than compensated by large decreases in feeding costs.)

The same argument might apply to kiwis. As a poultryman might choose small hens for minimal decrease in egg size with maximal decline in body weight, natural selection for smaller adults might markedly decrease the average body weight within a species with very little accompanying reduction in egg weight.

I believe that this general argument, applied to kiwis, may be



Proposed allometric explanation for the large egg of the kiwi. The kiwi probably evolved from a much larger bird by backing down the very shallow within-species slope (upper line). Most birds arrange themselves on the standard hummingbird-to-moa curve with its steeper slope (lower line). Therefore, a kiwi has a much heavier egg than predicted for a bird of its body size, BEN GAMIT. ADAPTED FROM JOE LEMONNIER. COURTESY OF *NATURAL HISTORY.*

defended on three strong grounds. First, as stated above, a general finding in allometric studies teaches us that within-species slopes for adults of one species are usually much lower than among-species slopes along mouse-to-elephant curves. Thus, any evolution of decreasing size along the within-species curve should produce a dwarfed descendant with more of the particular item being measured than an average nondwarfed species at the same body weight. Second, we have actual data, for domestic poultry at least, indicating that the within-species curve does have a substantially lower slope than the hummingbird-to-moa curve for our crucial measure of egg weight.

Third, I have studied many cases of dwarfism, and I believe we can state as a general phenomenon—rooted in the first point above—that decline in body size often far outstrips decrease in many particular features. Dwarfs, in several respects, always seem to have much more of certain body parts than related non-dwarfed species of the same body size. For example, I once studied tooth size in three species of dwarfed hippos (two fossil and the modern Liberian pygmy)—and found their molar teeth substantially larger, for each of three separate evolutionary events, than expected values for related hoofed mammals at their body size *(American Zoologist,* 1975).

In another example, the talapoin, a dwarfed relative of the rhesus monkey, has the largest relative brain weight among monkeys. Since within-species brain curves have substantially lower slopes than the two-thirds value for the marmoset-to-baboon curve, evolution to smaller size by backing down the within-species curve would yield a dwarf with a far larger brain than an ordinary monkey at the same body size.

Put all this together and a resolution fairly jumps at you for kiwis. Their enormous eggs require no special explanation if kiwis have evolved by marked decrease in size. Kiwi eggs exhibit the weight expected for backing down the within-species curve if natural selection operates only to decrease body size and no other factor intervenes to favor an active reduction in egg size—as we might anticipate in New Zealand, this easy land of no natural predators, where a female might waddle without fear as an enormous egg distends her abdomen during passage down the oviduct.

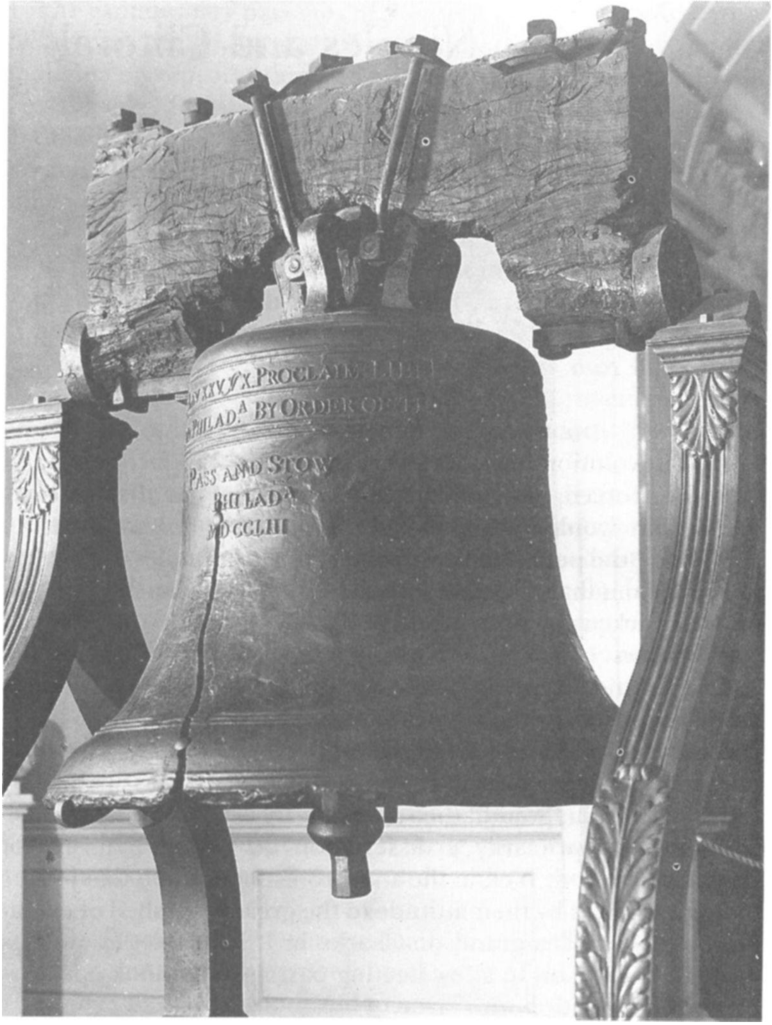
In this interpretation, if you ask me why kiwi eggs are so large, I reply, "Because kiwis are dwarfed descendants of larger birds, and just followed ordinary principles of scaling in their evolution." This answer differs sharply from the conventional form of evolutionary explanation: "Because these big eggs are good for something now, and natural selection favored them."

My answer will also strike many people as deeply unsatisfactory. It provides a reason rooted in history, pure and simple (with a bit of scaling theory thrown in)—kiwis are as they are because their ancestors were as they were. Don't we want answers that invoke general laws of nature rather than particular contingencies of history?

I would reply that my resolution is quite satisfactory, that evolutionary arguments are often properly resolved by such historical statements, and that we would do well to understand this important and neglected principle of reasoning—for we might save ourselves many a stumble in trying to apply preferred, but inappropriate, styles of explanation to situations encountered again and again in our daily lives.

To cite just one example where I learned, to my deep chagrin, that a peculiarity of history, rather than a harmonious generality, resolved an old personal puzzle: I had been troubled for a long time by something I didn't understand in the inscription on the Liberty Bell—not losing any sleep to be sure, but troubled nonetheless, for little things count. This national symbol bears, like most bells, an appropriate quotation: "Proclaim liberty throughout all the land unto all the inhabitants thereof" (Lev. 25:10). But the bell also says, "Pass and Stow." I assumed that this line must also be a quotation, fit to the purpose of the bell (as selection fits the features of organisms to their needs)—part of the general harmony and chosen plan. I pondered these cryptic words quite a bit because I didn't recognize the source. I consulted Bartlett's and found nothing. I constructed various possibilities: This too will pass, as we stow courage for the coming conflict; oh ye who pass by, remember, they prosper that stow and do not waste; pass the grass and stow the dough. Finally I asked the attendant on duty in Philadelphia. Of course, I should have figured it out, but I was too busy trying to make intrinsic sense of the inscription. The bell was cast by Messrs. John Pass and John Stow. Pass and Stow is a statement about the particular history of the bell; nothing more.

My odd juxtapositions sometimes cause consternation; some readers might view this particular comparison as outright sacrilege. Some may claim that the only conceivable similarity between kiwi eggs and the Liberty Bell is that both are cracked, but I reply that they stand united in owing their peculiarity and meaning to pathways of history.



The Liberty Bell on display in Philadelphia, advertising its makers, Mr. Pass and Mr. Slow, THE BEITMANN ARCHIVE.

Male Nipples and Clitoral Ripples*

THE MARQUIS DE CONDORCET, enthusiast of the French Revolution but not radical enough for the Jacobins—and therefore forced into hiding from a government that had decreed, and would eventually precipitate, his death—wrote in 1793 that "the perfectibility of man is really boundless. . . . It has no other limit than the duration of the globe where nature has set us " As Dickens so aptly remarked, "It was the best of times, it was the worst of times."

The very next year, as Condorcet lay dying in prison, a famous voice from across the channel published another paean to progress in a world that many judged on the brink of ruin. This treatise, called *Zoonomia, or the Laws of Organic Life,* was written by Erasmus Darwin, grandfather of Charles.

Zoonomia is primarily a dissertation on the mechanisms of human physiology. Yet, in the anachronistic tradition that judges biological works by their attitude to the great watershed of evolution, established by grandson Charles in 1859, *Zoonomia* owes its modern reputation to a few fleeting passages that look upon organic transmutation with favor.

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*The proper and most accurate title of this piece should be "Tits and Oils"—but such a label would be misread as sexist because people would not recognize the reference point as *male* tils. My wife, a master at titles, suggested this alternative. (During the short heyday of that most unnecessary of all commercially touted products—vaginal deodorants—she wanted to market a male counterpart to be known as "cocksure.") *Natural History* magazine, published by a group of line but slightly overcautious folks, first brought out this essay under their imposed title: "Freudian Slip." Not terrible; but not really descriptive either.

The evolutionary passages of *Zoonomia* occur in Item 8, Part 4, of Section 39, entitled, "Of Generation," Erasmus Darwin's thoughts on reproduction and embryology. He viewed embryology as a tale of continuous progress to greater size and complexity. Since his evolutionary speculations are strictly analogous to his concept of embryology, organic transformation also follows a single pathway to more and better:

> Would it be too bold to imagine that in the great length of time, since the earth began to exist . . . all warm-blooded animals have arisen from one living filament . . . possessing the faculty of continuing to improve by its own inherent activity, and of delivering down those improvements by generation to its posterity, world without end?

As the last sentence states, Erasmus Darwin's proposed mechanism of evolution lay in the inheritance of *useful* characters acquired by organisms during their lifetimes. This false theory of heredity has passed through later history under the label of Lamarckism, but the citation by Erasmus (a contemporary of Lamarck) illustrates the extent of this misnomer. Inheritance of acquired characters was the standard folk wisdom of the time, used by Lamarck to be sure, but by no means original or distinctive with him. For Erasmus, this mechanism of evolution required a concept of pervasive utility. New structures arose only when needed and by direct organic striving for an evident purpose. Erasmus discusses adaptations in three great categories: reproduction, protection and defense, and food. Of the last, he writes:

> All . . . seem to have been gradually produced during many generations by the perpetual endeavor of the creatures to supply the want of food, and to have been delivered to their posterity with constant improvement of them for the purposes required.

In this long section, Erasmus considers only one potential exception to the principle of pervasive utility: "the breasts and teats of all male quadrupeds, to which no use can be now assigned." He also suggests two exits from this potential dilemma: first, that male nipples are vestiges of a previous utility if, as Plato had suggested, "mankind with all other animals were originally hermaphrodites during the infancy of the world, and were in process of time separated into male and female"; and second, that some males may lactate and therefore help to feed their babies (in the absence of any direct evidence, Erasmus cites the milky-colored feeding fluids, produced in the crops of both male and female pigeons, as a possible analogue).

The tenacity of anomalies through centuries of changing beliefs can be truly astounding. As a consequence of writing these essays for so many years, I receive hundreds of letters from readers puzzled about one or another apparent oddity of nature. With so large a sample, I have obtained a pretty good feel for the issues and particulars of evolution that pose conundrums for well-informed nonscientific readers. I have been fascinated (and, I confess, surprised) over the years to discover that no single item has evoked more puzzlement than the very issue that Erasmus Darwin chose as a primary challenge to his concept of pervasive utility—male nipples. I have received more than a dozen requests to explain how evolution could possibly produce such a useless structure.

Consider my latest example from a troubled librarian. "I have a question that no one can answer for me, and I don't know where or how to look up the answer. Why do men have nipples? ... This question nags at me whenever I see a man's bare chest!"

I was fascinated to note that her two suggestions paralleled exactly the explanations floated by Erasmus Darwin. First, she reports, she asked a doctor. "He told me that men in primitive societies used to nurse babies." Finding this incredible, she tried Darwin's first proposal for nipples as a vestige of previous utility: "Can you tell me—was there once only one sex?"

If you are committed—as Erasmus was, and as a distressingly common version of "pop," or "cardboard," Darwinism still is—to a principle of pervasive utility for all parts of all creatures, then male nipples do raise an insoluble dilemma, hence (I assume) my voluminous correspondence. But as with so many persistent puzzles, the resolution does not lie in more research within an established framework but rather in identifying the framework itself as a flawed view of life.

Suppose we begin from a different point of view, focusing on rules of growth and development. The external differences between male and female develop gradually from an early embryo so generalized that its sex cannot be easily determined. The clitoris and penis are one and the same organ, identical in early form, but later enlarged in male fetuses through the action of testosterone. Similarly, the labia majora of women and the scrotal sacs of men are the same structure, indistinguishable in young embryos, but later enlarged, folded over, and fused along the midline in male fetuses.

I do not doubt that the large size and sensitivity of the female breast should count as an adaptation in mammals, but the smaller male version needs no adaptive explanation at all. Males and females are not separate entities, shaped independently by natural selection. Both sexes are variants upon a single ground plan, elaborated in later embryology. Male mammals have nipples because females need them—and the embryonic pathway to their development builds precursors in all mammalian fetuses, enlarging the breasts later in females but leaving them small (and without evident function) in males.

In a similar case that illuminates the general principle, the panda develops a highly functional false "thumb" from the radial sesamoid bone of its wrist. Interestingly, the corresponding bone of the foot, the tibial sesamoid, is also enlarged in the same manner (but not nearly so much), although increase of the tibial sesamoid has no apparent function.

As D. Dwight Davis argued in his great monograph on the giant panda (1964), evolution works on growth fields. Radial and tibial sesamoids are homologous structures, probably affected in concert by the same genetic factors. If natural selection operates for an enlarged radial sesamoid, a bigger tibial sesamoid will probably "come along for the ride." Davis drew a profound message from this case: Organisms are integral and constrained structures, "pushing back" against the force of selection to channel changes along permitted paths; complex animals are not a dissociable collection of independent, optimal parts. Davis wrote that "the effect seen in the sympathetic enlargement of the tibial sesamoid . . . strongly suggests that a very simple mechanism, perhaps involving a single factor, lies behind the hypertrophy of the radial sesamoid."

In my view of life, akin to Davis's concept of constraint and integration, male nipples are an expectation based on pathways of sexual differentiation in mammalian embryology.

At this point, readers might demur with the most crushing of all rejoinders: "Who cares?" Why worry about little items that ride piggyback on primary adaptations? Let's concentrate on the important thing—the adaptive value of the female breast—and leave aside the insignificant male ornament that arises as its consequence. Adaptations are preeminent; their side effects are nooks and crannies of organic design, meaningless bits and pieces. This argument is, I think, the standard position of strict Darwinian adaptationists.

I could defend the importance of structural nonadaptation with a long and abstruse general argument (I have done so in several technical papers). Let me proceed instead by the most compelling route I know by presenting a second example based on human sexuality, a case entirely comparable in concept with the origin of male nipples but differing in importance for human culture—a case, moreover, where the bias of utility has brought needless pain and anxiety into the lives of millions (where, indeed, one might argue that Freudian traditions have provided a manifestly false but potent weapon, however unintentional, for the subjugation of women). Consider the anatomical site of orgasm in human females.

As women have known since the dawn of our time, the primary site for stimulation to orgasm centers upon the clitoris. The revolution unleashed by the Kinsey report of 1953 has, by now, made this information available to men who, for whatever reason, had not figured it out for themselves by the more obvious routes of experience and sensitivity.

The data are unambiguous. Consider only the three most widely read of extensive surveys—the Kinsey report of 1953, Masters and Johnson's book of 1966, and *The I file Report* of 1976. In his study of genital anatomy, Kinsey reports that the female clitoris is as richly supplied with sensory nerves as the male penis—and therefore as capable of excitation. The walls of the vagina, on the other hand, "are devoid of end organs of touch and are quite insensitive when they are gently stroked or lightly pressed. For most individuals the insensitivity extends to every part of the vagina."

The data on masturbation are particularly convincing. Kinsey reports from his sample of 8,000 women that 84 percent of individuals who have ever masturbated depend "primarily on labial and/or clitoral techniques." *The Hite Report* on 3,000 individuals found that 79 percent of women who masturbate do so by directly stimulating the clitoris and surrounding vulva, while only 1.5 percent use vaginal entry.

The data on intercourse affirm this pattern. Shere Hite reports a frequency of orgasm with intercourse at 30 percent and often attained only with simultaneous stimulation of the clitoris by hand. She concludes: "*not* to have orgasm from intercourse is the experience of the majority of women." Masters and Johnson only included women who experienced orgasm with intercourse in their study. But they concluded that all orgasms are identical in physiology and clitoral in origin. These findings led Hite to comment that human copulation "sounds more like a Rube Goldberg scheme than a reliable way to orgasm. . . . Intercourse was never meant to stimulate women to orgasm." As Kinsey had said earlier with his characteristic economy and candor: "The techniques of masturbation and of petting are more specifically calculated to effect orgasm than the techniques of coitus itself."

This conclusion should be utterly unsurprising—once we grasp the proper role and limitation of adaptationist argument in evolutionary biology. I don't believe in the mystery style of writing essays: build up suspense but save the resolution until the end—for then readers miss the significance of details along the way for want of proper context. The reason for a clitoral site of orgasm is simple—and exactly comparable with the nonpuzzle of male nipples. The clitoris is the homologue of the penis—it is the same organ, endowed with the same anatomical organization and capacity of response.

Anatomy, physiology, and observed responses all agree. Why then do we identify an issue at all? Why, in particular, does the existence of clitoral orgasm seem so problematic? Why, for example, did Freud label clitoral orgasm as infantile and define feminine maturity as the shifting to an unattainable vaginal site?

Part of the reason, of course, must reside in simple male vanity. We (and I mean those of my sex, not the vague editorial pronoun) simply cannot abide the idea—though it flows from obvious biology—that a woman's sexual pleasure might not arise most reliably as a direct result of our own coital efforts. But the issue extends further. Clitoral orgasm is a paradox not only for the traditions of Darwinian biology but also for the bias of utility that underlies all functionally based theories of evolution (including Lamarck's and Darwin's) and, in addition, the much older tradition of natural theology that saw God's handiwork in the exquisite fit of organic form to function.

Consider the paradox of clitoral orgasm in any world of strict functionalism (I present a Darwinian version, but parallel arguments can be made for the entire range of functionalist thinking, from Paley's natural theology to Cuvier's creationism): Evolution arises from a struggle among organisms for differential reproductive success. Sexual pleasure, in short, must evolve as a stimulus for reproduction.

This formulation works for men since the peak of sexual excitement occurs during ejaculation—a primary and direct adjunct of intercourse. For men, maximal pleasure is linked with the greatest possibility of fathering offspring. In this perspective, the sexual pleasure of women should also be centered upon the act that causes impregnation—on intercourse itself. But how can our world be functional and Darwinian if the site of orgasm is divorced from the place of intercourse? How can sexual pleasure be so separated from its functional significance in the Darwinian game of life? (For the most divergent, but equally functionalist, view of some conservative Christians, sex was made by God to foster procreation; any use in any other context is blasphemy.)

Elisabeth Lloyd, a philosopher of science at Berkeley, has just completed a critical study of explanations recently proposed by evolutionary biologists for the origin and significance of female orgasm. Nearly all these proposals follow the lamentable tradition of speculative storytelling in the a priori adaptationist mode. In all the recent Darwinian literature, I believe that Donald Symons is the only scientist who presented what I consider the proper answer—that female orgasm is not an adaptation at all. (See his book, *The Evolution of Human Sexuality,* 1979.)

Many of these scientists don't even know the simple facts of the matter; they assume that female orgasms are triggered by intercourse and draw the obvious Darwinian conclusion. A second group recognizes the supposed paradox of nonassociation between orgasm and intercourse and then proposes another sort of adaptive explanation, usually based on maintenance of their pair bond by fostering close relationships through sexual pleasure. Desmond Morris *(The Naked Ape,* 1969), the most widely read promoter of this view, writes that female orgasm evolved for its role in promoting the pair bond by "the immense behavioral reward it brings to the act of sexual cooperation with the mated partner." Perhaps no popular speculation has been more androcentric than George Pugh's *(Biological Origin of Human Values,* 1977), who speaks about "the development of a female orgasm, which makes it easier for a female to be satisfied by one male, and which also operates psychologically to produce a stronger emotional bond in the female." Or Eibl-Eibesfeldt, who argues (1975) that the evolution of female orgasm "increases her readiness to submit and, in addition, strengthens her emotional bond to the partner."

This popular speculation about pair bonding usually rests upon an additional biological assumption—almost surely false—that capacity for female orgasm is an especially human trait. Yet Symons shows, in his admirable review of the literature, that whereas most female mammals do not experience orgasm during ordinary copulation, prolonged clitoral stimulation—either artificially in the laboratory (however unpleasant a context from the human point of view) or in nature by rubbing against another animal (often a female)—does produce orgasm in a wide range of mammals, including many primates. Symons concludes that "orgasm is most parsimoniously interpreted as a potential all female mammals possess."

Adaptive stories for female orgasm run the full gamut—leaving only the assumption of adaptation itself unquestioned. Sarah Hrdy (1981), for example, has taken up the cudgels against androcentrism in evolutionary speculation, not by branding the entire enterprise as bankrupt, but by showing that she can tell just as good an adaptive story from a female-centered point of view. She argues—turning the old pair-bond theory on its head—that the dissociation between orgasm and intercourse is an adaptation for promiscuous behavior, permitting females to enlist the support of several males to prevent any one from harming her babies. (In many species, a male that displaces a female's previous partner may kill her offspring, presumably to foster his own reproductive success by immediate remating.)

Indeed, no one surpasses Hrdy in commitment to the adaptationist assumption that orgasm must have evolved for Darwinian utility in promoting reproductive success. Chosen language so often gives away an underlying bias; note Hrdy's equation of nonadaptation both with despair in general and with the denigration of women's sexuality in particular.

> Are we to assume, then, that [the clitoris | is irrelevant? . . . It would be safer to suspect that, like most organs . . . it serves a purpose, or once did. . . . The lack of obvious purpose has left the way open for both orgasm, and female sexuality in general, to be dismissed as "nonadaptive."

But why are adaptationist arguments "safer," and why is nonadaptation a "dismissal"? I do not feel degraded because my nipples are concomitants of a general pattern in human development and not a sign that ancestors of my sex once lactated. In fact, I find this nonadaptationist explanation particularly fascinating, both because it teaches me something important about structural rules of development and because it counters a pervasive and constraining bias that has harmed evolutionary biology by restricting the range of permitted hypotheses. Why should the dissociation of orgasm from intercourse degrade women when it merely records a basic (if unappreciated) fact of human anatomy that happens to unite both sexes as variations of a common pattern in development? (Such an argument would only hold if adaptations were "good" and all other aspects of anatomy "irrelevant." I, for one, am quite attached to all my body parts and do not make such invidious rankings and distinctions among them.)

I could go on but will stop here for the obvious reason that this discussion, however amusing, might be deemed devoid of social importance. After all, these biologists may be enjoying themselves and promoting their view of life, but isn't all this strictly *entre nous?* I mean, after all, who cares about speculative ideas if they impose no palpable harm upon people's lives? But unfortunately, the history of psychology shows that one of the most influential theories of our century—a notion that had a direct and deeply negative effect upon millions of women—rested upon the false assumption that clitoral orgasm cannot be the natural way of a mature female. I speak, of course, about Sigmund Freud's theory of transfer from clitoral to vaginal orgasm.

In Freud's landmark and most influential book *Three Essays on the Theory of Sexuality* (1905, but first published in complete form in 1915), the third essay on "transformations of puberty" argues that "the leading erotogenic zone in female children is located at the clitoris." He also, as a scientist originally trained in anatomy, knows the reason—that the clitoris "is homologous to the masculine genital zone of the glans penis."

Freud continues: "All my experience concerning masturbation in little girls has related to the clitoris and not the regions of the external genitalia that are important in later sexual functioning." So far so good; Freud recognizes the phenomenon, knows its anatomical basis, and should therefore identify clitoral orgasm as a proper biological expression of female sexuality. Not at all, for Freud then describes a supposed transformation in puberty that defines the sexuality of mature women.

Puberty enhances the libido of boys but produces an opposite effect in girls—"a fresh wave of repression." Later, sexuality resumes in a new way. Freud writes:

> When at last the sexual act is permitted and the clitoris itself becomes excited, it still retains a function: the task, namely, of transmitting the excitation to the adjacent female sexual parts, just as—to use a simile—pine shavings can be kindled in order to set a log of harder wood on fire.

Thus, we encounter Freud's famous theory of female sexual maturity as a transfer from clitoral to vaginal orgasm:

> When erotogenic susceptibility to stimulation has been successfully transferred by a woman from the clitoris to the vaginal orifice, it implies that she has adopted a new leading zone for the purposes of her later sexual activity.

This dogma of transfer from clitoral to vaginal orgasm became a shibboleth of pop culture during the heady days of pervasive

Freudianism. It shaped the expectations (and therefore the frustration and often misery) of millions of educated and "enlightened" women told by a brigade of psychoanalysts and by hundreds of articles in magazines and "marriage manuals" that they must make this biologically impossible transition as a definition of maturity.

Freud's unbiological theory did further harm in two additional ways. First, Freud did not define frigidity only as an inability to perform sexually or as inefficacy in performance, but proposed as his primary definition a failure to produce this key transfer from clitoris to vagina. Thus, a woman who greatly enjoys sex, but only by clitoral stimulation, is frigid by Freud's terminology. "This anaesthesia," Freud writes, "may become permanent if the clitoridal zone refuses to abandon its excitability."

Second, Freud attributed a supposedly greater incidence of neurosis and hysteria in women to the difficulty of this transfer—for men simply retain their sexual zone intact from childhood, while women must undergo the hazardous switch from clitoris to vagina. Freud continues:

> The fact that women change their leading erotogenic zone in this way, together with the wave of repression at puberty . . . are the chief determinants of the greater proneness of women to neurosis and especially to hysteria. These determinants, therefore, are intimately related to the essence of femininity.

In short, Freud's error may be encapsulated by stating that he defined the ordinary biology of female sexuality as an aberration based on failure to abandon an infantile tendency.

The sources of Freud's peculiar theory are complex and involve many issues not treated in this essay (in particular his androcentric biases in interpreting the act of intercourse from a man's point of view and in defining both clitoral and penile stimulation in childhood as a fundamentally masculine form of sexuality that must be shunned by a mature woman). But another important source resides in the perspective underlying all the fanciful theories that I have discussed throughout this essay, from male nipples as sources of milk to clitoral orgasm as a clever invention to cement pair bonds—the bias of utility, or the exclusive commitment to functionalist explanations.

The more I read Kinsey, the more he wins my respect for his humane sensibility, and for his simple courage. (His 1953 report on *Sexual Behavior in the Human Female* appeared during the height of McCarthyism in America and led to a withdrawal of funding for his research and the effective end, during his lifetime, of his programs—see the essay "Of Wasps and WASPs" in my previous book, *The Flamingo's Smile*.) Kinsey was a measured man. He wrote in a dry and clinical fashion (probably more for reasons of necessity than inclinations of temperament). Yet, every once in a while, his passion spills forth and his rage erupts in a single, well-controlled phrase. Nowhere does Kinsey express more agitation than in his commentary on Freud's theory of the shift from clitoral to vaginal orgasm.

Kinsey locates his discussion of Freud in the proper context—in his section on sexual anatomy (Chapter 14, "Anatomy of Sexual Response and Orgasm"). He reports the hard data on adult masturbation and on the continuing clitoral site of orgasm in mature women. He locates the reason for clitoral orgasm not in any speculative theory about function but in the basic structure of sexual anatomy.

> In any consideration of the functions of the adult genitalia, and especially of their liability to sensory stimulation, it is important and imperative that one take into account the homologous origins of the structures in the two sexes.

Kinsey then provides a long and beautifully clear discussion of anatomical homologies, particularly the key unity of penis and clitoris. He concludes that "the vaginal walls are quite insensitive in the great majority of females. . . . There is no evidence that the vagina is ever the sole source of arousal, or even the primary source of erotic arousal in any female." Kinsey has now laid the foundation for a swift demolition of Freud's hurtful theory. He cites (in a long footnote, for his text is not contentious) a compendium of psychoanalytical proclamations from the Freudian heyday of the 1920s to 1940s. Consider just three items on his list:

1. (from 1936): "If this transition [from clitoris to vagina] is not successful, then the woman cannot experience satisfaction in the sexual act. . . . The first and decisive requisite of a normal orgasm is vaginal sensitivity."

2. (again from 1936): "The sole criterion of frigidity is the absence of the vaginal orgasm."

3. (from 1927): "In frigidity the pleasurable sensation is as a rule situated in the clitoris and the vaginal zone has none."

Kinsey's sole paragraph of evaluation ranks as the finest dismissal by understatement (and by incisive phrase at the end) that I have ever read.

> This question is one of considerable importance because much of the literature and many of the clinicians, including psychoanalysts and some of the clinical psychologists and marriage counselors, have expended considerable effort trying to teach their patients to transfer "clitoral responses" into "vaginal responses." Some hundreds of women in our own study and many thousands of the patients of certain clinicians have consequently been much disturbed by their failure to accomplish this biological impossibility.

I then must ask myself, why could Kinsey be so direct and sensible in 1953, while virtually all evolutionary discussion of female orgasm during the past twenty years has been not only biologically erroneous but also obtuse and purely speculative? I'm sorry to convert this essay into something of a broken record in contentious repetition, but the same point pervades the discussion all the way from Erasmus Darwin on male nipples to Sarah Hrdy on clitoral orgasm. The fault lies in a severely restrictive (and often false) functionalist view of life. Most functionalists have not misinterpreted male nipples, for their unobtrusive existence poses no challenge. But clitoral orgasm is too central to the essence of life for any explanation that does not focus upon the role of sexuality in reproductive success. And yet the obvious, nonadaptive structural alternative stares us in the face as the most elementary fact of sexual anatomy—the homology of penis and clitoris.

Kinsey's ability to cut through this morass right to the core of the strong developmental argument has interesting roots. Kinsey began his career by devoting twenty years to the taxonomy of gall-forming wasps. He pursued this work in the 1920s and 1930s before American evolutionary biology congealed around Darwinian funclionalism. In Kinsey's day, many (probably most) taxonomists accepted the nonadaptive nature of much small-scale geographic variability within species. Kinsey followed this structuralist tradition and never absorbed the bias of utility. He was therefore able to grasp the meaning of this elemental fact of homology between penis and clitoris—a fact that stares everyone in the face, but becomes invisible if the bias of utility be strong enough.

I well remember something that Francis Crick said to me many years ago, when my own functionalist biases were strong. He remarked, in response to an adaptive story I had invented with alacrity and agility to explain the meaning of repetitive DNA: "Why do you evolutionists always try to identify the value of something before you know how it is made?" At the time, I dismissed this comment as the unthinking response of a hidebound molecular reductionist who did not understand that evolutionists must always seek the "why" as well as the "how"—the final as well as the efficient causes of structures.

Now, having wrestled with the question of adaptation for many years, I understand the wisdom of Crick's remark. If all structures had a "why" framed in terms of adaptation, then my original dismissal would be justified for we would know that "whys" exist whether or not we had elucidated the "how." But I am now convinced that many structures (including male nipples and clitoral orgasm) have no direct adaptational "why." And we discover this by studying pathways of genetics and development—or, as Crick so rightly said to me, by first understanding how a structure is built. In other words, we must first establish "how" in order to know whether or not we should be asking "why" at all.

I began with Charles Darwin's grandpa Erasmus and end with his namesake, Desiderius Erasmus, the greatest of all Renaissance scholars. Of more than 3,000 proverbs from antiquity collected in his *Adagui* of 1508, perhaps two are best known and wonderfully apt for the point of this essay (which is not a diatribe against adaptation but a plea for expansion by alternative hypotheses and for fruitful competition and synthesis between functional and structural perspectives). First a comment on limitations of outlook: "No one is injured save by himself." Second, probably the most famous of zoological metaphors about human temperament: "The fox has many tricks, and the hedgehog only one, but that is the best of all." Some have taken the hedgehog's part in this dichotomy, but I will cast my lot for a diversity of options—for our complex world may offer many paths to salvation, and the hounds of hell press continually upon us.

Not Necessarily a Wing

FROM *Flesh Gordon* to *Alex in Wonderland,* title parodies have been a stock-in-trade of low comedy. We may not anticipate a tactical similarity between the mayhem of *Mad* magazine's movie reviews and the titles of major scientific works, yet two important nineteenth-century critiques of Darwin parodied his most famous phrases in their headings.

In 1887, E. D. Cope, the American paleontologist known best for his fossil feud with O. C. Marsh (see Essay 5) but a celebrated evolutionary theorist in his own right, published *The Origin of the Fittest*—a takeoff on Herbert Spencer's phrase, borrowed by Darwin as the epigram for natural selection: survival of the fittest. (Natural selection, Cope argued, could only preserve favorable traits that must arise in some other manner, unknown to Darwin. The fundamental issue of evolution cannot be the differential survival of adaptive traits, but their unexplained origin—hence the title parody.)

St. George Mivart (1817-1900), a fine British zoologist, tried to reconcile his unconventional views on religion and biology but ended his life in tragedy, rejected by both camps. At age seventeen, he abandoned his Anglican upbringing, became a Roman Catholic, and consequently (in a less tolerant age of state religion) lost his opportunity for training in natural history at Oxford or Cambridge. He became a lawyer but managed to carve out a distinguished career as an anatomist nonetheless. He embraced evolution and won firm support from the powerful T. H. Huxley, but his strongly expressed and idiosyncratic anti-Darwinian views led to his rejection by the biological establishment of Britain. He tried to unite his biology with his religion in a series of books and essays, and ended up excommunicated for his trouble six weeks before his death.

Cope and Mivart shared the same major criticism of Darwin—that natural selection could explain the preservation and increase of favored traits but not their origin. Mivart, however, went gunning for a higher target than Darwin's epigram. He shot for the title itself, naming his major book (1871) *On the Genesis of Species.* (Darwin, of course, had called his classic *On the Origin of Species.)*

Mivart's life may have ended in sadness and rejection thirty years later, but his *Genesis of Species* had a major impact in its time. Darwin himself offered strong, if grudging, praise and took Mivart far more seriously than any other critic, even adding a chapter to later editions of the *Origin of Species* primarily to counter Mivart's attack.

Mivart gathered, and illustrated "with admirable art and force" (Darwin's words), all objections to the theory of natural selection—"a formidable array" (Darwin's words again). Yet one particular theme, urged with special attention by Mivart, stood out as the centerpiece of his criticism. This argument continues to rank as the primary stumbling block among thoughtful and friendly scrutinizers of Darwinism today. No other criticism seems so troubling, so obviously and evidently "right" (against a Darwinian claim that seems intuitively paradoxical and improbable).

Mivart awarded this argument a separate chapter in his book, right after the introduction. He also gave it a name, remembered ever since. He called his objection "The Incompetency of 'Natural Selection' to Account for the Incipient Stages of Useful Structures." If this phrase sounds like a mouthful, consider the easy translation: We can readily understand how complex and fully developed structures work and how their maintenance and preservation may rely upon natural selection—a wing, an eye, the resemblance of a bittern to a branch or of an insect to a stick or dead leaf. But how do you get from nothing to such an elaborate something if evolution must proceed through a long sequence of intermediate stages, each favored by natural selection? You can't fly with 2 percent of a wing or gain much protection from an iota's similarity with a potentially concealing piece of vegetation.

How, in other words, can natural selection explain the incipient stages of structures that can only be used in much more elaborated form?

I take up this old subject for two reasons. First, I believe that Darwinism has, and has long had, an adequate and interesting resolution to Mivart's challenge (although we have obviously been mightily unsuccessful in getting it across). Second, a paper recently published in the technical journal *Evolution* has provided compelling experimental evidence for this resolution applied to its most famous case—the origin of wings.

The dilemma of wings—*the* standard illustration of Mivart's telling point about incipient stages—is set forth particularly well in a perceptive letter that I recently received from a reader, a medical doctor in California. He writes:

> How does evolutionary theory as understood by Darwin explain the emergence of items such as wings, since a small move toward a wing could hardly promote survival? I seem to be stuck with the idea that a significant quality of wing would have to spring forth all at once to have any survival value.

Interestingly, my reader's proposal that much or most of the wing must arise all at once (because incipient stages could have no adaptive value) follows Mivart's own resolution. Mivart first enunciated the general dilemma (1871, p. 23):

> Natural selection utterly fails to account for the conservation and development of the minute and rudimentary beginnings, the slight and infinitesimal commencements of structures, however useful those structures may afterwards become.

After fifty pages of illustration, he concludes: "Arguments may yet be advanced in favor of the view that new species have from time to time manifested themselves with suddenness, and by modifications appearing at once." Advocating this general solution for wings in particular, he concludes (p. 107): "It is difficult, then, to believe that the Avian limb was developed in any other way than by a comparatively sudden modification of a marked and important kind."

Darwin's theory is rooted in the proposition that natural selection acts as the primary creative force in evolutionary change. This creativity will be expressed only if the fortuitous variation forming the raw material of evolutionary change can be accumulated sequentially in tiny doses, with natural selection acting as the sieve of acceptance. If new species arise all at once in an occasional lucky gulp, then selection has no creative role. Selection, at best, becomes an executioner, eliminating the unfit following this burst of good fortune. Thus, Mivart's solution—bypassing incipient stages entirely in a grand evolutionary leap—has always been viewed, quite rightly, as an anti-Darwinian version of evolutionary theory.

Darwin well appreciated the force, and potentially devastating extent, of Mivart's critique about incipient stages. He counterattacked with gusto, invoking the standard example of wings and arguing that Mivart's solution of sudden change presented more problems than it solved—for how can we believe that so complex a structure as a wing, made of so many coordinated and coadapted parts, could arise all at once:

> He who believes that some ancient form was transformed suddenly through an internal force or tendency into, for instance, one furnished with wings, will be . . . compelled to believe that many structures beautifully adapted to all the other parts of the same creature and to the surrounding conditions, have been suddenly produced; and of such complex and wonderful co-adaptations, he will not be able to assign a shadow of an explanation... . To admit all this is, as it seems to me, to enter into the realms of miracle, and to leave those of Science.

(This essay must now go in other directions but not without a small, tangential word in Mivart's defense. Mivart did appreciate the problem of complexity and coordination in sudden origins. He did not think that any old complex set of changes could arise all at once when needed—*that* would be tantamount to miracle. Most of Mivart's book studies the regularities of embryology and comparative anatomy to learn which kinds of complex changes might be possible as expressions and elaborations of developmental programs already present in ancestors. He advocates these changes as possible and eliminates others as fanciful.)

Darwin then faced his dilemma and developed the interestingly paradoxical resolution that has been orthodox ever since (but more poorly understood and appreciated than any other principle in evolutionary theory). If complexity precludes sudden origin, and the dilemma of incipient stages forbids gradual development in functional continuity, then how can we ever get from here to there? Darwin replies that we must reject an unnecessary hidden assumption in this argument—the notion of functional continuity. We will all freely grant that no creature can fly with 2 percent of a wing, but why must the incipient stages be used for flight? If incipient stages originally performed a different function suited to their small size and minimal development, natural selection might superintend their increase as adaptations for this original role until they reached a stage suitable for their current use. In other words, the problem of incipient stages disappears because these early steps were not inadequate wings but well-adapted something-elses. This principle of *functional change in structural continuity* represents Darwin's elegant solution to the dilemma of incipient stages.

Darwin, in a *beau geste* of argument, even thanked Mivart for characterizing the dilemma so well—all the better to grant Darwin a chance to elaborate his solution. Darwin writes: "A good opportunity has thus been afforded [by Mivart] for enlarging a little on gradations of structure, often associated with changed functions—an important subject, which was not treated at sufficient length in the former editions of this work." Darwin, who rarely added intensifiers to his prose, felt so strongly about this principle of functional shift that he wrote: "In considering transitions of organs, it is so important to bear in mind the probability of conversion from one function to another."

Darwin presented numerous examples in Chapters 5 and 7 of the final edition of the *Origin of Species.* He discussed organs that perform two functions, one primary, the other subsidiary, then relinquish the main use and elaborate the formerly inconspicuous operation. He then examined the flip side of this phenomenon—functions performed by two separate organs (fishes breathing with both lungs and gills). He argues that one organ may assume the entire function, leaving the other free for evolution to some other role (lungs for conversion to air bladders, for example, with respiration maintained entirely by gills). He does not, of course, neglect the classic example of wings, arguing that insects evolved their organs of flight from tracheae (or breathing organs—a minority theory today, but not without supporters). He writes: "It is therefore highly probable that in this great class organs which once served for respiration have been actually converted into organs of flight."

Darwin's critical theory of functional shift, usually (and most unfortunately) called the principle of "preadaptation,"* has been with us for a century. I believe that this principle has made so little headway not only because the basic formulation seems paradoxical and difficult, but mainly because we have so little firm, direct evidence for such functional shifts. Our technical literature contains many facile verbal arguments—little more than plausible "just-so" stories. The fossil record also presents some excellent examples of sequential development through intermediary stages that could not work as modern organs do—but we lack a rigorous mechanical analysis of function at the various stages.

Let us return, as we must, to the classic case of wings. *Archaeopteryx,* the first bird, is as pretty an intermediate as paleontology

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"This dreadful name has made a difficult principle even harder to grasp and understand. Preadaptation seems to imply that the proto-wing, while doing something else in its incipient stages, knew where it was going—predestined for a later conversion to flight. Textbooks usually introduce the word and then quickly disclaim any odor of foreordination. (But a name is obviously ill-chosen if it cannot be used without denying its literal meaning.) Of course, by "preadaptation" we only mean that some structures are fortuitously suited to other roles if elaborated, not that they arise with a different future use in view—now there I go with the standard disclaimer. As another important limitation, preadaptation does not cover the important class of features that arise without functions (as developmental consequences of other primary adaptations, for example) but remain available for later co-optation. I suspect, for example, that many important functions of the human brain are co-opted consequences of building such a large computer for a limited set of adaptive uses. For these reasons. Kli/abetb Vrba and I have proposed that the restrictive and confusing word "preadaptation" be dropped in favor of the more inclusive term "exaplation"—for any organ not evolved under natural selection for its current use—either because it performed a different function in ancestors (classical preadaptation) or because it represented a nonfunctional part available for later co-optation. See our technical article, "Exaplation: A Missing Term in the Science of Form," *Paleobiology,* **1981.**

could ever hope to find—a complex melange of reptilian and avian features. Scientists are still debating whether or not it could fly. If so, *Archaeopteryx* worked like the Wrights' biplane to a modern eagle's Concorde. But what did the undiscovered ancestors *of Archaeopteryx* do with wing rudiments that surely could not produce flight? Evolutionists have been invoking Darwin's principle of functional shift for more than 100 years, and the list of proposals is long. Proto-wings have been reconstructed as stabilizers, sexual attractors, or insect catchers. But the most popular hypothesis identifies thermoregulation as the original function of incipient stages that later evolved into feathered wings. Feathers are modified reptilian scales, and they work very well as insulating devices. Moreover, if birds evolved from dinosaurs (as most paleontologists now believe), they arose from a lineage particularly subject to problems with temperature control. *Archaeopteryx* is smaller than any dinosaur and probably arose from the tiniest of dinosaur lineages. Small animals, with high ratios of surface area to volume, lose heat rapidly and may require supplementary devices for thermoregulation. Most dinosaurs could probably keep warm enough just by being large. Surface area (length **X** length, or length squared) increases more slowly than volume (length **X** length **X** length, or length cubed) as objects grow. Since animals generate heat over their volumes and lose it through their surfaces, small animals (with their relatively large surface areas) have most trouble keeping warm.

There I go again—doing what I just criticized. I have presented a plausible story about thermoregulation as the original function of organs that later evolved into wings. But science is tested evidence, not tall tales. This lamentable mode of storytelling has been used to illustrate Darwin's principle of functional shift only */ante de mieux*—because we didn't have the goods so ardently desired. At least until recently, when my colleagues Joel G. Kingsolver and M. A. R. Koehl published the first hard evidence to support a shift from thermoregulation to flight as a scenario for the evolution of wings. They studied insects, not birds—but the same argument has long been favored for nature's smaller and far more abundant wings (see their article, "Aerodynamics, Thermoregulation, and the Evolution of Insect Wings: Differential Scaling and Evolutionary Change," in *Evolution,* 19S.>).

In preparing this essay, I spent several days reading the classical literature on the evolution of insect flight—and emerged with a deeper understanding of just how difficult Darwin's principle of functional shift can be, even for professionals. Most of the literature hasn't even made the first step of applying functional shift at all, not to mention the later reform of substituting direct evidence for verbal speculation. Most reconstructions are still trying to explain the incipient stages of insect wings as somehow involved in airborne performance from the start—not for flapping flight, of course, but still for some aspect of motion aloft rather than, as Darwin's principle would suggest, for some quite different function.

To appreciate the dilemma of such a position (so well grasped by Mivart more than 100 years ago), consider just one recent study (probably the best and most widely cited) and the logical quandaries that a claim of functional continuity entails. In 1964, J. W. Flower presented aerodynamic arguments for wings evolved from tiniest rudiment to elaborate final form in the interest of airborne motion. Flower argues, supporting an orthodox view, that wings evolved from tiny outgrowths of the body used for gliding prior to elaboration for sustained flight. But Flower recognizes that these incipient structures must themselves evolve from antecedents too small to function as gliding planes. What could these very first, slight outgrowths of the body be for? Ignoring Darwin's principle of functional shift, Flower searches for an aerodynamic meaning even at this very outset. He tries to test two suggestions: E. H. Hinton's argument that initial outgrowths served for "attitude control," permitting a falling insect to land in a suitable position for quick escape from predators; and a proposal of the great British entomologist Sir Vincent Wigglesworth (wonderful name for an insect man, I always thought) that such first stages might act as stabilizing or controlling devices during takeoff in small, passively aerial insects.

Flower proceeded by performing aerodynamic calculations on consequences of incipient wings for simple body shapes when dropped—and he quickly argued himself into an inextricable logical corner. He found, first of all, that tiny outgrowths might help, as Wigglesworth, Hinton, and others had suggested. But the argument foundered on another observation: The same advantages could be gained far more easily and effectively by another, readily available alternative route—evolution to small size (where increased surface/volume ratios retard falling and enhance the probability of takeoff). Flower then realized that he would have to specify a reasonably large body size for incipient wings to have any aerodynamic effect. But he then encountered another problem: At such sizes, legs work just as well as, if not better than, proto-wings for any suggested aerodynamic function. Flower admitted:

> The first conclusion to be drawn from these calculations is that the selective pressure in small insects is towards smaller insects, which would have no reason to evolve wings.

I would have stopped and searched elsewhere (in Darwin's principle of functional shift) at this point, but Flower bravely continued along an improbable path:

> The main conclusions, however, are that attitude control of insects would be by the use of legs or by very small changes in body shape [*i.e.*, by evolving small outgrowths, or proto-wings).

Flower, in short, never considered an alternative to his assumption of functional continuity based upon some aspect of aerial locomotion. He concluded:

> At first they [proto-wings] would affect attitude; later they could increase to a larger size and act as a true wing, providing lift in their own right. Eventually they could move, giving the insect greater maneuverability during descent, and finally they could "flap," achieving sustained flight.

As an alternative to such speculative reconstructions that work, in their own terms, only by uncomfortable special pleading, may I suggest Darwin's old principle of functional shift (preadaptation—ugh—for something else).

The physiological literature contains voluminous testimony to the thermodynamic efficiency of modern insect wings: in presenting, for example, a large surface area to the sun for quick heating (see B. Heinrich, 1981). If wings can perform this subsidiary function now, why not suspect thermoregulation as a primary role at the outset? M. M. Douglas (1981), for example, showed that, in *Colias* butterflies, only the basal one-third of the wing operates in thermoregulation—an area approximately equal to the thoracic lobes (proto-wings) of fossil insects considered ancestral to modern forms.

Douglas then cut down some *Colias* wings to the actual size of these fossil ancestral lobes and found that insects so bedecked showed a 55 percent greater increase in body temperature than bodies deprived of wings entirely. These manufactured proto-wings measured 5 by 3 millimeters on a body 15 millimeters long. Finally, Douglas determined that no further thermoregulatory advantage could be gained by wings longer than 10 millimeters on a 15-millimeter body.

Kingsolver and Koehl performed a host of elaborate and elegant experiments to support a thermoregulatory origin of insect proto-wings. As with so many examples of excellent science producing clear and interesting outcomes, the results can be summarized briefly and cleanly.

Kingsolver and Koehl begin by tabulating all the aerodynamic hypotheses usually presented in the literature as purely verbal speculations. They arrange these proposals of functional continuity (the explanations that do not follow Darwin's solution of Mivart's dilemma) into three basic categories: proto-wings for gliding (aerofoils for steady-state motion), for parachuting (slowing the rale of descent in a falling insect), and attitude stability (helping an insect to land right side up). They then transcended the purely verbal tradition by developing aerodynamic equations for exactly how proto-wings should help an insect under these three hypotheses of continuity in adaptation (increasing the lift/drag ratio as the major boost to gliding, increasing drag to slow the descent rate in parachuting, measuring the moment about the body axis produced by wings for the hypothesis of attitude stability).

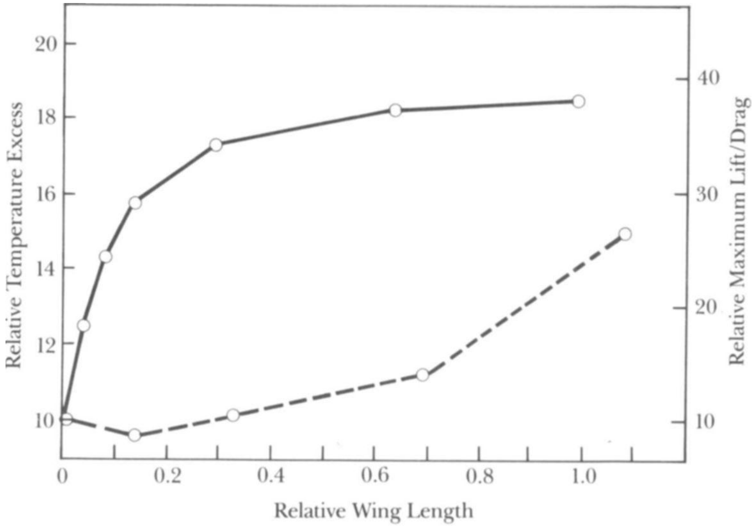
They then constructed insect models made of wire, epoxy, and other appropriate materials to match the sizes and body shapes of flying and nonflying forms among early insect fossils. To these models, they attached wings (made of copper wire enclosing thin, plastic membranes) of various lengths and measured the actual aerodynamic effects for properties predicted by various hypotheses of functional continuity. The results of many experiments in wind tunnels are consistent and consonant: Aerodynamic benefits begin for wings above a certain size, and they increase as wings get larger. But at the small sizes of insect proto-wings, aerodynamic advantages are absent or insignificant and do not increase with growing wing length. These results are independent of body shape, wind velocity, presence or placement of legs, and mounting position of wings. In other words, large wings work well and larger wings work better—but small wings (at the undoubted sizes of Mivart's troubling incipient stages) provide no aerodynamic edge.

Kingsolver and Koehl then tested their models for thermoregulatory effects, constructing wings from two materials with different thermal conductivities (construction paper and aluminum foil) and measuring the increased temperature of bodies supplied with wings of various lengths versus wingless models. They achieved results symmetrically opposite to the aerodynamic experiments. For thermoregulation, wings work well at the smallest sizes, with benefits increasing as the wing grows. However, beyond a measured length, further increase of the wing confers no additional effect. Kingsolver and Koehl conclude:

> At any body size, there is a relative wing length above which there is no additional thermal effect, and below which there is no significant aerodynamic effect.

The accompanying chart illustrates these combined results. Note how the thermoregulatory effect of excess body temperature due to wings (solid line) increases rapidly at small wing sizes but not at all above an intermediate wing length. Conversely, the aerodynamic effect of lift/drag ratio does not increase at all until intermediate wing length, but grows rapidly thereafter.

We could not hope for a more elegant experimental confirmation of Darwin's solution to Mivart's challenge. Kingsolver and Koehl have actually measured the functional shift by showing that incipient wings aid thermoregulation but provide no aerodynamic benefit—while larger wings provide no further thermoregulatory oomph but initiate aerodynamic advantage and increase the benefits steadily thereafter. The crucial intermediate



The thermoregulatory (upper curve) and aerodynamic (lower curve) advantages for increasing wing length in insects. Note that thermodynamic benefits accrue rapidly when the wing is very small (too small for flight), but scarcely increase at all for wings of larger size. Aerodynamic advantages, on the other hand, are insignificant for small size, but increase rapidly at larger wing dimensions, just as the thermodynamic benefits cease, BEN GAMIT. ADAPTED FROM JOE LEMONNIER. COURTESY OF *NATURAL HISTORY.*

wing length, where thermoregulatory gain ceases and aerodynamic benefits begin, represents a domain of functional shift, as aerodynamic advantages pick up the relay from waning thermoregulation to continue the evolutionary race to increasing wing size.

But what might push an insect across the transition? Why reach this crucial domain at all? If wings originally worked primarily for thermoregulation, why not just stop as the length of maximum benefit approached? Here, Kingsolver and Koehl present an interesting speculation based on another aspect of their data. They found that the domain of transition between thermal and aerial effects varied systematically with body size: The larger the body, the sooner the transition (in terms of relative wing length). For a body 2 centimeters long, the transition occurred with wings 40 to 60 percent of body length; but a 10-centimeter body switches to aerodynamic advantage at only 10 percent of body length.

Now suppose that incipient ancestral wings worked primarily for thermoregulation and had reached a stable, optimum size for greatest benefit. Natural selection would not favor larger wings and a transition to the available domain of aerodynamic advantage. But if body size increased for other reasons, an insect might reach the realm of aerial effects simply by growing larger, without any accompanying change of body shape or relative wing length.

We often think, naively, that size itself should make no profound difference. Why should just more of the same have any major effect beyond simple accumulation? Surely, any major improvement or alteration must require an extensive and explicit redesign, a complex reordering of parts with invention of new items.

Nature does not always match our faulty intuitions. Complex objects often display the interesting and paradoxical property of major effect for apparently trifling input. Internal complexity can translate a simple quantitative change into a wondrous alteration of quality. Perhaps that greatest and most effective of all evolutionary inventions, the origin of human consciousness, required little more than an increase of brain power to a level where internal connections became rich and varied enough to force this seminal transition. The story may be much more complex, but we have no proof that it must be.

Voltaire quipped that "God is always for the big battalions." More is not always better, but more can be very different.

Life's Little Joke

I STILL DON'T UNDERSTAND why a raven is like a writing desk, but I do know what binds Hernando Cortes and Thomas Henry Huxley together.

On February 18, 1519, Cortes set sail for Mexico with about 600 men and, perhaps more important, 16 horses. Two years later, the Aztec capital of Tenochtitlan lay in ruins, and one of the world's great civilizations had perished.

Cortes's victory has always seemed puzzling, even to historians of an earlier age who did not doubt the intrinsic superiority of Spanish blood and Christian convictions. William H. Prescott, master of this tradition, continually emphasizes Cortes's diplomatic skill in making alliances to divide and conquer—and his good fortune in despoiling Mexico during a period of marked internal dissension among the Aztecs and their vassals. (Prescott published his *History of the Conquest of Mexico* in 1843; it remains among the most exciting and literate books ever written.)

Prescott also recognized Cortes's two "obvious advantages on the score of weapons"—one inanimate and one animate. A gun is formidable enough against an obsidian blade, but consider the additional impact of surprise when your opponent has never seen a firearm. Cortes's cavalry, a mere handful of horses and their riders, caused even more terror and despair, for the Aztecs, as Prescott wrote,

> had no large domesticated animals, and were unacquainted with any beast of burden. Their imaginations were bewildered when they beheld the strange apparition of the horse

> and his rider moving in unison and obedient to one impulse, as if possessed of a common nature; and as they saw the terrible animal, with "his neck clothed in thunder," bearing down their squadrons and trampling them in the dust, no wonder they should have regarded him with the mysterious terror felt for a supernatural being.

On the same date, February 18, in 1870, Thomas Henry Huxley gave his annual address as president of the Geological Society of London and staked his celebrated claim that Darwin's ideal evidence for evolution had finally been uncovered in the fossil record of horses—a sequence of continuous transformation, properly arrayed in temporal order:

> It is easy to accumulate probabilities—hard to make out some particular case, in such a way that it will stand rigorous criticism. After much search, however, I think that such a case is to be made out in favor of the pedigree of horses.

Huxley delineated the famous trends to fewer toes and higher-crowned teeth that we all recognize in this enduring classic among evolutionary case histories. Huxley viewed this lineage as a European affair, proceeding from fully three-toed *Anchitherium,* to *Hipparion* with side toes "reduced to mere dew-claws [that] do not touch the ground," to modern *Equus,* where, "finally, the crowns of the grinding-leeth become longer. . . . The phalanges of the two outer toes in each foot disappear, their metacarpal and metatarsal bones being left as the 'splints.' "

In *Cat's Cradle,* Kurt Vonnegut speaks of the subtle ties that can bind people across worlds and centuries into aggregations forged by commonalities so strange that they must be meaningful. Cortes and Huxley must belong to the same karass (Vonnegut's excellent word for these associations)—for they both, on the same date, unfairly debased America with the noblest of animals. Huxley was wrong and Cortes, by consequence, was ever so lucky.

Horses evolved in America, through a continuity that extends unbroken across 60 million years. Several times during this history, different branches migrated to Europe, where Huxley arranged three (and later four) separate incursions as a false *m*

continuity. But horses then died in America at the dawn of human history in our hemisphere, leaving the last European migration as a source of recolonization by conquest. Huxley's error became Montezuma's sorrow, as an animal more American than Babe Ruth or apple pie came home to destroy her greatest civilization. (Montezuma's revenge would come later, and by another route.)

During our centennial year of 1876, Huxley visited America to deliver the principal address for the founding of Johns Hopkins University. He stopped first at Yale to consult the eminent paleontologist Othniel C. Marsh. Marsh, ever gracious, offered Huxley an architectural tour of the campus, but Huxley had come for a purpose and would not be delayed. He pointed to the buildings and said to Marsh: "Show me what you have got inside them; I can see plenty of bricks and mortar in my own country." Huxley was neither philistine nor troglodyte; he was simply eager to study some particular fossils: Marsh's collection of horses.

Two years earlier, Marsh had published his phylogeny of American horses and identified our continent as the center stage, while relegating Huxley's European sequence to a periphery of discontinuous migration. Marsh began with a veiled and modest criticism *(American Journal of Science,* 1874):

> Huxley has traced successfully the later genealogy of the horse through European extinct forms, but the line in America was probably a more direct one, and the record is more complete.

Later, he stated more baldly (p. 258): "The line of descent appears to have been direct, and the remains now known supply every important intermediate form."

Marsh had assembled an immense collection from the American West (prompted largely by a race for priority in his bitter feud with Edwin 1). (lope—see Essay 5 for another consequence of this feud!). For every query, every objection that Huxley raised, Marsh produced a specimen. Leonard Huxley describes the scene in his biography of his father:

> At each inquiry, whether he had a specimen to illustrate such and such a point or to exemplify a transition from earlier and less specialized forms to later and more special-

> ized ones, Professor Marsh would simply turn to his assistant and bid him fetch box number so and so, until Huxley turned upon him and said, "I believe you are a magician; whatever I want, you just conjure it up."

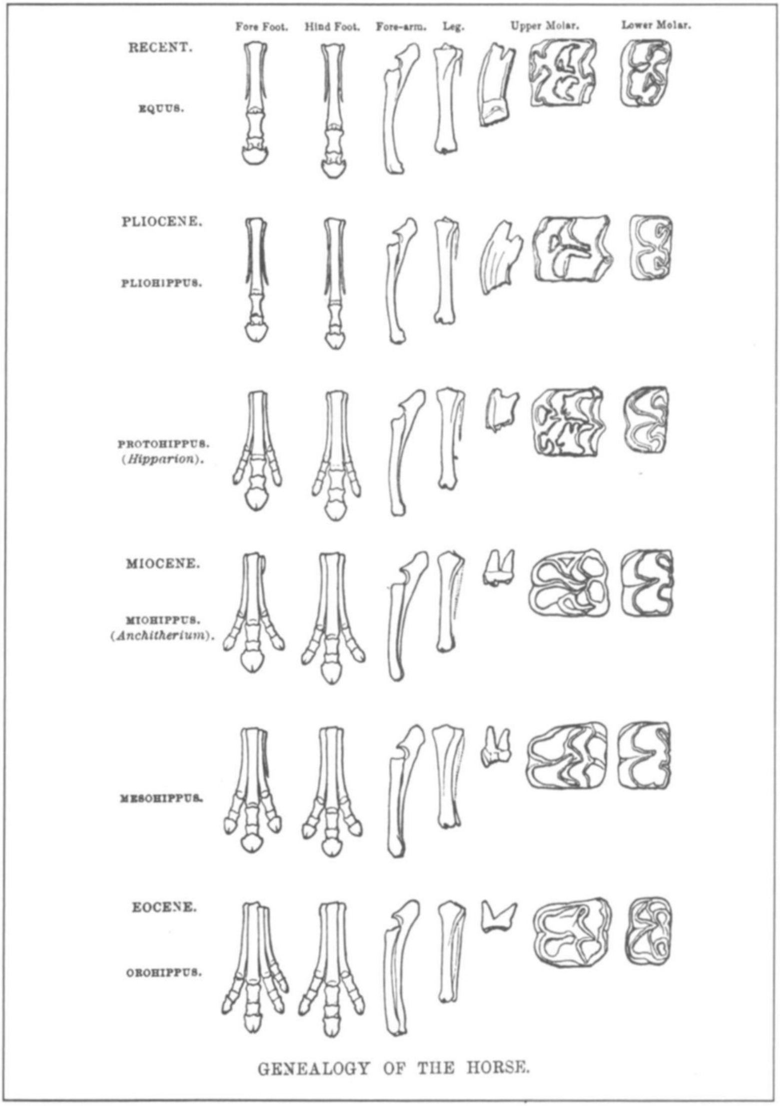
Years before, T. H. Huxley had coined a motto; now he meant to live by it: "Sit down before fact as a little child, be prepared to give up every preconceived notion." He capitulated to Marsh's theory of an American venue. Marsh, with growing pleasure and retreating modesty, reported his impression of personal triumph:

> He [Huxley] then informed me that this was new to him, and that my facts demonstrated the evolution of the horse beyond question, and for the first time indicated the direct line of descent of an existing animal. With the generosity of true greatness, he gave up his own opinions in the face of new truth and took my conclusions.

A few days later, Huxley was, if anything, more convinced. He wrote to Marsh from Newport, his next stop: "The more I think of it the more clear it is that your great work is the settlement of the pedigree of the horse." But Huxley was scheduled to lecture on the evolution of horses less than a month later in New York. As he traveled about eastern America, Huxley rewrote his lecture from scratch. He also enlisted Marsh's aid in preparing a chart that would show the new evidence to his New York audience in pictorial form. Marsh responded with one of the most famous illustrations in the history of paleontology—the first pictorial pedigree of the horse.

Scholars are trained to analyze words. But primates are visual animals, and the key to concepts and their history often lies in iconography. Scientific illustrations are not frills or summaries; they are foci for modes of thought. The evolution of the horse—both in textbook charts and museum exhibits—has a standard iconography. Marsh began this traditional display in his illustration for Huxley. In so doing, he also initialed an error that captures pictorially the most common of all misconceptions about the shape and pattern of evolutionary change.

Errors in science are diverse enough to demand a taxonomy of



The celebrated original figure drawn by O.C. Marsh for T.H. Huxley's New York lecture on the evolution of horses. This version appeared in an article by Marsh in the *American Journal of Science* for 1879. NEG. NO. 123823. COURTESY DEPARTMENT OF LIBRARY SERVICES, AMERICAN MUSEUM OF NATURAL HISTORY.

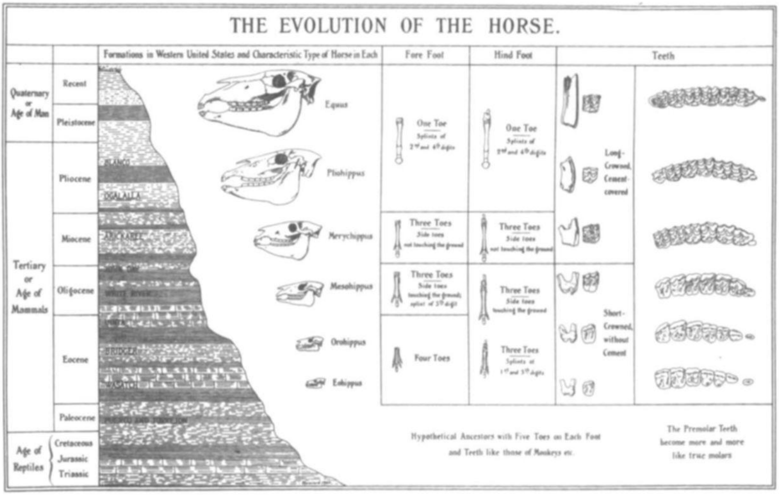
categories. Some make me angry, particularly those that arise from social prejudice, masquerade as objectively determined truth, and directly limit the lives of those caught in their thrall (scientific justifications for racism and sexism, as obvious examples). Others make me sad because honest effort ran headlong into unresolvable complexities of nature. Still others, as errors of logic that should not have occurred, bloat my already extended ego when I discover them. But I reserve a special place in perverse affection for a small class of precious ironies—errors that pass nature through a filter of expectation and reach a particular conclusion only because nature really works in precisely the opposite way. This result, I know, sounds both peculiar and unlikely, but bear with me for the premier example of life's little joke—as displayed in conventional iconography (and interpretation) for the most famous case study of all, the evolution of the horse.

In his original 1874 article, Marsh recognized the three trends that define our traditional view of old dobbin's genealogy: increase in size, decrease in the number of toes (with the hoof of modern horses made from a single digit, surrounded by two vestigial splints as remnants of side toes), and increase in the height and complexity of grinding teeth. (I am not treating the adaptive significance of these changes here, but wish to record the conventional explanation for the major environmental impetus behind trends in locomotion and dentition: a shift from browsing on lush lowland vegetation to grazing of newly evolved grasses upon drier plains. Tough grasses with less food value require considerably more dental effort.)

Marsh's famous chart, drawn for Huxley, depicts these trends as an ascending series—a ladder of uninterrupted progress toward one toe and tall, corrugated teeth (by scaling all his specimens to the same size, Marsh does not show the third "classic" trend toward increasing bulk).

We are all familiar with this traditional picture—the parade of horses from little eohippus (properly called *Hyracotherium),* with four toes in front and three behind, to Man o' War. *{Hyracotherium* is always described as "fox terrier" in size. Such traditions disturb and captivate me. I know nothing about fox terriers but have dutifully copied this description. I wonder who said it first, and why this simile has become so canonical. I also wonder what the textbook tradition of endless and thoughtless copying has done to retard the spread of original ideas.*)

In conventional charts and museum displays, the evolution of horses looks like a line of schoolchildren all pointed in one direction and arrayed in what my primary-school drill instructors called "size place" (also stratigraphic order in this case). The most familiar of all illustrations, first drawn early in the century for the American Museum of Natural History's pamphlet on the evolution of horses, by W. D. Matthew, but reproduced hundreds of times since then, shows the whole story: size, toes, and teeth arranged in a row by order of appearance in the fossil record. To cite just one example of this figure's influence, George W. Hunter reproduced Matthew's chart as the primary illustration of



Most widely reproduced of all illustrations showing the evolution of horses as a ladder towards progress. Note increase in skull size, decrease in the number of toes, and increase in the height of teeth. The skulls are also arranged in stratigraphic order. W.D. Matthew used this illustration in several publications. This version comes from an article in the *Quarterly Review of Biology* for 1926. NEG. NO. 37909. COURTESY DEPARTMENT OF LIBRARY SERVICES, AMERICAN MUSEUM OF NATURAL HISTORY.

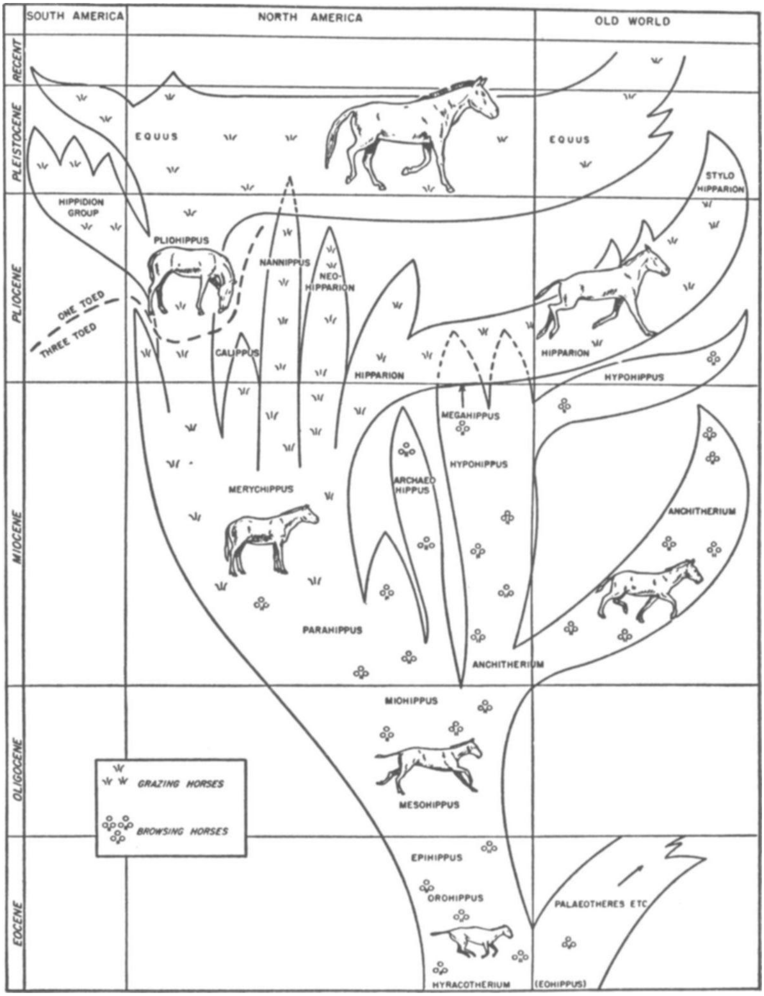
•This parenthetical comment inspired Roger Angell's letter and led directly to research and writing of the essay preceding this piece.

evolution in his high-school textbook of 1914, *A Civic Biology.* John Scopes assigned this book to his classes in Tennessee and was convicted for teaching its chapters on evolution, as William Jennings Bryan issued his last hurrah (see Essay 28): "No more repulsive doctrine was ever proclaimed by man . . . may heaven defend the youth of our land from [these] impious babblings."

But what is so wrong with these evolutionary ladders? Surely we can trace an unbroken continuity from *Hyracotherium* to modern horses. Yes, but continuity comes in many more potential modes than the lock step of the ladder. Evolutionary genealogies are copiously branching bushes—and the history of horses is more lush and labyrinthine than most. To be sure, *Hyracotherium* is the base of the trunk (as now known), and *Equus* is the surviving twig. We can, therefore, draw a pathway of connection from a common beginning to a lone result. But the lineage of modern horses is a twisted and tortuous excursion from one branch to another, a path more devious than the road marked by Ariadne's thread from the Minotaur at the center to the edge of our culture's most famous labyrinth. Most important, the path proceeds not by continuous transformation but by lateral stepping (with geological suddenness when punctuated equilibrium applies, as in this lineage, at least as read by yours truly, who must confess his bias as coauthor of the theory).

Each lateral step to a new species follows one path among several alternatives. Each extended lineage becomes a set of decisions at branching points—only one among hundreds of potential routes through the labyrinth of the bush. There is no central direction, no preferred exit to this maze—just a series of indirect pathways to every twig that ever graced the periphery of the bush.

As an example of distortions imposed by converting tortuous paths through bushes into directed ladders, consider the men associated with the two classical iconographies reproduced here. When Huxley made his formal capitulation to Marsh's interpretation in print (1880), he extended the ladder of horses as a metaphor for all vertebrates. Speaking of modern reptiles and teleost fishes, Huxley wrote (1880, p. 661): "They appear to me to be off the main line of evolution—to represent, as it were, side tracks starting from certain points of that line." But teleosts (modern bony fishes) are an enormously successful group. They stock the world's oceans, lakes, and rivers and maintain nearly 100 times as many species as primates (and more than all mammals combined). How can we call them "off the main line" just because we



The evolution of horses depicted as at least a modest bush by G.G. Simpson in 1951. NEG. NO. 328907. COURTESY DEPARTMENT OF LIBRARY SERVICES, AMERICAN MUSEUM OF NATURAL HISTORY.

can trace our own pathway back to a common ancestry with theirs more than 300 million years ago?

W. D. Matthew slipped into an equally biased assessment of value because his designation of one pathway as a ladder forced an interpretation of all others as diversions. Matthew (1926, p. 164) designated his ladder as the "direct line of succession," but acknowledged that "there are also a number of side branches, more or less closely related." Three pages later, Matthew adds the opprobrium of near indecency to his previous charge of mere laterality, as he describes (p. 167) "a number of side branches leading up in a similar manner to aberrant specialized Equidae now extinct." But in what way are extinct lineages more specialized than a modern horse or in any sense more peculiar? Their historical death is the only possible rationale for a designation of aberrancy, but more than 99 percent of all species that ever lived are extinct—and disappearance cannot be the biological equivalent of a scarlet letter. We might as well call modern horses aberrant because, much to Montezuma's later sorrow, they became extinct in the land of their birth.

Yet we have recognized the bushiness of horse evolution from the very beginning. How else did Marsh forestall Huxley but by convincing him that his European "genealogy" of horses formed a stratigraphic sequence of discontinuous stages, falsely linking several side branches that had disappeared without issue?

As an example of bushiness, and a plug for the value of appropriate metaphors in general, consider the finest book on the evolution of horses ever written for popular audiences—G. G. Simpson's *Horses* (1951). Simpson redrew the genealogy of horses as a modest bush with no preferred main line. He also criticized the conceptual lock imposed by the bias of the ladder when he noted that modern one-toed horses are a side branch and extinct three-toed creatures the main line (if any center can be designated at all).

> As nearly as there is a straight line in horse evolution, it culminated and ended with these animals [the three-toed anchitheres], which, like their ancestors, were multiple-toed browsers. From this point of view, it is the line leading to modern horses that was the side branch, even though it outlasted the straighter line of horse evolution [p. 130].

Yet Simpson, who held a lifelong commitment to the predominant role of evolution by transformational change within populations rather than by accumulation across numerous events of discrete, branching speciation, could not entirely let go of biases imposed by the metaphor of the ladder. In one revealing passage, he accepts bushiness, but bemoans the complexities thus introduced, as though they clouded evolution's essence of transformational change:

> *Miohippus* . . . intergraded with several different descendant groups. It is sad that this introduces possible confusion into the story, but there is not much point in criticizing nature for something that happened some millions of years ago. It would also be foolish to try to ignore the complications, which did occur and which are a very important part of the record.

But these "complications" are not a veil upon the essence of lineal descent; they are the primary stuff of evolution itself.

Moreover, Simpson restricted his bushiness as much as possible and retained linearity wherever he could avoid an inference of branching. In particular, he proposes the specific and testable hypothesis (see his illustration) that the early part of the record—the sequence of *Hyracotherium—Orohippus—Epihippus—Mesohippus—Miohippus—Hypohippus*—tells a story of linear descent, only later interrupted by copious branching among three-toed browsers: "The line from *Eohippus* to *Hypohippus,* for example, exemplifies a fairly continuous phyletic evolution" (p. 217). Simpson especially emphasizes the supposedly gradual and continuous transformation from *Mesohippus* to *Miohippus* near the top of this sequence:

> The more progressive horses of the middle Oligocene and all the horses of the late Oligocene are placed by convention in a separate genus, *Miohippus.* In fact *Mesohippus* and *Miohippus* intergrade so perfectly and the differences between them are so slight and variable that even experts find it difficult, at times nearly impossible, to distinguish them clearly.

The enormous expansion of collections since Simpson proposed this hypothesis has permitted a test by vertebrate paleontologists Don Prothero and Neil Shubin. Their results falsify Simpson's gradual and linear sequence for the early stages of horse evolution and introduce extensive bushiness into this last stronghold of the ladder.

Prothero and Shubin have made four major discoveries in the crucial segment of history that Simpson designated as the strongest case for a gradualistic sequence of lineal transformation—the transition from *Mesohippus* to *Miohippus.*

1. Previous experts were so convinced about the imperceptibly gradual transition between these two genera that they declared any search for distinguishing characters as vain, and arbitrarily drew the division between *Mesohippus* and *Miohippus* at a stratigraphic boundary. But far richer material available to Prothero and Shubin has permitted the identification of characters that cleanly distinguish the two genera. (Teeth are the hardest part of a vertebrate skeleton and the fossil record of mammals often contains little else. A technical course in the evolution of mammals is largely an exercise in the identification of teeth, and an old professional quip holds that mammalian evolution is the interbreeding of two sets of teeth to produce some slightly modified descendant choppers. *Miohippus* and *Mesohippus* do not have distinctive dentitions, and previous failure to find a clear separation should not surprise us. The new material is rich in skull and limb bones.) In particular, Prothero and Shubin found that *Miohippus* develops a distinctive articulation, absent in ancestral *Mesohippus,* between the enlarging third metatarsal (the foot bone of the digit that will become the entire hoof of modern horses) and the cuboid bone of the tarsus (ankle) above.

2. *Mesohippus* does not turn into *Miohippus* by insensible degrees of gradual transition. Rather, *Miohippus* arises by branching from a *Mesohippus* stock that continues to survive long afterward. The two genera overlap in time by at least 4 million years.

3. Each genus is itself a bush of several related species, not a rung on a ladder of progress. These species often lived and interacted in the same area at the same time (as different species of zebra do in Africa today). One set of strata in Wyoming, for example, has yielded three species of *Mesohippus* and two of *Miohippus,* all contemporaries.

4. The species of these bushes tend to arise with geological suddenness, and then to persist with little change for long periods. Evolutionary change occurs at the branch points themselves, and trends are not continuous marches up ladders, but concatenations of increments achieved at nodes of branching on evolutionary bushes. Of this phenomenon Prothero and Shubin write:

> There is no evidence of long-term changes within these well-defined species [of *Mesohippus* and *Mwhippus]* through time. Instead, they are strikingly static through millions of years. Such stasis is apparent in most Neogene [later] horses as well, and in *Hyracotherium.* This is contrary to the widely-held myth about horse species as gradualistically-varying parts of a continuum, with no real distinctions between species. Throughout the history of horses, the species are well-marked and static over millions of years. At high resolution, the gradualistic picture of horse evolution becomes a complex bush of overlapping, closely related species.

Bushiness now pervades the entire phylogeny of horses.

We can appreciate this fundamental shift in iconography and meaning, but where is the "precious irony" that I promised? What is "life's little joke" of my title? Simply this. The model of the ladder is much more than merely wrong. It never could provide the promised illustration of evolution progressive and triumphant— for *it could only be applied to unsuccessful lineages.*

Bushes represent the proper topology of evolution. Ladders are false abstractions, made by running a steamroller over a labyrinthine pathway that hops from branch to branch through a phylogenetic bush. We cannot force a successful bush of evolution into a ladder because we may follow a thousand pathways through the maze of twigs, and we cannot find a criterion for preferring one route over another. Who ever heard of the evolutionary trend of rodents or of bats or of antelopes? Yet these are the greatest success stories in the history of mammals. Our proudest cases do not become our classic illustrations because we can draw no ladder of progress through a vigorous bush with hundreds of surviving twigs.

But consider the poor horses. Theirs was once a luxuriant bush, yet they barely survive today. Only one twig (the genus *Equus,* with horses, zebras, and asses) now carries all the heritage of a group that once dominated the history of hoofed mammals—and with fragility at that, for *Equus* died in the land of its birth and had to be salvaged from a stock that had migrated elsewhere. (In a larger sense, horses form one of three dwindling lines—tapirs and rhinos are the others—that now represent all the diversity of the formerly dominant order Perissodactyla, or odd-toed ungulates, among hoofed mammals. This mighty group once included the giant titanotheres, the clawed chalicotheres, and *Balurhitherium,* the largest land mammal that ever lived. It now hangs on as a remnant in a world increasingly dominated by the Artiodactyla, or even-toed ungulates—cows, deer, antelope, camels, hippos, giraffes, pigs, and their relatives.)

This is life's little joke. By imposing the model of the ladder upon the reality of bushes, we have guaranteed that our classic examples of evolutionary progress can only apply to unsuccessful lineages on the very brink of extermination—for we can linearize a bush only if it maintains but one surviving twig that we can falsely place at the summit of a ladder. I need hardly remind everybody that at least one other mammalian lineage, preeminent among all in our attention and concern, shares with horses the sorry state of reduction from a formerly luxuriant bush to a single surviving twig—the very property of extreme tenuousness that permits us to build a ladder reaching only to the heart of our own folly and hubris.

Literary Bias on the Slippery Slope

EVERY PROFESSION has its version: Some speak of "Sod's law"; others of "Murphy's law." The formulations vary, but all make the same point—if anything bad can happen, it will. Such universality of attribution can only arise for one reason—the principle is true (even though we know that it isn't).

The fieldworker's version is simply stated: You always find the most interesting specimens at the very last moment, just when you absolutely must leave. The effect of this phenomenon can easily be quantified. It operates weakly for localities near home and easily revisited and ever more strongly for distant and exotic regions requiring great effort and expense for future expeditions. Everyone has experienced this law of nature. I once spent two weeks on Great Abaco, visiting every nook and cranny of the island and assiduously proving that two supposed species of *Cerion* (my favorite land snail) really belonged to one variable group. On the last morning, as the plane began to load, we drove to the only unexamined place, an isolated corner of the island with the improbable name Hole-in-the-Wall. There we found hundreds of large white snails, members of the second species.

Each profession treasures a classic, or canonical, version of the basic story. The paleontological "standard," known to all my colleagues as a favorite campfire tale and anecdote for introductory classes, achieves its top billing by joining the most famous geologist of his era with the most important fossils of any time. The story, I have just discovered, is also entirely false (more than a bit embarrassing since I cited the usual version to begin an earlier essay in this series).

Charles Doolittle Walcott (1850-1927) was both the world's leading expert on Cambrian rocks and fossils (the crucial time for the initial flowering of multicellular life) and the most powerful scientific administrator in America. Walcott, who knew every president from Teddy Roosevelt to Calvin Coolidge, and who persuaded Andrew Carnegie to establish the Carnegie Institute of Washington, had little formal education and began his career as a fieldworker for the United States Geological Survey. He rose to chief, and resigned in 1907 to become secretary (their name for boss) of the Smithsonian Institution. Walcott had his finger, more accurately his fist, in every important scientific pot in Washington.

Walcott loved the Canadian Rockies and, continuing well into his seventies, spent nearly every summer in tents and on horseback, collecting fossils and indulging his favorite hobby of panoramic photography. In 1909, Walcott made his greatest discovery in Middle Cambrian rocks exposed on the western flank of the ridge connecting Mount Field and Mount Wapta in eastern British Columbia.

The fossil record is, almost exclusively, a tale told by the hard parts of organisms. Soft anatomy quickly disaggregates and decays, leaving bones and shells behind. For two basic reasons, we cannot gain an adequate appreciation for the full range of ancient life from these usual remains. First, most organisms contain no hard parts at all, and we miss them entirely. Second, hard parts, especially superficial coverings, often tell us very little about the animal within or underneath. What could you learn about the anatomy of a snail from the shell alone?

Paleontologists therefore treasure the exceedingly rare soft-bodied faunas occasionally preserved when a series of unusual circumstances coincide—rapid burial, oxygen-free environments devoid of bacteria or scavengers, and little subsequent disturbance of sediments.

Walcott's 1909 discovery—called the Burgess Shale—surpasses all others in significance because he found an exquisite fauna of soft-bodied organisms from the most crucial of all times. About 570 million years ago, virtually all modern phyla of animals made their first appearance in an episode called "the Cambrian explosion" to honor its geological rapidity. The Burgess

Shale dates from a time just afterward and offers our only insight into the true range of diversity generated by this most prolific of all evolutionary events.

Walcott, committed to a conventional view of slow and steady progress in increasing complexity and diversity, completely misinterpreted the Burgess animals. He shoehorned them all into modern groups, interpreting the entire fauna as a set of simpler precursors for later forms. A comprehensive restudy during the past twenty years has inverted Walcott's view and taught us the most surprising thing we know about the history of life: The fossils from this one small quarry in British Columbia exceed, in anatomical diversity, all modern organisms in the world's oceans today. Some fifteen to twenty Burgess creatures cannot be placed into any modern phylum and represent unique forms of life, failed experiments in metazoan design. Within known groups, the Burgess range far exceeds what prevails today. Taxonomists have described almost a million living species of arthropods, but all can be placed into three great groups—insects and their relatives, spiders and their kin, and crustaceans. In Walcott's single Canadian quarry, vastly fewer species include about twenty more basic anatomical designs! The history of life is a tale of decimation and later stabilization of few surviving anatomies, not a story of steady expansion and progress.

But this is another story for another time (see my book *Wonderful Life,* 1989). I provide this epitome only to emphasize the context for paleontology's classic instance of Sod's law. These are no ordinary fossils, and their discoverer was no ordinary man.

I can provide no better narration for the usual version than the basic source itself—the obituary notice for Walcott published by his longtime friend and former research assistant Charles Schuchert, professor of paleontology at Yale. (Schuchert was, by then, the most powerful paleontologist in America, and Yale became the leading center of training for academic paleontology. The same story is told far and wide in basically similar versions, but I suspect that Schuchert was the primary source for canonization and spread. I first learned the tale from my thesis adviser, Norman D. Newell. He heard it from his adviser, Carl Dunbar, also at Yale, who got it directly from Schuchert.) Schuchert wrote in 1928:

> One of the most striking of Walcott's faunal discoveries came at the end of the field season of 1909, when Mrs. Walcott's horse slid in going down the trail and turned up a slab that at once attracted her husband's attention. Here was a great treasure—wholly strange Crustacea of Middle Cambrian time—but where in the mountain was the mother rock from which the slab had come? Snow was even then falling, and the solving of the riddle had to be left to another season, but next year the Walcotts were back again on Mount Wapta, and eventually the slab was traced to a layer of shale—later called the Burgess shale—3,000 feet above the town of Field, British Columbia, and 8,000 feet above the sea.

Stories are subject to a kind of natural selection. As they propagate in the retelling and mutate by embellishment, most eventually fall by the wayside to extinction from public consciousness. The few survivors hang tough because they speak to deeper themes that stir our souls or tickle our funnybones. The Burgess legend is a particularly good story because it moves from tension to resolution, and enfolds within its basically simple structure two of the greatest themes in conventional narration—serendipity and industry leading to its just reward. We would never have known about the Burgess if Mrs. Walcott's horse hadn't slipped going downslope on the very last day of the field season (as night descended and snow fell, to provide a dramatic backdrop of last-minute chanciness). So Walcott bides his time for a year in considerable anxiety. But he is a good geologist and knows how to find his quarry (literally in this case). He returns the next summer and finally locates the Burgess Shale by hard work and geological skill. He starts with the dislodged block and traces it patiently upslope until he finds the mother lode. Schuchert doesn't mention a time, but most versions state that Walcott spent a week or more trying to locate the source. Walcott's son Sidney, reminiscing sixty years later, wrote in 1971: "We worked our way up, trying to find the bed of rock from which our original find had been dislodged. A week later and some 750 feet higher we decided that we had found the site."

I can imagine two basic reasons for the survival and propagation of this canonical story. First, it is simply too good a tale to pass into oblivion. When both good luck and honest labor combine to produce victory, we all feel grateful to discover that fortune occasionally smiles, and uplifted to learn that effort brings reward. Second, the story might be true. And if dramatic and factual value actually coincide, then we have a real winner.

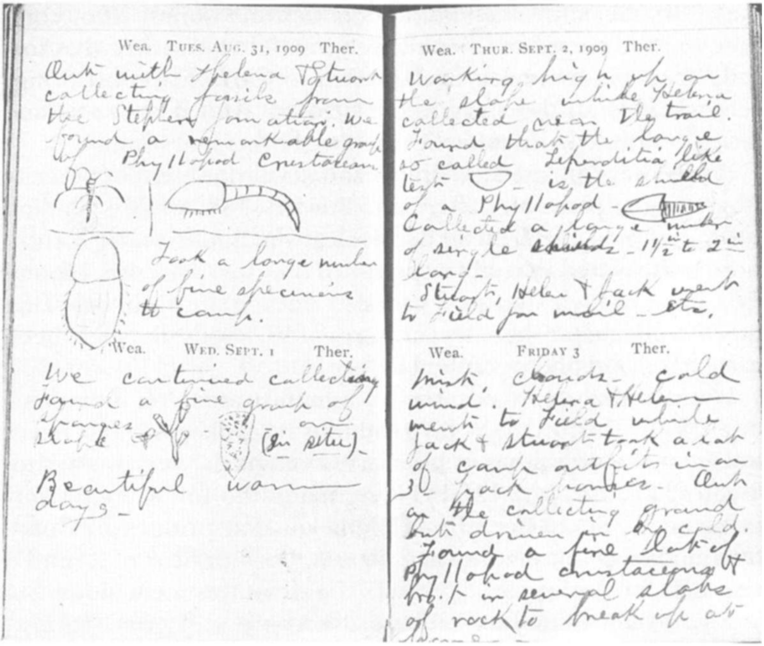
I had alwav s grasped the drama and never doubled the veracity (the story is plausible, after all). But in 1988, while spending several days in the Walcott archives at the Smithsonian Institution, I discovered that all key points of the story are false. I found that some of my colleagues had also tracked down the smoking gun before me, for the relevant pages of Walcott's diary had been earmarked and photographed before.

Walcott, the great conservative administrator, left a precious gift to future historians by his assiduous recordkeeping. He never missed a day of writing in his diary. Even at the very worst moment of his life, July 11, 1911, he made the following, crisply factual entry about his wife: "Helena killed at Bridgeport Conn, by train being smashed up at 2:30 **A.M**. Did not hear of it until 3 **P.M**. Left for Bridgeport 5:35 **P.M**." (Walcott was meticulous, but please do not think him callous. Overcome with grief the next day, he wrote on July 12: "My love—my wife—my comrade for 24 years. I thank God I had her for that time. Her untimely fate I cannot now understand.")

Walcott's diary for the close of the 1909 field season neatly dismisses part one of the canonical tale. Walcott found the first soft-bodied fossils on Burgess ridge either on August 30 or 31. His entry for August 30 reads:

> Out collecting on the Stephen formation [the unit that includes what Walcott later called the Burgess Shale] all day. Found many interesting fossils on the west slope of the ridge between Mounts Field and Wapta [the right locality for the Burgess Shale]. Helena, Helen, Arthur, and Stuart [his wife, daughter, assistant, and son] came up with remainder of outfit at 4 **P.M.**

On the next day, they had clearly discovered a rich assemblage of soft-bodied fossils. Walcott's quick sketches (see figure) are so clear that I can identify the three genera he depicts—*Marrella* (upper left), the most common Burgess fossil and one of the



Wea. TUES. AUG. 31, 1909 Ther.
Out with Helena & Stuart
collecting fossils from
the Stephen formation. We
found a remarkable group
of Phyllopod Crustaceans
Took a large number
of fine specimens
to camp.

Wea. WED. SEPT. 1 Ther.
We continued collecting
found a fine group of
sponges on
slope & - (in situ) -
Beautiful warm
days -

Wea. THUR. SEPT. 2, 1909 Ther.
Working high up on
the slope while Helena
collected near the trail.
Found that the large
so called Lepeditia like
test - is the shield
of a Phyllopod -
Collected a large number
of single shields - 1½ in to 2 in
long -
Stuart, Helen & Jack went
to Field for mail - etc.

Wea. FRIDAY 3 Ther.
Mist, clouds - cold
wind. Helena & Helen
went to Field while
Jack & Stuart took a lot
of camp outfits in an
30 pack [illegible]. Out
on the collecting ground
but driven in by cold.
Found a fine lot of
Phyllopod crustaceans &
brt. in several slabs
of rock to break up at
[illegible]

The smoking gun for exploding a Burgess Shale legend. Walcott's diary for the end of August and the beginning of September, 1909. He collected for an entire week in good weather. SMITHSONIAN INSTITUTION.

unique arthropods beyond the range of modern designs; *H'aptia,* a bivalved arthropod (upper right); and the peculiar trilobite *Naraoia* (lower left). Walcott wrote: "Out with Helena and Stuart collecting fossils from the Stephen formation. We found a remarkable group of Phyllopod crustaceans. Took a large number of fine specimens to camp."

What about the horse slipping and the snow falling? If this incident occurred at all, we must mark the date as August 30, when Walcott's family came up the slope to meet him in the late afternoon. They might have turned up the slab as they descended for the night, returning the next morning to find the specimens that Walcott drew on August 31. This reconstruction gains some support from a letter that Walcott wrote to Marr (for whom he later named the "lace crab" *Mairella)* in October 1909:

> When we were collecting from the Middle Cambrian, a stray slab of shale brought down by a snow slide showed a fine Phyllopod crustacean on a broken edge. Mrs. W. and I worked on that slab from 8 in the morning until 6 in the evening and took back with us the finest collection of Phyllopod crustaceans that I have ever seen.

(Phyllopod, or "leaf-footed," is an old name for marine arthropods with rows of lac\ '_;ills. often used for swimming, on one branch of their legs.)

Transformation can be subtle. A snow slide becomes a snowstorm, and the night before a happy day in the field becomes a forced and hurried end to an entire season. But far more important, Walcott's field season did not finish with the discoveries of August 30 and 31. The party remained on Burgess ridge until September 7! Walcott was thrilled by his discovery and collected with avidity every day thereafter. The diaries breathe not a single word about snow, and Walcott assiduously reported the weather in every entry. His happy week brought nothing but praise for Mother Nature. On September 1 he wrote: "Beautiful warm days."

Finally, I strongly suspect that Walcott located the source for his stray block during the last week of his 1909 field season—at least the basic area of outcrop, if not the very richest layers. On September 1, the day after he drew the three arthropods, Walcott wrote: "We continued collecting. Found a fine group of sponges on slope (in *situ)* [meaning undisturbed and in their original position]." Sponges, containing some hard parts, extend beyond the richest layers of soft-bodied preservation, but the best specimens come from the strata of the Burgess mother lode. On each subsequent day, Walcott found abundant soft-bodied specimens, and his descriptions do not read like the work of a man encountering a lucky stray block here and there. On September 2, he discovers that the supposed shell of an ostracode really houses the body of a Phyllopod: "Working high up on the slope while Helena collected near the trail. Found that the large so-called Leperditia-like test is the shield of a Phyllopod." The Burgess quarry is "high up on the slope," while stray blocks would slide down toward the trail.

On September 3, Walcott was even more successful: "Found a fine lot of Phyllopod crustaceans and brought in several slabs of rock to break up at camp." In any event, he continued to collect, and put in a full day for his last hurrah on September 7: "With Stuart and Mr. Rutter went up on fossil beds. Out from 7 A.M. to 6:30 P.M. Our last day in camp for 1909."

If I am right about his discovery of the main beds in 1909, then the second part of the canonical tale—the week-long patient tracing of errant block to source in 1910—should be equally false. Walcott's diary for 1910 supports my interpretation. On July 10, champing at the bit, he hiked up to the Burgess Pass campground, but found the area too deep in snow for any excavations. Finally, on July 29, Walcott reports that his party set up "at Burgess Pass campground of 1909." On July 30, they climbed neighboring Mount Field and collected fossils. Walcott indicates that they made their first attempt to locale the Burgess beds on August 1:

> All out collecting the Burgess formation until 4 P.M. when a cold wind and rain drove us into camp. Measured section of the Burgess formation—420 feet thick. Sidney with me. Stuart with his mother and Helen puttering about camp.

("Measuring a section" is geological jargon for tracing the vertical sequence of strata and noting the rock types and fossils. If you wished to find the source of an errant block dislodged and tumbled below, you would measure the section above, trying to match your block to its most likely layer.)

I think that Charles and Sidney Walcott located the Burgess beds on this very first day, because Walcott writes for his next entry of August 2: "Out collecting with Helena, Stuart, and Sidney. We found a fine lot of 'lace crabs' and various odds and ends of things." "Lace crab" was Walcott's informal field term for *Marrella,* and *Marrella* is the marker of the mother lode—the most common animal in the Burgess Shale. If we wish to give the canonical tale all benefit of doubt, and argue that these lace crabs of August 2 came from dislodged blocks, we still cannot grant a week of strenuous effort for locating the mother lode, for Walcott writes just two days later on August 4: "Helena worked out a lot of Phyllopod crustaceans from 'Lace Crab layer.' " From then on, until the end of summer, they quarried the lace crab layer, now known as the Burgess Shale.

The canonical tale is more romantic and inspiring, but the plain facluality of the diary makes more sense. I have been to the Burgess ridge. The trail lies just a few hundred feet below the main Burgess beds. The slope is simple and steep, with strata well exposed. Tracing an errant block to its source should not have presented a major problem—for Walcott was more than a good geologist; he was a great geologist. He should have located the main beds right away, in 1909, since he had a week to work after first discovering soft-bodied fossils. He was not able to quarry in 1909—the only constraint imposed by limits of time. But he found many fine fossils and probably the main beds themselves. He knew just where to go in 1910 and set up shop in the right place as soon as the snows melted.

Memory is a fascinating trickster. Words and images have enormous power and can easily displace actual experience over the years. As an intriguing testimony to the power of legend, consider the late memories of Walcott's son Sidney. In 1971, more than sixty years after the events, Sidney wrote a short article for *Smithsonian,* "How I Found My Own Fossil." (The largest Burgess arthropod bears the name *Sidneyia inexpectans* in honor of his discovery.) Sidney must have heard the canonical tale over and over again across the many years (think of him enduring mounds of rubber chicken and endless repetitions of the anecdote in after-dinner speeches)—and his actual experience faded as the conventional myth took root.

Sidney's version includes the two main ingredients—serendipity in the chance discovery of a dislodged slab blocking the pathway of packhorses, and assiduous effort in the patient, week-long tracing of block to source. But Sidney places the packhorse incident on his watch in 1910, not on his mother's the previous year:

> Father suddenly told me to halt the packlrain. I signaled, and the horses started to browse at the side of the trail. Often on our summer camping trips I had seen Father throw stones and logs out of the trail to make the going a bit easier for the horses. So it was no surprise to see him upend a slab, worn white by the shoes of horses slipping on it for

> years. He hit it a few times along its edge with his geological hammer and it split open. "Look Sidney," he called. I saw several extraordinary fossils on the rock surface. "Let's look further tomorrow. . . . We won't go to Field tonight." To our family, back in 1910, it seemed a miracle that Father's simple act of thoughtfulness for the comfort and safety of a few packhorses led to this discovery.

A lovely story, but absolutely nothing about it can be true. Sidney knew the canonical yarn about slabs and packhorses, but moved the tale a year forward. We cannot believe that slabs could have blocked paths for two years running, with fossils always on their upturned edges, especially since an unanticipated discovery in 1909 precludes a similar surprise the next year. Moreover, Sidney could not have remembered an actual incident of the first season, and then mixed up the years, because he wasn't there in 1909!

Sidney's second ingredient, his tale of a week-long search for the mother lode (cited previously in this essay), is equally false from the evidence of Walcott's diary, and similarly read into memory from the repetition of legend, not the recall of actual events.

Why am I bothering with all this detail? To be sure, truth has a certain moral edge over falsehood, but few people care much about corrections to stories they never heard about people they never knew. If the only lesson in this little reversal of Burgess orthodoxy exhorts us to be careful lest a tendency to embellish or romanticize stifle the weakly flickering flame of truth, then this essay is as banal as the sentence I just wrote. But I would defend my effort on two grounds. First, the Burgess animals happen to be the world's most important fossils, and the purely factual issues surrounding their discovery therefore demand more than the usual care and attention to accuracy. We might not challenge a family legend about Uncle Joe in the interests of domestic peace and benevolence, but we really would like to know how Jesus lived and died because different views have had such palpable effects upon billions of lives. Second, I believe that our tendencies to construct legends raise an issue far more interesting than watchdog warnings about eternal verity.

I would begin by asking why almost every canonical tale is false in the same way—a less interesting reality converted to a simple story with a message. Do we need these stories so badly because life isn't heroic or thrilling most of the time? Sean O'Casey said that the stage must be larger than life, and few poets or playwrights can succeed by fidelity to the commonplace. It takes the artistry of James Joyce to make a masterpiece from one day in the life of an ordinary man. Most of our existence is eating, sleeping, walking, and breathing. Even the life of a soldier, if expressed in real time, would be almost uninterrupted tedium—for an old motto identifies this profession as long periods of boredom interspersed with short moments of terror.

Astute scientists understand that political and cultural bias must impact their ideas, and they strive to recognize these inevitable influences. But we usually fail to acknowledge another source of error that might be called literary bias. So much of science proceeds by telling stories—and we are especially vulnerable to constraints of this medium because we so rarely recognize what we are doing. We think that we are reading nature by applying rules of logic and laws of matter to our observations. But we are often telling stories—in the good sense, but stories nonetheless. Consider the traditional scenarios of human evolution—tales of the hunt, of campfires, dark caves, rituals, and toolmaking, coming of age, struggle and death. How much is based on bones and artifacts and how much on the norms of literature?

If these reconstructions are stories, then they are bound by the rules of canonical legendmaking. And if we construct our stories to be *unlike* life—the main point of this essay—then our literary propensities are probably derailing our hope to understand the quotidian reality of our evolution. Stories only go in certain ways—and these paths do not conform to patterns of actual life.

This constraint does not apply only to something so clearly ripe for narration and close to home as "the rise of man from the apes" (to choose a storylike description that enfolds biases of gender and progress into its conventionality). Even the most distant and abstract subjects, like the formation of the universe or the principles of evolution, fall within the bounds of necessary narrative. Our images of evolution are caught in the web of tale telling. They involve progress, pageant; above all, ceaseless motion somewhere. Even revisionist stories that question ideas of gradual progress—the sort that I have been spinning for years in these essays—are tales of another kind about good fortune, unpredictability, and contingency (the kingdom lost for want of a horseshoe nail). But focus on almost any evolutionary moment, and nothing much is happening. Evolution, like soldiering and life itself, is daily repetition almost all the time. Evolutionary days may be generations, but as the Preacher said, one passeth away and another cometh, but the earth abideth forever. The fullness of time, of course, does provide a sufficient range for picking out rare moments of activity and linking them together into a story. But we must understand that nothing happens most of the time—and we don't because our stories don't admit this theme—if we hope to grasp the dynamics of evolutionary change. (This sentence may sound contradictory, but it isn't. To know the reasons for infrequent change, one must understand the ordinary rules of stability.) The Burgess Shale teaches us that, for the history of basic anatomical designs, almost everything happened in the geological moment just before, and almost nothing in more than 500 million years since.

Included in this "almost nothing," as a kind of geological afterthought of the last few million years, is the first development of self-conscious intelligence on this planet—an odd and unpredictable invention of a little twig on the mammalian evolutionary bush. Any definition of this uniqueness, embedded as it is in our possession of language, must involve our ability to frame the world as stories and to transmit these tales to others. If our propensity to grasp nature as story has distorted our perceptions, I shall accept this limit of mentality upon knowledge, for we receive in trade both the joys of literature and the core of our being.

Glow, Big Glowworm

SMALL MISUNDERSTANDINGS are often a prod to insight or victory. For such a minor error with major consequences, Laurel and Hardy got into terminal trouble with the toymaster in *March of the Wooden Soldiers*—they got fired for building 100 soldiers six feet high, when Santa had ordered 600 at one foot. But the six-footers later saved Toyland from the invasion of Barnaby and his bogeymen.

In insects that undergo a complete metamorphosis, cells that will form adult tissues are already present in the bodies of larvae as isolated patches called imaginal disks. For many years, I regarded this term as one of the oddest in all biology—for I always read "imaginal" as "imaginary" and thought I was being told that this substrate of maturity really didn't exist at all.

When I learned the true origin of this term, I realized that I had not only misunderstood but had made an absolutely backward interpretation. I also discovered thai my resolution had taught me something interesting—about ways of looking at the world, not about any fads of nature per se—and I therefore judged my former error as fruitful.

Linnaeus himself, father of taxonomy, named the stages of insect development. He designated the feeding stage that hatched from the egg as a larva (the caterpillar of a moth or the maggot of a housefly), and he called the sexually mature adult an imago, hence imaginal disk for precursors of adult tissues within the larva.

The etymologies of these terms provided my insight—a larva is a mask; an imago, the image or essential form of a species. Linnaeus, in other words, viewed the development of insects as progress toward fulfillment. The first stage is only preparatory; it hides the true and complete representation of a species. The final form embodies the essence of louseness, thripsness, or flyness. Imaginal disks, by both etymology and concept, are bits of higher reality lurking within initial imperfection—no sign of "let's pretend" here.

Most impediments to scientific understanding are conceptual locks, not factual lacks. Most difficult to dislodge are those biases that escape our scrutiny because they seem so obviously, even ineluctably, just. We know ourselves best and tend to view other creatures as mirrors of our own constitution and social arrangements. (Aristotle, and nearly two millennia of successors, designated the large bee that leads the swarm as a king.)

Few aspects of human existence are more basic than our life cycle of growth and development. For all the glories of childhood, we in the West have generally viewed our youngsters as undeveloped and imperfect adults—smaller, weaker, and more ignorant. Adulthood is a termination; childhood, an upward path. How natural, then, that we should also interpret the life cycles of other organisms as a linear path from imperfect potential to final realization—from the small, ill-formed creature that first develops from an egg to the large and complex fruition that produces the egg of the next generation.

How obvious, in particular, that insect larvae are imperfect juveniles and imagoes realized adults. Linnaeus's etymology embodies this traditional interpretation imposed from human life upon the development of insects. When we combine this dubious comparison of human and insect life cycles with our more general preference for viewing developmental sequences as ladders of progress (a prejudice that has hampered our understanding of evolution even more than our resolution of embryology), insect larvae seem doomed to easy dismissal by an aggregation of biases—etymological, conceptual, and parochial.

If we turn to two leading works of popular science, published five years after Darwin's *Origin of Species*—one on life cycles in general, the other on insects—we obtain a good sense of these traditional biases. A. de Quatrefages, great French student of that economic leader among insect larvae, the silkworm, wrote in his *Metamorphosis of Man and the Lower Animals* (1864) that "larvae . . . are always incomplete beings; they are true first sketches, which are rendered more and more perfect at each developmental phase."

An Introduction to Entomology, by William Kirby, rector of Barham, and William Spence, wins first prize among British works of popular science for celebrity, for longevity (its first edition appeared in 1815), and for prose in the most preciously purple tradition of "nature writing," as satirized by example in James Joyce's *Ulysses:* "Note the meanderings of some purling rill as it babbles on its way, fanned by the gentlest zephyrs tho' quarrelling with the stony obstacles, to the tumbling waters of Neptune's blue domain. . . ." To which, Mr. Dedalus replies: "Agonizing Christ, wouldn't it give you a heartburn on your arse." And for which (among other things) *Ulysses* was once banned from the United Slates as obscene—although I would sooner exclude that purling rill than a heartburn on any part of the anatomy.

In their first post-Darwinian edition (1863), Kirby and Spence make no bones about their preference for well-formed imagoes and their distaste for grubby larvae (a redundancy for emphasis of my point—grubs are larvae, and we owe this adjective to the same prejudice):

> That active little fly, now an unbidden guest at your table, whose delicate palate selects your choicest viands, while extending his proboscis to the margin of a drop of wine, and then gaily flying to take a more solid repast from a pear or peach; now gamboling with his comrades in the air, now gracefully currying his furled wings with his taper feet, was but the other day a disgusting grub, without wings, without legs, without eyes, wallowing, well pleased, in the midst of a mass of excrement.

The adult, they write, is called an imago "because, having laid aside its mask [larva), and cast off its swaddling bands [the pupal cocoon, or chrysalis], being no longer disguised [larva] or confined [pupa), or in any other respect imperfect, it is now become a true representative or image of its species."

The burden of metaphor becomes immeasurably heavier for larvae when Kirby and Spence then drag out that oldest of all insect analogies from an age of more pervasive Christianity—the life cycle of a butterfly to the passage of a soul from first life in the imperfect prison of a human body (larval caterpillar), to death and entombment (pupal chrysalis), to the winged freedom of resurrection (imago, or butterfly). This simile dates to the great Dutch biologist Jan Swammerdam, child of Cartesian rationalism but also, at heart, a religious mystic, who first discovered the rudimentary wings of butterflies, enfurled in late stages of larval caterpillars. Swammerdam wrote near the end of the seventeenth century: "This process is formed in so remarkable a manner in butterflies, that we see therein the resurrection painted before our eyes, and exemplified so as to be examined by our hands." Kirby and Spence then elaborated just a bit:

> To see a caterpillar crawling upon the earth sustained by the most ordinary kinds of food, which when . . . its appointed work being finished, passes into an intermediate state of seeming death, when it is wound up in a kind of shroud and encased in a coffin, and is most commonly buried under the earth . . . then, when called by the warmth of the solar beam, they burst from their sepulchres, cast off their raiments . . . come forth as a bride out of her chamber—to survey them, I say, arrayed in their nuptial glory, prepared to enjoy a new and more exalted condition of life, in which all their powers are developed, and they are arrived at the perfection of their nature . . . who that witnesses this interesting scene can help seeing in it a lively representation of man in his threefold state of existence. . . .The butterfly, the representative of the soul, is prepared in the larva for its future state of glory; . . . it will come to its state of repose in the pupa, which is its Hades; and at length, when it assumes the imago, break forth with new powers and beauty to its final glory and the reign of love.

But must we follow this tradition and view larvae as harbingers of better things? Must all life cycles be conceptualized as paths of progress leading to an adult form? Human adults control the world's media—and the restriction of this power to one stage of our life cycle imposes a myopic view. I would be happy to counter this prejudice (as many have) by emphasizing the creativity and specialness of human childhood, but this essay speaks for insects.

I will admit that our standard prejudice applies, in one sense, to creatures like ourselves. Our bodies do grow and transform in continuity. A human adult is an enlarged version of its own childhood; we grown-ups retain the same organs, reshaped a bit and often increased a great deal. (Many insects with simple life cycles, or so-called incomplete metamorphoses, also grow in continuity. This essay treats those insects that cycle through the classic stages of complete metamorphosis: egg, larva, pupa, and imago.)

But how can we apply this bias of the upward path to complex life cycles of other creatures? In what sense is the polyp of a cnidarian (the phylum of corals and their allies) more—or less—complete than the medusa that buds from its body? One stage feeds and grows; the other mates and lays eggs. They perform different and equally necessary functions. What else can one say? Insect larvae and imagoes perform the same division—larvae eat and imagoes reproduce. Moreover, larvae do not grow into imagoes by increase and complication of parts. Instead, larval tissues are sloughed off and destroyed during the pupal stage, while the imago largely develops from small aggregations of cells—the imaginal disks of this essay's beginning—that resided, but did not differentiate, within the larva. Degenerating larval tissues are often used as a culture medium for growth of the imago within the pupa. Larva and imago are different and discrete, not before and shadowy versus later and complete.

Even Kirby and Spence sensed this true distinction between objects equally well suited for feeding and reproduction, though they soon buried their insight in cascading metaphors about progress and resurrection:

> Were you ... to compare the internal conformation of the caterpillar with that of the butterfly, you would witness changes even more extraordinary. In the former you would find some thousands of muscles, which in the latter are replaced by others of a form and structure entirely different. Nearly the whole body of the caterpillar is occupied by a capacious stomach. In the butterfly it has become converted into an almost imperceptible thread-like viscus; and the abdomen is now filled by two large packets of eggs.

If we break through the tyranny of our usual bias, to a different view of larvae and imagoes as separate and potentially equal devices for feeding and reproduction, many puzzles are immediately resolved. Each stage adapts in its own way, and depending upon ecology and environment, one might be emphasized, the other degraded to insignificance in our limited eyes. The "degraded" stage might be the imago as well as the larva—more likely, in fact, since feeding and growth can be rushed only so much, but mating, as poets proclaim, can be one enchanted evening. Thus, I used to feel sorry for the mayfly and its legendary one day of existence, but such brevity only haunts the imago, and longer-lived larvae also count in the total cycle of life. And what about the seventeen-year "locust" (actually a cicada)? Larvae don't lie around doing nothing during this dog's age, waiting patiently for their few days of visible glory. They have an active-life underground, including long stretches of dormancy to be sure, but also active growth through numerous molts.

Thus, we find our best examples of an alternative and expansive view of life cycles among species that emphasize the size, length, and complexity of larval life at the apparent expense of imaginal domination—where, to borrow Butler's famous line with only minor change in context, a hen really does seem to be the egg's way of manufacturing another egg. I recently encountered a fine case during a visit to New Zealand—made all the more dramatic because human perceptions focus entirely upon the larva and ignore the imago.

After you leave the smoking and steaming, the boiling and puffing, the sulfurous stench of geysers, fumaroles, and mud pots around Rotorua, you arrive at the second best site on the standard tourist itinerary of the North Island—the glowworm grotto of Waitomo Cave. Here, in utter silence, you glide by boat into a spectacular underground planetarium, an amphitheater lit with thousands of green dots—each the illuminated rear end of a fly larva (not a worm at all). (I was dazzled by the effect because I found it so unlike the heavens. Stars are arrayed in the sky at random with respect to the earth's position. Hence, we view them as clumped into constellations. This may sound paradoxical, but my statement reflects a proper and unappreciated aspect of random distributions. Evenly spaced dots are well ordered for cause. Random arrays always include some clumping, just as we will flip several heads in a row quite often so long as we can make enough tosses—and our sky is not wanting for stars. The glowworms, on the other hand, are spaced more evenly because larvae compete with, and even eat, each other—and each constructs an exclusive territory. The glowworm grotto is an ordered heaven.)

These larval glowworms are profoundly modified members of the family Mycetophilidae, or fungus gnats. Imagoes of this species are unremarkable, but the larvae rank among the earth's most curious creatures. Two larval traits (and nothing imaginal) inspired the name for this peculiar species—*Arachnocampa luminosa,* honoring both the light and the silken nest that both houses the glowworm and traps its prey (for Arachne the weaver, namesake of spiders, or arachnids, as well). The imagoes of *Arachnocampa luminosa* are small and short-lived mating machines. The much larger and longer-lived larvae have evolved three complex and coordinated adaptations—carnivory, light, and webbing—that distinguish them from the simpler larval habits of ancestral fungus gnats: burrowing into mushrooms, munching all the way.

In a total life cycle (egg to egg) often lasting eleven months, *Arachnocampa luminosa* spends eight to nine months as a larval glowworm. Larvae molt four times and grow from 3- to 5-millimeter hatchlings to a final length of some 30 to 40 millimeters. (By contrast, imagoes are 12 to 16 millimeters in length, males slightly smaller than females, and live but one to four days, males usually longer than females.)

Carnivory is the focus of larval existence, the coordinating theme behind a life-style so different from the normal course of larval herbivory in fungus gnats. Consider the three principal ingredients:

Luminescence: The light organ of *A. luminosa* forms at the rear end of the larva from enlarged tips of four excretory tubes. These tubes carry a waste product that glows in the presence of luciferase, an enzyme also produced by the larva. This reaction requires a good supply of oxygen, and the four excretory tubes lie embedded in a dense network of respiratory tubules that both supply oxygen to fuel the reaction and then reflect and direct the light downward. This complex and specially evolved system functions to attract insects (mostly small midges) to the nest. Pupae and imagoes retain the ability to luminesce. The light of female pupae and adults attracts males, but the glow of adult males has no known function.

The Nest and Feeding Threads: From glands in its mouth, the glowworm exudes silk and mucus to construct a marvel of organic architecture. The young larva first builds the so-called nest—really more of a hollow tube or runway—some two to three times the length of its body. A network of fine silk threads suspends this nest from the cave's ceiling. The larva drops a curtain of closely spaced feeding threads from its nest. These "fishing lines" may number up to seventy per nest and may extend almost a foot in length (or ten times the span of the larva itself). Each line is studded along its entire length with evenly spaced, sticky droplets that catch intruding insects; the entire structure resembles, in miniature, a delicate curtain of glass beads. Since the slightest current of air can cause these lines to tangle, caves, culverts, ditches, and calm spaces amidst vegetation provide the limited habitats for *A. luminosa* in New Zealand.

Carnivory: Using its lighted rear end as a beacon, *A. luminosa* attracts prey to its feeding threads. Two posterior papillae contain sense organs that detect vibrations of ensnared prey. The larva then crawls partway down the proper line, leaving half to two-thirds of its rear in the nest, and hauls up both line and meal at a rate of some 2 millimeters per second.

The rest of the life cycle pales by comparison with this complexity of larval anatomy and behavior. The pupal stage lasts a bit less than two weeks and already records a marked reduction in size (15 to 18 millimeters for females, 12 to 14 for males). I have already noted the imago's decrease in body size and duration of life. Imaginal behavior also presents little in the way of diversity or complexity. Adult flies have no mouth and do not feed at all. We commit no great exaggeration by stating that they behave as unipurpose mating and egg-laying machines during their brief existence. Up to three males may congregate at a female pupa, awaiting her emergence. They jockey for positon and fight as the female fly begins to break through her encasement. As soon as the tip of her abdomen emerges, males (if present) begin to mate. Thus, females can be fertilized even before they break fully from the pupal case. Females may then live for less than a day (and no more than three), doing little more before they expire than finding an appropriate place for some 100 to 300 eggs, laid one at a time in clumps of 40 to 50. Males may live an additional day (up to four); with luck, they may find another female and do it again for posterity.

As a final and grisly irony, emphasizing larval dominance over the life cycle of *A. luminosa,* a rapacious glowworm will eat anything that touches its feeding threads. The much smaller imagoes often fly into the lines and end up as just another meal for their own children.*

Please do not draw from this essay the conclusion that larvae

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•To throw in a tidbit for readers interested in the history of evolutionary theory, this lightly coordinated complex of larval adaptations so intrigued Richard Goldschmidt that he once wrote an entire article to argue that light, carnivory, and nest building could not have arisen by gradual piecemeal, since each makes no sense without the others—and that all, therefore, must have appeared at once as a fortuitous consequence of a large mutational change, a "hopeful monster," in his colorful terminology.

This proposal (published in English in *Rn>ue Scienlifique,* 1948) inspired a stern reaction from orthodox Darwinians. Although I have great sympathy for Goldschmidt's iconoclasm, he was, I think, clearly wrong in this case. As J. F. Jackson pointed out (1974), Goldschmidt made an error in the taxonomic assignment of *.-/. luminosa* among the Mycetophilidae. He ranked this species in the subfamily Bolitophilinae. All larvae of this group burrow into soft mushrooms, and none shows even incipient development of any among the three linked features that mark the unique form and behavior of *A. luminosa.* Hence, Goldschmidt argued for all or nothing.

But .-I. *luminosa* probably belongs in another subfamily, the Keroplatinae—and, unknown to Goldschmidt, several species within this group do display a series of plausible transitions. *Leptomorphus* catches and eats fungal spores trapped on a sheetlike nest slung below a mushroom. Some species of *Macrocera* and *Keroplatus* also build trap nets for fungal spores but will eat small arthropods that also become ensnared. Species of *Orfelia, Apemon,* and Plalyura build webs of similar form but not associated with mushrooms—and they live exclusively on a diet of trapped insects. Finally, *Orfelia aeropiscator* (literally, air fisher) both builds a nest and hangs vertical feeding threads but does not possess a light.

These various "intermediates" are, of course, not ancestral to *A. luminosa.* Each represents a well-adapted species in its own right, not a transitional stage to the threefold association of New Zealand glowworms. But this array does show that each step in a plausible sequence of structurally intermediate stages can work as a successful organism. This style of argument follows Darwin's famous resolution for a potential evolutionary origin for the extraordinary complexity of the vertebrate eye. Darwin identified a series of structural intermediates, from simple light-sensitive dots to cameralike lens systems—not actual ancestors (for these are lost among nonpreservable eyes in a fossil record of hard parts) but plausible sequences disproving the "commonsense" notion that nothing in between is possible in principle.

are really more important than imagoes, either in *A. luminosa* or in general. I have tried to show that larvae must not be dismissed—as preparatory, undeveloped, or incomplete—by false analogy to a dubious (but socially favored) interpretation of human development. If any "higher reality" exists, we can only specify the life cycle itself. Larva and imago are but two stages of a totality—and you really can't have one without the other. Eggs need hens as much as hens need eggs.

I do try to show that child-adult is the wrong metaphor for understanding larva-imago. I have proceeded by discussing a case where larvae attract all our attention—literally as a source of beauty; structurally in greater size, length of life, and complexity of anatomy and behavior; and evolutionarily as focus of a major transformation from a simpler and very different ancestral style—while imagoes have scarcely modified their inherited form and behavior at all. But our proper emphasis on the larva of *A. luminosa* does not mark any superiority.

We need another metaphor to break the common interpretation that degrades larvae to a penumbra of insignificance. (How many of you include maggot in your concept of fly? And how many have ever considered the mayfly's longer larval life?) The facts of nature are what they are, but we can only view them through spectacles of our mind. Our mind works largely by metaphor and comparison, not always (or often) by relentless logic. When we are caught in conceptual traps, the best exit is often a change in metaphor—not because the new guideline will be truer to nature (for neither the old nor the new metaphor lies "out there" in the woods), but because we need a shift to more fruitful perspectives, and metaphor is often the best agent of conceptual transition.

If we wish to understand larvae as working items in their own right, we should replace the developmental metaphor of child-adult with an economic simile that recognizes the basic distinction in function between larvae and imagoes—larvae as machines built for feeding and imagoes as devices for reproduction. Fortunately, an obvious candidate presents itself on the very first page of the founding document itself—Adam Smith's *Wealth of Nations.* We find our superior metaphor in the title of Chapter 1, "On the Division of Labor," and in Smith's opening sentence:

> The greatest improvement in the productive powers of labor, and the greater part of the skill, dexterity, and judgment with which it is anywhere directed, or applied, seem to have been the effects of the division of labor.

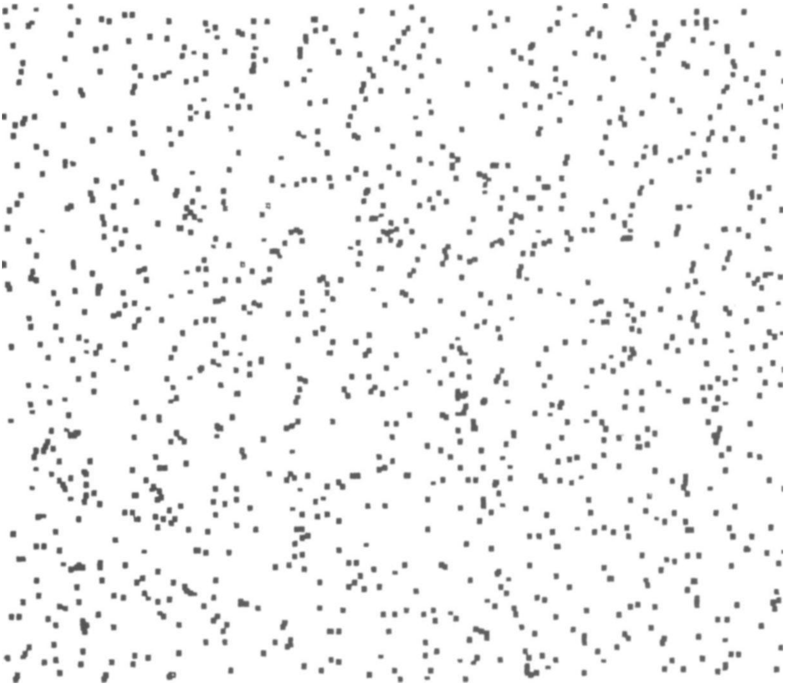
By allocating the different, sometimes contradictory, functions of feeding and reproduction to sequential phases of the life cycle, insects with complete metamorphosis have achieved a division of labor that permits a finer adaptive honing of each separate activity.

If you can dredge up old memories of your first college course in economics, you will remember that Adam Smith purposely chose a humble example to illustrate the division of labor—pin making. He identifies eighteen separate actions in drawing the wire, cutting, pointing, manufacture of the head, fastening head to shaft, and mounting the finished products in paper for sale. One man, he argues, could make fewer than twenty pins a day if he performed all these operations himself. But ten men, sharing the work by rigid division of labor, can manufacture about 48,000 pins a day. A human existence spent pointing pins or fashioning their heads or pushing them into paper may strike us as the height of tedium, but larvae of./, *luminosa* encounter no obvious psychic stress in a life fully devoted to gastronomy.

Hobbyists and professional entomologists will, no doubt, have recognized an unintended irony in Smith's selection of pin making to illustrate the division of labor. Pins are the primary stock-in-trade of any insect collector. They are used to fasten the dry and chitinous imagoes—but not the fat and juicy larvae—to collecting boards and boxes. Thus, the imagoes of *A. luminosa* may end their natural life caught in a larval web, but if they happen to fall into the clutches of a human collector, they will, instead, be transfixed by the very object that symbolizes their fall from conceptual dominance to proper partnership.

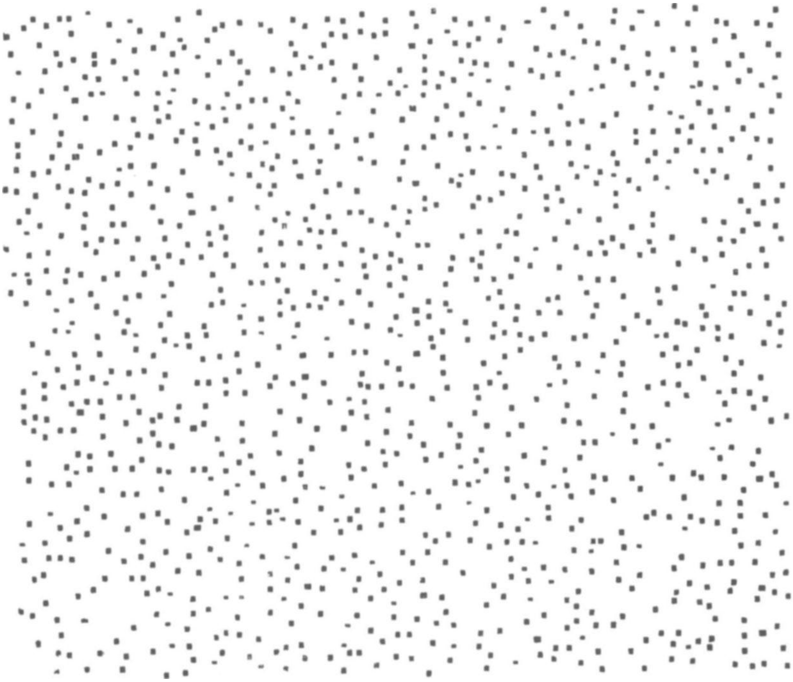
Postscript

Nothing brings greater pleasure to a scholar than utility in extension—the fruitfulness of a personal thought or idea when devel-



Output from Ed Purcell's computer program for arranging dots by the "stars," ABOVE (random), and the "worms," FACING PAGE (ordered by fields of inhibition around each dot), options. Note the curious psychological effect. Most of us would see order in the strings and clumps of the figure just above, and would interpret the figure on the opposite-page, with its lack of apparent pattern, as random. In fact, the opposite is true, and our ordinary conceptions are faulty.

oped by colleagues beyond the point of one's own grasp. I make a tangential reference in this essay to a common paradox—the apparent pattern of random arrays versus the perceived absence of sensible order in truly rule-bound systems. This paradox arises because random systems are highly clumped, and we perceive clumps as determined order. I gave the example of the heavens—



where we "see" constellations because stars are distributed at random relative to the earth's position. I contrasted our perception of heavenly order with the artificial "sky" of Waitomo Cave—where "stars" are the self-illuminated rear ends of fly larvae. Since these carnivorous larvae space themselves out in an ordered array (because they eat anything in their vicinity and therefore set up "zones of inhibition" around their own bodies), the Waitomo "sky" looks strange to us for its absence of clumping.

My favorite colleague, Ed Purcell (Nobel laureate in physics and sometime collaborator on baseball statistics), read this tangential comment and wrote a quick computer program to illustrate the effect. Into an array of square cells (144 units on the X-axis and 96 on the Y-axis for a total of 13,824 positions), Purcell placed either "stars" or "worms" by the following rules of randomness and order (following the heavens versus the fly larvae of Waitomo). In the stars option, squares are simply occupied at random (a random number generator spits out a figure between 1 and 13,824 and the appropriate square is inked in). In the worms option, the same generator spits out a number, but the appropriate square is inked in only if it and all surrounding squares are unoccupied (just as a worm sets up a zone of inhibition about itself). Thus, worm squares are spaced out by a principle of order; star squares are just filled in as the random numbers come up.

Now examine the patterns produced with 1,500 stars and worms (still less than 50 percent capacity for worms, since one in four squares could be occupied, and 3,456 potential worm holes therefore exist). By ordinary vernacular perception, we could swear that the "stars" program must be generating causal order, while the "worms" program, for apparent lack of pattern, seems to be placing the squares haphazardly. Of course, exactly the opposite is true. In his letter to me, Ed wrote:

> What interests me more in the random field of "stars" is the overpowering impression of "features" of one sort or another. It is hard to accept the fact that any perceived feature—be it string, clump, constellation, corridor, curved chain, lacuna—is a totally meaningless accident, having as its only cause the avidity for pattern of my eye and brain! Yet that is perfectly true in this case.

I don't know why our brains (by design or culture) equip us so poorly as probability calculators—but this nearly ubiquitous failure constitutes one of the chief, and often dangerous, dilemmas of both intellectual and everyday life (the essays of Section 9, particularly number 31 on Joe DiMaggio's hitting streak, discuss this subject at greater length). Ed Purcell adds, emphasizing the pervasiveness of misperception, even among people trained in probability:

> If you ask a physics student to take pen in hand and sketch a random pattern of 1,500 dots, I suspect the result will look more like the "worms" option than the "stars."

To Be a Platypus

LONG AGO, garrulous old Polonius exalted brevity as the soul of wit, but later technology, rather than sweet reason, won his day and established verbal condensation as a form of art in itself. The telegram, sent for cash on the line and by the word, made brevity both elegant and economical—and the word *telegraphic* entered our language for a style that conveys bare essentials and nothing else.

The prize for transmitting most meaning with least verbosity must surely go to Sir Charles Napier, who subdued the Indian province of Sind and announced his triumph, via telegram to his superiors in London, with the minimal but fully adequate *"Peccavi.* " This tale, in its own telegraphic way, speaks volumes about the social order and education of imperial Britain. In an age when all gentlemen studied Latin, and could scarcely rise in government service without a boost from the old boys of similar background in appropriate public schools, Napier never doubted that his superiors would remember the first-person past tense of the verb *peccare*—and would properly translate his message and pun: I have sinned.

The most famous telegram from my profession did not quite reach this admirable minimum, but it must receive honorable mention for conveying a great deal in few words. In 1884, W. H. Caldwell, a young Cambridge biologist, sent his celebrated telegram from Australia to a triumphant reading at the Annual Meeting of the British Association in Montreal. Caldwell wired: "Monotremes oviparous, ovum meroblastic."

This message may lack the ring of *peccavi* and might be viewed by the uninitiated as pure mumbo jumbo. But all professional biologists could make the translation and recognize that Caldwell had solved a particularly stubborn and vexatious problem of natural history. In essence, his telegram said: The duckbilled platypus lays eggs.

(Each word of Caldwell's telegram needs some explication. Oviparous animals lay eggs, while viviparous creatures give birth to live young; ovoviviparous organisms form eggs within their bodies, and young hatch inside their mothers. Sorry for the jargon so early in the essay, but these distinctions become important later on. Monotremes are that most enigmatic group of mammals from the Australian region—including the spiny echidna, actually two separate genera of anteaters, and the duckbilled platypus, an inhabitant of streams and creeks. An ovum is an egg cell, and meroblastic refers to a mode of cleavage, or initial division into embryonic cells, after fertilization. Yolk, the egg's food supply, accumulates at one end of the ovum, called the vegetal pole. Cleavage begins at the other end, called the animal pole. If the egg is very yolky, the cleavage plane cannot penetrate and divide the vegetal end. Such an egg shows incomplete, or meroblastic, cleavage—division into discrete cells at the animal pole but little or no separation at the yolky end. Egg-laying land vertebrates, reptiles and birds, tend to produce yolky egg cells with meroblastic cleavage, while most mammals show complete, or holoblastic, cleavage. Therefore, in adding "ovum meroblastic" to "monotremes oviparous," Caldwell emphasized the reptilian character of these paradoxical mammals—not only do they lay eggs but the eggs are typically reptilian in their yolkiness.)

The platypus surely wins first prize in anybody's contest to identify the most curious mammal. Harry Burrell, author of the classic volume on this anomaly *(The Platypus: Its Discovery, Position, Form and Characteristics, Habits and Life History,* 1927), wrote: "Every writer upon the platypus begins with an expression of wonder. Never was there such a disconcerting animal!" (I guess I just broke tradition by starting with the sublime *Hamlet.)*

The platypus sports an unbeatable combination for strangeness: first, an odd habitat with curiously adapted form to match; second, the real reason for its special place in zoological history—its engimatic melange of reptilian (or birdlike), with obvious mammalian, characters. Ironically, the feature that first suggested premammalian affinity—the "duckbill" itself—supports no such meaning. The platypus's muzzle (the main theme of this column) is a purely mammalian adaptation to feeding in fresh waters, not a throwback to ancestral form—although the duckbill's formal name embodies this false interpretation: *Ornithorhynchus anatinus* (or the ducklike bird snout).

Chinese taxidermists had long fooled (and defrauded) European mariners with heads and trunks of monkeys stitched to the hind parts of fish—one prominent source for the persistence of mermaid legends. In this context, one can scarcely blame George Shaw for his caution in first describing the platypus (1799):

> Of all the Mammalia yet known it seems the most extraordinary in its conformation, exhibiting the perfect resemblance of the beak of a Duck engrafted on the head of a quadruped. So accurate is the similitude, that, at first view, it naturally excites the idea of some deceptive preparation.

But Shaw could find no stitches, and the skeleton was surely discrete and of one functional piece (the premaxillary bones of the upper jaw extend into the bill and provide its major support). Shaw concluded:

> On a subject so extraordinary as the present, a degree of scepticism is not only pardonable but laudable; and I ought perhaps to acknowledge that I almost doubt the testimony of my own eyes with respect to the structure of this animal's beak; yet must confess that I can perceive no appearance of any deceptive preparation . . . nor can the most accurate examination of expert anatomists discover any deception.

The frontal bill may have provoked most astonishment, but the rear end also provided numerous reasons for amazement. The platypus sported only one opening, the cloaca, for all excretory and reproductive business (as in reptiles, but not most mammals, with their multiplicity of orifices for birth and various forms of excretion; Monotremata, or "one-holed," the technical name for the platypus and allied echidna, honors this unmammalian feature).

Internally, the puzzle only increased. The oviducts did not unite into a uterus, but extended separately into the cloacal tube. Moreover, as in birds, the right ovary had become rudimentary, and all egg cells formed in the left ovary. This configuration inevitably led to a most troubling hypothesis for biologists committed, as most were in these pre-Darwinian days, to the division of nature into unambiguous, static categories: no uterus, no internal space to form a placenta, a reproductive tract reptilian in form. All this suggested the unthinkable for a mammal—birth from eggs. The neighboring marsupials, with their pouches and tinyjoeys, had already compromised the noble name of mammal. Would Australia also yield the ultimate embarrassment of fur from eggs?

As anatomists studied this creature early in the nineteenth century, the mystery only deepened. The platypus looked like a perfectly good mammal in all "standard" nonreproductive traits. It sported a full coat of hair and the defining anatomical signature of mammals—one bone, the dentary, in its lower jaw and three, the hammer, anvil, and stirrup, in its middle ear. (Reptiles have several jawbones and only one ear bone. Two reptilian jawbones became the hammer and anvil of the mammalian ear.) But premammalian characters also extended beyond the reproductive system. In particular, the platypus grew an interclavicle bone in its shoulder girdle—a feature of reptiles shared by no placental mammal.

What could this curious melange be, beyond a divine test of faith and patience? Debate centered on modes of reproduction, for eggs had not yet been found and Caldwell's telegram lay half a century in the future. All three possibilities boasted their vociferous and celebrated defenders—for no great biologist could avoid such a fascinating creature, and all leaders of natural history entered the fray. Meckel, the great German anatomist, and his French colleague Blainville predicted viviparity, argued that eggs would never be found, and accommodated the monotremes among ordinary mammals. E. Home, who first described the platypus in detail (1802), and the renowned English anatomist Richard Owen chose the middle pathway of ovoviviparity and argued that failure to find eggs indicated their dissolution within the female's body. But the early French evolutionists, Lamarck and Etienne Geoffroy Saint-Hilaire, insisted that anatomy could not lie and that the platypus must be oviparous. Eggs, they argued, would eventually be found.

Geoffroy, by the way, coined the name *monotreme* in an interesting publication that reveals as much about French social history as *peccavi* indicated for imperial Britain. This issue of the *Bulletin des sciences* is labeled *Therniidor, an 11 de la Republique.* With revolutionary fervor at its height, France broke all ties with the old order and started counting again from year one (1793). They also redivided the year into twelve equal months, and renamed the months to honor the seasons rather than old gods and emperors. Thus, Geoffroy christened the monotremes in a summer month (Thermidor) during the eleventh year (1803) of the Republic (see Essay 24 for more on the French revolutionary calendar).

Just one incident in the pre-Caldwell wars will indicate the intensity of nineteenth-century debate about platypuses and the relief at Caldwell's resolution. When the great naturalists delineated their positions and defined the battleground, mammary glands had not been found in the female platypus—an apparent argument for those, like Geoffroy, who tried to distance monotremes as far as possible from mammals. Then, in 1824, Meckel discovered mammary glands. But since platypuses never do anything by the book, these glands were peculiar enough to spur more debate rather than conciliation. The glands were enormous, extending nearly from the forelegs to the hind limbs—and they led to no common opening, for no nipples could be found. (We now know that the female excretes milk through numerous pores onto a portion of her ventral surface, where the baby platypus laps it up.) Geoffroy, committed to oviparity and unwilling to admit anything like a mammalian upbringing, counterattacked. Meckel's glands, he argued, were not mammary organs, but homologues of the odiferous flank glands of shrews, secreting substances for attraction of mates. When Meckel then extracted a milky substance from the mammary gland, Geoffroy admitted that the secretion must be food of some sort, but not milk. The glands, he now argued, are not mammary but a special feature of monotremes, used to secrete thin strands of mucus that thicken in water to provide food for young hatched from the undiscovered eggs.

Owen then counterattacked to support Meckel for three reasons: The glands are largest shortly after the inferred time of birth (though Geoffroy expected the same for mucus used in feeding). The female echidna, living in sand and unable to thicken mucus in water, possesses glands of the same form. Finally, Owen suspended the secretion in alcohol and obtained globules, like milk, not angular fragments, like mucus (an interesting commentary upon the rudimentary slate of chemical analysis during the 1830s).

Geoffroy held firm—both to oviparity (correctly) and to the special status of feeding glands (incorrectly, for they are indeed mammary). In 1822, Geoffroy formally established the Monotremata as a fifth class of vertebrates, ranking equally with fishes, reptiles (then including amphibians), birds, and mammals. We may view Geoffroy as stubborn, and we certainly now regard the monotremes as mammals, however peculiar—but he presents a cogent and perceptive argument well worth our attention. Don't shoehorn monotremes into the class Mammalia to make everything neat and foreclose discussion, he pleads. Taxonomies are guides to action, not passive devices for ordering. Leave monotremes separate and in uncomfortable limbo—"which suggests the necessity of further examination [and] is far better than an assimilation to normality, founded on strained and mistaken relations, which invites indolence to believe and slumber" (letter to the Zoological Society of London, 1833).

Geoffroy also kept the flame of oviparity alive, arguing that the cloaca and reproductive tract bore no other interpretation: "Such as the organ is, such must be its function; the sexual apparatus of an oviparous animal can produce nothing but an egg." So Caldwell arrived in Australia in September 1883—and finally resolved the great debate, eighty years after its inception.

Caldwell, though barely a graduate, proceeded in the grand imperial style (he soon disappeared from biological view and became a successful businessman in Scotland). He employed 150 aboriginals and collected nearly 1,400 echidnas—quite a hecatomb for monotreme biology. On the subject of social insights, this time quite uncomfortable, Caldwell described his colonial style of collecting:

> The blacks were paid half-a-crown for every female, but the price of flour, tea, and sugar, which I sold to them, rose with

> the supply of Echidna. The half-crowns were, therefore, always just sufficient to buy food enough to keep the lazy blacks hungry.

It was, of course, often done—but rarely said so boldly and without apology. In any case, Caldwell eventually found the eggs of the platypus (usually laid two at a time and easily overlooked at their small size of less than an inch in length).

Caldwell solved a specific mystery that had plagued zoology for nearly a century, but he only intensified the general problem. He had proved irrevocably that the platypus is a melange, not available for unambiguous placement into any major group of vertebrates. Geoffroy had been right about the eggs; Meckel about the mammary glands.

The platypus has always suffered from false expectations based on human foibles. (This essay discusses the two stages of this false hoping, and then tries to rescue the poor platypus in its own terms.) During the half-century between its discovery and Darwin's *Origin of Species,* the platypus endured endless attempts to deny or mitigate its true melange of characters associated with different groups of vertebrates. Nature needed clean categories established by divine wisdom. An animal could not both lay eggs and feed its young with milk from mammary glands. So Geoffroy insisted upon eggs and no milk; Meckel upon milk and live birth.

Caldwell's discovery coincided with the twenty-fifth anniversary of Darwin's *Ongin.* By this time, evolution had made the idea of intermediacy (and melanges of characters) acceptable, if not positively intriguing. Yet, freed of one burden, the platypus assumed another—this time imposed by evolution, the very idea that had just liberated this poor creature from uncongenial shoving into rigid categories. The platypus, in short, shouldered (with its interclavicle bone) the burden of primitiveness. It would be a mammal, to be sure—but an amoeba among the gods; a tawdry, pitiable little fellow weighted down with the reptilian mark of Cain.

Caldwell dispatched his epitome a century ago, but the platypus has never escaped. I have spent the last week as a nearly full-time reader of platypusology. With a few welcome exceptions (mostly among Australian biologists who know the creature intimately), nearly every article identifies something central about the platypus as undeveloped or inefficient relative to placental mammals—as if the undoubted presence of premammalian characters condemns each feature of the platypus to an unfinished, blundering state.

Before I refute the myth of primitiveness for the platypus in particular, I should discuss the general fallacy that equates early with inefficient and still underlies so much of our failure to understand evolution properly. The theme has circulated through these essays for years—ladders and bushes. But I try to provide a new twist here—the basic distinction between *early branching* and *undeveloped,* or *inefficient, structure.*

If evolution were a ladder toward progress, with reptiles on a rung below mammals, then I suppose that eggs and an interclavicle would identify platypuses as intrinsically wanting. But the Old Testament author of Proverbs, though speaking of wisdom rather than evolution, provided the proper metaphor, *etz chayim:* She is a *tree of life* to them who take hold upon her. Evolution proceeds by branching, and not (usually) by wholesale transformation and replacement. Although a lineage of reptiles did evolve into mammals, reptiles remain with us in all their glorious abundance of snakes, lizards, turtles, and crocodiles. Reptiles are doing just fine in their own way.

The presence of premammalian characters in platypuses does not brand them as inferior or inefficient. But these characters do convey a different and interesting message. They do signify an early branching of monotreme ancestors from the lineage leading to placental mammals. This lineage did not lose its reptilian characters all at once, but in the halting and piecemeal fashion so characteristic of evolutionary trends. A branch that split from this central lineage after the defining features of mammals had evolved (hair and an earful of previous jawbones, for example) might retain other premammalian characters (birth from eggs and an interclavicle) as a sign of early derivation, not a mark of backwardness.

The premammalian characters of the platypuses only identify the antiquity of their lineage as a separate branch of the mammalian tree. If anything, this very antiquity might give the platypus more scope (that is, more time) to become what it really is, in opposition to the myth of primitivity: a superbly engineered creature for a particular, and unusual, mode of life. The platypus is an elegant solution for mammalian life in streams—not a primitive relic of a bygone world. Old does not mean hidebound in a Darwinian world.

Once we shuck the false expectation of primitiveness, we can view the platypus more fruitfully as a bundle of adaptations. Within this appropriate theme of *'good* design, we must make one further distinction between shared adaptations of all mammals and particular inventions of platypuses. The first category includes a coat of fur well adapted for protecting platypuses in the (often) cold water of their streams (the waterproof hair even traps a layer of air next to the skin, thus providing additional insulation). As further protection in cold water and on the same theme of inherited features, platypuses can regulate their body temperatures as well as most "higher" mammals, although the assumption of primitivity stalled the discovery of this capacity until 1973—before that, most biologists had argued that platypus temperatures plummeted in cold waters, requiring frequent returns to the burrow for warming up. (My information on the ecology of modern platypuses comes primarily from Tom Grant's excellent book, *The Platypus,* New South Wales University Press, 1984, and from conversations with Frank Carrick in Brisbane. Grant and Carrick are Australia's leading professional students of platypuses, and I thank them for their time and care.)

These features, shared In passive inheritance with oilier mammals, certainly benefit the platypus, but they provide no argument for my theme of direct adaptation—the replacement of restraining primitivity by a view of the platypus as actively evolving in its own interest. Many other features, however, including nearly everything that makes the platypus so distinctive, fall within the second category of special invention.

Platypuses are relatively small mammals (the largest known weighed just over five pounds and barely exceeded two feet from tip to tail). They construct burrows in the banks of creeks and rivers: long (up to sixty feet) for nesting; shorter for daily use. They spend most of their life in the water, searching for food (primarily insect larvae and other small invertebrates) by probing into bottom sediments with their bills.

The special adaptations of platypuses have fitted them in a subtle and intricate way for aquatic life. The streamlined body moves easily through water. The large, webbed forefeet propel the animal forward by alternate kicks, while the tail and partially webbed rear feet act as rudders and steering devices (in digging a burrow, the platypus anchors with its rear feet and excavates with its forelimbs). The bill works as a feeding structure par excellence, as I shall describe in a moment. Other features undoubtedly serve in the great Darwinian game of courtship, reproduction, and rearing—but we know rather little about this vital aspect of platypus life. As an example, males bear a sharp, hollow spur on their ankles, attached by a duct to a poison gland in their thighs. These spurs, presumably used in combat with competing males, grow large during the breeding season. In captivity, males have killed others with poison from their spurs, and many platypuses, both male and female, sport distinctive punctures when captured in the wild.

Yet even this long and impressive list of special devices has been commonly misrepresented as yet another aspect (or spin-off) of pervasive primitiveness. Burrell, in his classic volume (1927), actually argued that platypuses develop such complex adaptations because simple creatures can't rely upon the flexibility of intelligence and must develop special structures for each required action. Burrell wrote:

> Man . . . has escaped the need for specialization because his evolution has been projected outside himself into an evolution of tools and weapons. Other animals in need of tools and weapons must evolve them from their own bodily parts; we therefore frequently find a specialized adaptation to environmental needs grafted on to primitive simplicity of structure.

You can't win in such a world. You are either primitive prima facie or specialized as a result of lurking and implicit simplicity! From such a Catch-22, platypuses can only be rescued by new concepts, not additional observations.

As a supreme irony, and ultimate defense of adaptation versus ineptitude, the structure that built the myth of primitivity—the misnamed duckbill itself—represents the platypus's finest special invention. The platypus bill is not a homologue of any feature in birds. It is a novel structure, uniquely evolved by monotremes (the echidna carries a different version as its long and pointed snout). The bill is not simply a hard, inert horny structure. Soft skin covers the firm substrate, and this skin houses a remarkable array of sensory organs. In fact, and strange to tell, the platypus, when under water, shuts down all its other sensory systems and relies entirely upon its bill to locate obstacles and food. Flaps of skin cover tiny eyes and nonpinnate ears when a platypus dives, while a pair of valves closes off the nostrils under water.

E. Home, in the first monograph of platypus anatomy (1802), made an astute observation that correctly identified the bill as a complex and vital sensory organ. He dissected the cranial nerves and found almost rudimentary olfactory and optic members but a remarkably developed trigeminal, carrying information from the face to the brain. With great insight, Home compared the platypus bill to a human hand in function and subtlety. (Home never saw a live platypus and worked only by inference from anatomy.) He wrote:

> The olfactory nerves are small and so are the optic nerves; but the fifth pair which supplies the muscles of the face are uncommonly large. We should be led from this circumstance to believe, that the sensibility of the different parts of the bill is very great, and therefore it answers to the purpose of a hand, and is capable of nice discrimination in its feeling.

Then, in the same year that Caldwell discovered eggs, the English biologist E. B. l'oulton found the primary sensory organs of the bill. He located numerous columns of epithelial cells, each underlain by a complex of neural transmitters. He called them "push rods," arguing by analogy with electrical bells that a sensory stimulus (a current of water or an object in bottom sediments) would depress the column and ignite the neural spark.

A set of elegant experiments in modern neurophysiology by R. C. Bohringer and M.J. Rowe (1977 and 1981) can only increase our appreciation for the fine-tuned adaptation of the platypus bill. They found Poulton's rods over the bill's entire surface, but four to six times more densely packed at the anterior border of the upper bill, where platypuses must first encounter obstacles and food items. They noted different kinds of nerve receptors under the rods, suggesting that platypuses can distinguish varying kinds of signals (perhaps static versus moving components or live versus dead food). Although individual rods may not provide sufficient information for tracing the direction of a stimulus, each rod maps to a definite location on the brain, strongly implying that the sequence of activation among an array of rods permits the platypus to identify the size and location of objects.

Neurophysiologists can locate areas of the brain responsible for activating definite parts of the body and draw a "map" of the body upon the brain itself. (These experiments proceed from either direction. Either one stimulates a body part and records the pattern of activity in a set of electrodes implanted into the brain, or one pulses a spot on the brain and determines the resulting motion of body parts.) We have no finer demonstrations of evolutionary adaptation than numerous brain maps that record the importance of specially developed organs by their unusually enlarged areas of representation upon the cortex. Thus, a raccoon's brain map displays an enormous domain for its forepaws, a pig's for its snout, a spider monkey's for its tail. Bohringer and Rowe have added the platypus to this informative array. A map of the platypus's cortex is mostly bill.

We have come a long way from the first prominent evolutionary interpretation ever presented for the platypus bill. In 1844, in the major pre-Darwinian defense of evolution written in English, Robert Chambers tried to derive a mammal from a bird in two great leaps, via the intermediate link of a duckbilled platypus. One step, Chambers wrote,

> would suffice in a goose to give its progeny the body of a rat, and produce the ornithorhynchus, or might give the progeny of an ornithorhynchus the mouth and feet of a true rodent, and thus complete at two stages the passage from the aves to the mammalia.

The platypus, having suffered such slings and arrows of outrageous fortune in imposed degradation by human hands, has cast its arms (and its bill) against a sea of troubles and vindicated itself. The whips and scorns of time shall heal. The oppressor's wrong, the proud man's contumely have been reversed by modern studies—enterprises of great pith and moment. The platypus is one honey of an adaptation.

Bligh's Bounty

IN 1789, a British naval officer discovered some islands near Australia and lamented his inability to provide a good description:

> Being constantly wet, it was with the utmost difficulty I could open a book to write, and I am sensible that what I have done can only serve to point out where these lands are to be found again, and give the idea of their extent.

As he wrote these lines, Captain William Bligh was steering a longboat with eighteen loyal crew members into the annals of human heroism at sea—via his 4,000-mile journey to Timor, accomplished without loss of a single man, and following the seizure of his ship. *The Bounty,* in history's most famous mutiny.

Bligh may have been overbearing; he surely wins no awards for insight into human psychology. But history and Charles Laughton have not treated him fairly either. Bligh was committed, meticulous, and orderly to a fault—how else, in such peril, could he have bothered to describe some scattered pieces of new Pacific real estate.

Bligh's habit of close recording yielded other benefits, including one forgotten item to science. Obsessed by the failure of his *Bounty* mission to bring Tahitian breadfruit as food for West Indian slaves, Bligh returned to Tahiti aboard *the Providence* and successfully unloaded 1,200 trees at Port Royal, Jamaica, in 1793 (his ship was described as a floating forest). En route, he stopped in Australia and had an interesting meal.

George Tobin, one of Bligh's officers, described their quarry as

> a kind of sloth about the size of a roasting pig with a proboscis 2 or 3 inches in length. . . . On the back were short quills like those of the Porcupine. . . . The animal was roasted and found of a delicate flavor.

Bligh himself made a drawing of his creature before the banquet. The officers of the *Providence* had eaten an echidna, one of Australia's most unusual mammals—an egg-laying anteater closely related to the duckbilled platypus.

Bligh brought his drawing back to England. In 1802, it appeared as a figure (reproduced here) accompanying the first technical description of the echidna's anatomy by Everard Home in the *Philosophical Transactions of the Royal Society* (G. Shaw had published a preliminary and superficial description in 1792).

Home discovered the strange mix of reptilian and mammalian features that has inspired interest and puzzlement among biologists ever since. He also imposed upon the echidna, for the first time, the distinctive burden of primitivity that has continually hampered proper zoological understanding of all monotremes, the egg-laying mammals of Australia. Home described the echidna as not quite all there in mammalian terms, a lesser form stamped with features of lower groups:

> These characters distinguish [the echidna] in a very remarkable manner, from all other quadrupeds, giving this new tribe a resemblance in some respects to birds, in others to the Amphibia; so that it may be considered as an intermediate link between the classes of Mammalia, Aves, and Amphibia.

Unfortunately, Home could not study the organ that most clearly belies the myth of primitivity. "The brain," he wrote, "was not in a state to admit of particular examination." Home did have an opportunity to infer the echidna's anomalously large brain from the internal form of its skull, well drawn on the plate just preceding Bligh's figure (and also reproduced here). But Home said nothing about this potential challenge to his general interpretation.

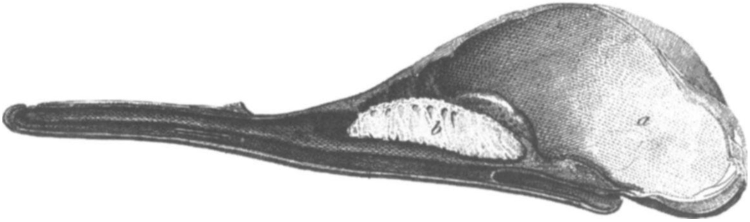
Original drawing of an echidna by none other than Captain Bligh of *Bounty* fame. NEC. NO. 337535. COURTESY DEPARTMENT OE LIBRARY SERVICES, AMERICAN MUSEUM OF NATURAL HISTORY.

And so the burden of primitivity stuck tenaciously to echidnas, and continues to hold fast in our supposedly more sophisticated age. Some great zoologists have struggled against this convenient fallacy, most notably the early French evolutionist Etienne Geoffroy Saint-Hilaire, who coined the name Monotremala (see

Essay 18) and labored unsuccessfully to establish the echidna and platypus as a new class of vertebrates, separate from both mammals and reptiles and not merely inferior to placentals. By his own manifesto, he chose his strategy explicitly to avoid the conceptual lock that assumptions of primitivity would clamp upon our understanding of monotremes. He wrote in 1827:

> What is defective, I repeat, is our manner of perception, our way of conceiving the organization of monotremes; that is, our determination, made a priori, to join them violently to mammals [by *violemment,* Geoffroy means, of course, "without any conceptual justification"), to place them in the same class and, after our disappointments and false judgments, then to make our unjust grievances heard, as when we speak of them as mammals essentially and necessarily outside the rules.

But Geoffroy's legitimate complaint, so eloquently expressed, did not prevail, and the myth of primitivity continues, despite its blatant flaw. As I argue in the preceding essay on platypuses, the myth of primitivity rests upon a logical confusion between early branching from the ancestors of placental mammals (the true meaning of reptilian characters retained by monotremes) and structural inferiority. Unless geological age of branching is a sure guide to level of anatomical organization—as it is not—egg laying and interclavicle bones do not brand platypuses and echidnas as inferior mammals.



Everard Home's 1802 figure of an echidna's skull. The large size of the brain was apparent even then. NEG. NO. 337429. COURTESY DEPARTMENT OF LIBRARY SERVICES, AMERICAN MUSEUM OF NATURAL HISTORY.

Beyond this general defense, echidnas can provide ample specific evidence of their adequacy. They are, first of all, a clear success in ecological terms. Echidnas live all over the Australian continent (and extend into Papua-New Guinea), the only native mammal with such a wide range. Moreover, *the* echidna, as a single struggling relict, ranks with *the* rat and *the* monkey (those meaningless synecdoches of the psychological literature) as an absurd abstraction of nature's richness. Echidnas come as two species in two separate genera and with quite different habits. *Tachyglossus aruleatus* (the Australian form with Papuan extensions) rips apart ant and termite nests with its stout forelimbs and collects the inhabitants on its sticky tongue. The larger and longer-snouted *Zaglossus bruijni* of Papua-New Guinea lives on a nearly exclusive diet of earthworms. Moreover, three other species, including the "giant" echidna, *Zaglossus hacketti,* have been found as fossils in Australia. Echidnas are a successful and at least modestly varied group.

But echidnas hold a far more important ace in the hole as their ultimate defense against charges of primitivity. The same cultural biases that lead us to classify creatures as primitive or advanced have established the form and function of brains as our primary criterion of ranking. Echidnas have big and richly convoluted brains. Scientists have recognized this anomaly in the tale of primitivity for more than a century—and they have developed an array of arguments, indeed a set of traditions, for working around such an evident and disconcerting fact. Large brains undoubtedly serve echidnas well; but they also help to instruct us about an important issue in the practice of science—how do scientists treat factual anomalies? What do we do with evidence that challenges a comfortable view of nature's order?

The echidna's brain refutes the myth of primitivity with a double whammy—size and conformation. (I discuss only the Australian species, *Tachyglossus aruleatus;* its larger Papua-New Guinea relative, *Zaglossus,* remains virtually unknown to science—for basic information about echidnas, see the two books by M. Griffiths listed in the bibliography.) Since mammalian brains increase more slowly than body weight along the so-called mouse-to-elephant curve, we can use neither absolute nor relative brain weight as a criterion. (Big mammals have absolutely large brains as an uninteresting consequence of body size, while small mammals have relatively large brains because brains increase more slowly than bodies.) Biologists have therefore developed a standard criterion: measured brain weight relative to expected brain weight for an average mammal of *the same* body size. This ratio, dubbed EQ, (or encephalization quotient) in amusing analogy with you know what, measures 1.0 for mammals right on the mouse-to-elephant curve, above 1.0 for brainier than average mammals, and less than 1.0 for brain weights below the norm.

To provide some feel for the range of EOJs, so-called basal insectivores—a selected stem group among the order traditionally ranked lowest among placental mammals—record a mean of 0.311. Adding advanced insectivores, the average rises to 0.443. Rodents, a perfectly respectable group (and dominant among mammals by sheer number), weigh in with a mean EQ of 0.652. (Primates and carnivores rank consistently above 1.0.) Monotremes are not, by this criterion, mental giants—their EOJs range from 0.50 to 0.75—but they rank way above the traditional primitives among placentals and right up there with rodents and other "respected" groups. Monotremes continue to shine by other standards of size as well. Some neurologists regard the ratio of brain to spinal cord as a promising measure of mental advance. Fish generally dip below 1:1 (spinal cord heavier than brain). We top-heavy humans tip the scale at 50:1; cats score 4:1. The "lowly" echidna waddles in front of tabby at approximately 6:1.

By conformation, rather than simple size alone, echidnas are even more impressive. The neocortex, the putative site of higher mental functions, occupies a larger percentage of total brain weight in supposedly advanced creatures. The neocortex of basal insectivores averages 13 percent of brain weight; the North American marsupial opossum records 22 percent. Echidnas score 43 percent (platypuses 48 percent), right up there with the prosimians (54 percent), basal group of the lordly primates. (All my figures for brain sizes come from H. J. Jerison, 1973, and P. PirlotandJ. Nelson, 1978.)

The neocortex of echidnas is not only expanded and nearly spherical as in primates; its surface is also richly convoluted in a series of deep folds and bumps (sulci and gyri), a traditional criterion of mental advance in mammals. (Curiously, by comparison, the platypus neocortex, while equally expanded and spherical, is almost completely smooth.)

Many famous nineteenth-century neuroanatomists studied monotreme brains, hoping to understand the basis of human mental triumph by examining its lowly origins. Echidnas provided an endless source of puzzlement and frustration. William Henry Flower dissected an echidna in 1865 and wrote of "this most remarkable brain, with its largely developed and richly convoluted hemispheres." He admitted: "It is difficult to see in many of the peculiarities of their brain even an approach in the direction of that of the bird." And Grafton Elliot Smith, the great Australian anatomist who later fell for I'iltdown Man in such a big way, wrote with evident befuddlement in 1902:

> The most obtrusive feature of this brain is the relatively enormous development of the cerebral hemispheres. . . . In addition, the extent of the cortex is very considerably increased by numerous deep sulci. The meaning of this large neopallium is quite incomprehensible. The factors which the study of other mammalian brains has shown to be the determinants of the extent of the cortex fail completely to explain how it is that a small animal of the lowliest status in the mammalian series comes to possess this large cortical apparatus.

One might have anticipated that scientists, so enlightened by monotreme mentality, would simply abandon the myth of primitivity. But prompt submission to items of contrary evidence is not, despite another prominent myth (this time about scientific procedure), the usual response of scientists to nature's assaults upon traditional beliefs. Instead, most students of monotreme brains have recorded their surprise and then sought different criteria, again to affirm the myth of primitivity.

A favorite argument cites the absence in monotremes (and marsupials as well) of a corpus callosum—the bundle of fibers connecting the right and left hemispheres of "higher" mental processing in placental mammals. In a wonderful example of blatantly circular logic, A. A. Abbie, one of Australia's finest natural historians, wrote in a famous article of 1941 (commissures, to a neuroanatomist, are connecting bands of neural tissue, like the corpus callosum):

> Since in mammals cerebral evolution and with it any progressive total evolution is reflected so closely in the state of the cerebral commissures it is clear that the taxonomic significance of these commissures far transcends that of any other physical character.

In other words, since we know (a priori) that monotremes are primitive, search for the character that affirms a lowly status (lack of a corpus callosum) and proclaim this character, ipso facto, more important than any other (size of brain, convolutions, or any other indication of monotreme adequacy). (I shall have more to say about commissures later on, but let me just mention for now that lack of a corpus callosum does not preclude communication across the cerebral hemispheres. Monotremes possess at least two other commissures—the hippocampal and the anterior—capable of making connections, though by a route more circuitous than the pathway of the corpus callosum.)

This tradition of switching to another criterion continues in modern studies. In their 1978 article on monotreme brain sizes, for example, Pirlot and Nelson admit, after recording volumes and convolutions for echidnas: "It is very difficult to isolate criteria that clearly establish the 'primitiveness' of monotreme brains." But they seek and putatively find, though they honorably temper their good cheer with yet another admission of the puzzling size of the monotreme neocortex:

> This cortex could be considered to be among the most primitive mammalian cortices on the basis of the low number and low density of large, especially pyramidal neurons. It is surprising to find that a very high proportion of cortex is neocortex. This does not necessarily mean an advanced degree of progressiveness, although the two are usually related.

The basic data on size and external conformation of echidna brains have been recorded (and viewed as troubling) for more than a century. More sophisticated information on neural fine structure and actual use of the cortical apparatus in learning has been gathered during the past twenty years—all affirming, again and again, the respectability of echidna intelligence.

In 1964, R. A. Lende published the first extensive map of localized sensory and motor areas on the echidna's cerebral cortex. (I discuss the general procedures of such study in the preceding essay on platypus brains. P. S. Ulinski, 1984, has recently confirmed and greatly extended Lende's work in a series of elegant experiments.) Lende discovered a surprising pattern of localization, basically mammalian in character but different from placental mappings. He identified separate areas for visual, auditory, and sensory control (the motor area overlapped the sensory region and extended forward to an additional section of the cortex), all demarcated one from the other by constant sulci (fissures of the cortex) and located together at the rear of the cortex.

Most surprisingly, these areas abut one another without any so-called association cortex in between. (Association cortex includes areas of the cerebral surface that do not control any specific sensory or motor function and may play a role in coordinating and integrating the basic inputs. For this reason, amount and position of association cortex have sometimes been advanced as criteria of "higher" mental function. But such negative definitions are troubling and should not be pushed too hard or far.) In any case, Lende identified a relatively enormous area of unspecified (perhaps association) cortex in front of his mapped sensory and motor areas. Lende concluded, in a statement oft-quoted against those who maintain the myth of primitivity:

> Ahead of the posteriorly situated sensory and motor areas established in this study there is relatively more "frontal cortex" than in any other mammal, including man, the function of which remains unexplained.

Other studies have tried to push the echidna brain to its practical limits by imposing upon these anteaters all the modern apparatus of mazes, levers, and food rewards so favored by the science of comparative psychology. Echidnas have performed remarkably well in all these studies, again confuting the persistent impression of stupidity still conveyed by textbooks, and even by the most "official" of all sources—the Australian Museum's *Complete*

Book of Australian Mammals, edited by R. Strahan (1983), which insists without evidence:

> In this last respect [brainpower], monotremes are inferior to typical placental mammals and, probably, to typical marsupials. The paucity of living monotremes may therefore be due to their being less bright, less adaptable in their behavior, than other mammals.

To cite just three studies among several of similar intent and conclusion:

1. Saunders, Chen, and Pridmore (1971) ran echidnas through a simple two-choice T-maze (down a central channel, then either right or left into a bin of food or a blank wall). They trained echidnas to move in one direction (location of the chow, of course), then switched the food box to the other arm of the T. In such studies of so-called habit-reversal learning, most fish never switch, birds learn very slowly, mammals rapidly. Echidnas showed quick improvement with a steady reduction in errors—and at typically mammalian rates. Half the experiments (seven of fifteen) on well-trained echidnas yielded the optimal performance of "one-trial reversal" (you switch the food box and the animal goes the wrong way—where the food used to be—the first time, then immediately cottons on and heads in the other direction, toward the chow, each lime). Rats often show one-trial reversal learning, birds never.

2. Buchmann and Rhodes (1978) tested echidnas for their ability to learn positional (right or left) and visual-tactile (black and rough versus white and smooth) cues—with echidnas pushing the appropriate lever to gain their food reward. As an obvious testimony to mental adequacy, they report that "unsuccessful (unrewarded) responses were often associated with vigorous kicking at the operanda." Echidnas learned at a characteristic rate for placental mammals and also remembered well. One animal, retested a month later, performed immediate one-trial reversals.

Buchmann and Rhodes compared their echidnas with other animals tested in similar procedures. Crabs and goldfish did not show improvement (did not learn) over time. Echidnas displayed great variation in their speed of learning—one improved faster (and one slower) than rats; all echidnas performed better than cats, lake these results (and the reward for success as well) with a grain of salt because numbers are limited and procedures varied widely among studies—but still, the single best performer on the entire chart was an echidna.

Buchmann and Rhodes conclude: "There is no evidence that the performance of echidnas is inferior to eutherian [placental] or metatherian [marsupial| mammals." They end by ridiculing the "quaint, explicitly or tacitly-held views that echidnas are little more than animated pin-cushions, or, at the best, glorified reptiles."

3. Gates (1978) studied learning in visual discrimination (black versus white, and various complex patterns of vertical and horizontal striping). His results parallel the other studies—echidnas learned quickly, at typical mammalian rates. But he added an interesting twist that confutes the only serious, direct argument ever offered from brain anatomy for monotreme inferiority—the claim that absence of a corpus callosum precludes transfer between the cerebral hemispheres, thereby compromising "higher" mental functions.

Gates occluded one eye and taught echidnas to distinguish black from while panels with the other eye. They reached "criterion performance" in an average of 100 trials. He then uncovered the occluded eye, bandaged the one that had overseen the initial learning, and did the experiment again. If no information passes from one cerebral hemisphere to the other, then previous learning on one side of the brain should offer no help to the other, and the 100-trial average should persist. But echidnas only needed 40 trials to reach criterion with the second eye.

Gates conjectures that information is either passing across the other two commissures in the absence of a corpus callosum, or via the few optic fibers that do not cross to the other side of the brain. (In vertebrate visual systems, inputs from the right eye go to the left hemisphere of the brain, left eye to the right hemisphere; thus, each eye "informs" the opposite hemisphere. But about 1 percent of optic fibers do not cross over, and therefore map to their own hemisphere. These few fibers may sneak a little learning to the hemisphere dependent upon the occluded eye.) In addition, direct evidence of electrical stimulation has shown that inputs to one hemisphere can elicit responses in corresponding parts of the other hemisphere—information clearly gets across in the absence of a corpus callosum.

The solution to the paradox of such adequate intelligence in such a primitive mammal is stunningly simple. The premise—the myth of primitivity itself—is dead wrong. To say it one more, and one last, time: The reptilian features of monotremes only record their early branching from the ancestry of placental mammals—and time of branching is no measure of anatomical complexity or mental status.

Monotremes have evolved separately from placentals for a long time—more than enough for both groups to reach, by parallel evolution in independent lineages, advanced levels of mental functioning permitted by their basic, shared mammalian design. The primary evidence for parallel evolution has been staring us in the face for a century, forming part of the standard literature on echidnas, well featured even in primary documents that uphold the myth of primitivity. We know that the echidna's brain attained its large size by an independent route. The platypus has a smooth (if bulbous) brain. The echidna evolved complex ridges and folds on its cerebral surface as a special feature of its own lineage. These sulci and gyri cannot be identified (homologized) with the well-known convolutions of placental brains. The echidna brain is so different, by virtue of a separate evolution to large size, that its convolutions have been named by Greek letters to avoid any misplaced comparison with the different ridges and folds of placental brains. And Grafton Elliot Smith, the man most puzzled by echidna brains, did the naming—apparently without realizing that the very need for such separate designations provided the direct evidence that could refute the myth of primitivity.

In his eloquent plea for monotremes (1827), Geoffroy Saint-Hilaire wrote brilliantly about the subtle interplay of fact and theory in science. He recognized the power of theory to guide the discovery of fact and to set a context for fruitful interpretation. ("To limit our efforts to the simple practicalities of an ocular examination would be to condemn the activities of the mind.") But he also acknowledged the flip side of useful guidance, the extraordinary power of theory to restrict our vision, in particular to render "obvious" facts nearly invisible, by denying them a sensible context. ("At first useless, these facts had to remain unperceived until the moment when the needs and progress of science provoked us to discover them.") Or as Warner Oland, the Swedish pseudo-Oriental Charlie Chan, once said in one of his most delightfully anachronistic pseudo-Confucian sayings *(Charlie Chan in Egypt,* 1935): "Theory like mist on eyeglasses. Obscure facts."

Here Goes Nothing

GOLIATH PAID THE HIGHEST of prices to learn the most elementary of lessons—thou shall not judge intrinsic quality by external appearance. When the giant first saw David, "he disdained him: for he was but a youth, and ruddy, and of a fair countenance" (1 Sam. 17:42). Saul had been similarly unimpressed when David presented himself as an opponent for Goliath and savior of Israel. Saul doubled out loud: "for thou art but a youth, and he a man of war from his youth" (1 Sam. 17:33). But David persuaded Saul by telling him that actions speak louder than appearances—for David, as a young shepherd, had rescued a lamb from a predatory lion: "I went out after him, and smote him, and delivered it out of his mouth" (1 Sam. 17:35).

This old tale presents a double entendre to introduce this essay—first as a preface to my opening story about a famous insight deceptively clothed in drab appearance; and second as a quirky lead to the body of this essay, a tale of animals that really do deliver from their mouths: *Rheobatrachus silus,* an Australian frog that swallows its fertilized eggs, broods tadpoles in its stomach, and gives birth to young frogs through its mouth.

Henry Walter Bates landed at Para (now Belem), Brazil, near the mouth of the Amazon, in 1848. He arrived with Alfred Russel Wallace, who had suggested the trip to tropical jungles, arguing that a direct study of nature at her richest might elucidate the origin of species and also provide many fine specimens for sale. Wallace returned to England in 1852, but Bates remained for eleven years, collecting nearly 8,000 new species (mostly insects) and exploring the entire Amazon valley.

In 18(33, Bates published his two-volume classic, perhaps the greatest work of nineteenth-century natural history and travel, *The Naturalist on the River Amazons.* But two years earlier, Bates had hidden his most exciting discovery in a technical paper with a disarmingly pedestrian title: "Contributions to an Insect Fauna of the Amazon Valley," published in the *Transactions of the Linnaean Society.* The reviewer of Bates's paper *(Natural History Reviews,* 18()3, pp. 219-224) lauded Bates's insight but lamented the ill-chosen label: "From its unpretending and somewhat indefinite title," he wrote, "we fear [that Bates's work] may be overlooked in the ever-flowing rush of scientific literature." The reviewer therefore sought to rescue Bates from his own modesty by providing a bit of publicity for the discovery. Fortunately, he had sufficient oomph to give Bates a good send-off. The reviewer was Charles Darwin, and he added a section on Bates's insight to the last edition of the *Origin of Species.*

Bates had discovered and correctly explained the major style of protective mimicry in animals. In Batesian mimicry (for the phenomenon now bears his name), uncommon and tasty animals (the mimics) gain protection by evolving uncanny resemblance to abundant and foul-tasting creatures (the models) that predators learn to avoid. The viceroy butterfly is a dead ringer for the monarch, which, as a caterpillar, consumes enough noxious poisons from its favored plant foods to sicken any untutored bird. (Vomiting birds have become a cliche of natural history films. Once afflicted, twice shy, as the old saying goes. The tale may be more than twice told, but many cognoscenti do not realize that the viceroy's name memorializes its mimicry—for this butterfly is the surrogate, or vice-king, to the ruler, or monarch, itself.)

Darwin delighted in Bates's discovery because he viewed mimicry as such a fine demonstration of evolution in action. Creationism, Darwin consistently argued, cannot be disproved directly because it claims to explain everything. Creationism becomes impervious to test and, therefore, useless to science. Evolutionists must proceed by showing that any creationist explanation becomes a *reductio ad absurdum* by twists of illogic and special pleading required to preserve the idea of God's unalterable will in the face of evidence for historical change.

In his review of Bates's paper, Darwin emphasizes that creationists must explain the precision of duplicity by mimics as a simple act of divine construction—"they were thus clothed from the hour of their creation," he writes. Such a claim, Darwin then argues, is even worse than wrong because it stymies science by providing no possible test for truth or falsity—it is an argument "made at the expense of putting an effectual bar to all further inquiry." Darwin then presents his *reductio ad absurdum,* showing that any fair-minded person must view mimicry as a product of historical change.

Creationists had made a central distinction between true species, or entities created by God, and mere varieties, or products of small changes permitted within a created type (breeds of dogs or strains of wheat, for example). But Bates had shown that some mimics are true species and others only varieties of species that lack mimetic features in regions not inhabited by the model. Would God have created some mimics from the dust of the earth but allowed others to reach their precision by limited natural selection within the confines of a created type? Is it not more reasonable to propose that mimicking species began as varieties and then evolved further to become separate entities? And much worse for creationists: Bates had shown that some mimicking species resemble models that are only varieties. Would God have created a mimic from scratch to resemble another form that evolved (in strictly limited fashion) to its current state? God may work in strange ways, his wonders to perform—but would he really so tax our credulity? The historical explanation makes so much more sense.

But if mimicry became a source of delight for Darwin, it also presented a serious problem. We may easily grasp the necessity for a historical account. We may understand *how* the system works once all its elements develop, but *why* does this process of mimicry ever begin? What starts it off, and what propels it forward? Why, in Darwin's words, "to the perplexity of naturalists, has nature condescended to the tricks of the stage?" More specifically: Any butterfly mimic, in the rich faunas of the Amazon valley, shares its space with many potential models. Why does a mimic converge upon one particular model? We can understand how natural selection might perfect a resemblance already well established, but what begins the process along one of many potential pathways—especially since we can scarcely imagine that a 1 or 2 percent resemblance to a model provides much, if any.

advantage for a mimic. This old dilemma in evolutionary theory even has a name in the jargon of my profession—the problem of the "incipient stages of useful structures." Darwin had a good answer for mimicry, and I will return to it after a long story about frogs—the central subject of this essay and another illustration of the same principle that Darwin established to resolve the dilemma of incipient stages.

We remember Darwin's *Beagle* voyage primarily for the big and spectacular animals that he discovered or studied: the fossil *Toxodon* and the giant Galapagos tortoises. But many small creatures, though less celebrated, brought enormous scientific reward—among them a Chilean frog appropriately named *Rhinoderma darwini.* Most frogs lay their eggs in water and then allow the tadpoles to make their own way, but many species have evolved various styles of parental care, and the range of these adaptations extols nature's unity in diversity.

In *R. danvini,* males ingest the fertilized eggs and brood them in the large throat pouches usually reserved for an earlier act of courtship—the incessant croaking that defines territory and attracts females. Up to fifteen young may fill the pouch, puffing out all along the father's ventral (lower) surface and compressing the vital organs above. G. B. Howes ended his classic account of this curious life-style *(Proceedings of the Zoological Society of London,* 1888) with a charming anthropomorphism. Previous students of *Rhinoderma,* he noted, had supposed that the male does not feed while carrying his young. But Howes dissected a brooding male and found its stomach full of beetles and flies and its large intestine clogged with "excreta like that of a normal individual." He concluded, with an almost palpable sigh of relief, "that this extraordinary paternal instinct does not lead up to that self-abnegation" postulated by previous authors.

But nature consistently frustrates our attempts to read intrinsic solicitude into her ways. In November 1973, two Australian scientists discovered a form of parental care that must preclude feeding, for these frogs brood their young in their stomachs and then give birth through their mouths. And we can scarcely imagine that a single organ acts as a nurturing uterus and a site of acid digestion at the same time.

Rheobatrachus silus, a small aquatic frog living under stones or in rock pools of shallow streams and rills in a small area of southeast

Queensland, was first discovered and described in 1973. Later that year, C.J. Corben and G.J. Ingram of Brisbane attempted to transfer a specimen from one aquarium to another. To their astonishment, it "rose to the surface of the water and, after compression of the lateral body muscles, propulsively ejected from the mouth six living tadpoles" (from the original description published by Corben, Ingram, and M.J. Tyler in 1974). They initially assumed, from their knowledge of *Rhinoderma,* that their brooder was a male rearing young in its throat pouch. Eighteen days later, they found a young frog swimming beside its parent; two days later, a further pair emerged unobserved in the night. At that point, they decided (as the euphemism goes) to "sacrifice" their golden goose. But the parent, when grasped, "ejected by propulsive vomiting eight juveniles in the space of no more than two seconds. Over the next few minutes a further five juveniles were ejected." They then dissected the parent and received their biggest surprise. The frog had no vocal sac. It was a female with "a very large, thin-walled, dilated stomach"—the obvious home of the next generation.

Natural birth had not yet been observed in *Rheobatrachm.* All young had either emerged unobserved or been vomited forth as a violent reaction after handling. The first young had greeted the outside world prematurely as tadpoles (since development clearly proceeds all the way to froghood in the mother's stomach, as later births demonstrated).

Art then frustrated nature, and a second observation also failed to resolve the mode of natural birth. In January 1978, a pregnant female was shipped express airfreight from Brisbane to Adelaide for observation. But the poor frog was—yes, you guessed it—"delayed" by an industrial dispute. The mother, still hanging on, eventually arrived surrounded by twenty-one dead young; a twenty-second frog remained in her stomach upon dissection. Finally, in 1979, K. R. McDonald and D. B. Carter successfully transported two pregnant females to Adelaide—and the great event was finally recorded. The first female, carefully set up for photography, frustrated all hopes by vomiting six juveniles "at great speed, flying upwards . . . for approximately one meter ... a substantial distance relative to the body size of the female." But the second mother obliged. Of her twenty-six offspring, two appeared gently and, apparently, voluntarily. The mother "partially emerged from the water, shook her head, opened her mouth, and two babies actively struggled out." The photo of a fully formed baby frog, resting on its parent's tongue before birth, has already become a classic of natural history. This second female, about two inches long, weighed 11.62 grams after birth. Her twenty-six children weighed 7.66 grams, or 66 percent of her weight without them. An admirable effort indeed!

Rheobalrachus inspired great excitement among Australian scientists, and research groups in Adelaide and Brisbane have been studying tins frog intensively, with all work admirably summarized and discussed in a volume edited by M.J. Tyler (1983). Rarely has such extensive and coordinated information been presented on a natural oddity, and we are grateful to these Australian scientists for bringing together their work in such a useful way.

This volume also presents enough detail (usually lacking in technical publications) to give nonscientists a feel for the actual procedures of research, warts and all (an appropriate metaphor for the subject), (ilen Ingram's article on natural history, for example, enumerates all the day-to-day dilemmas that technical papers rarely mention: slippery bodies that elude capture; simple difficulties in seeing a small, shy frog that lives in inaccessible places (Ingram learned to identify *Rheobalrachus* by characteristic ripples made by its jump into water); rain, fog, and dampness; and regeneration that frustrates identification (ecologists must recognize individual animals in order to monitor size and movement of populations by mark-recapture techniques; amphibians and reptiles are traditionally marked by distinctive patterns of toe clipping, a painless and unobtrusive procedure, but *Rheobatrachus* frustrates tradition by regenerating its clipped toes, and Ingram could not reidentify his original captures). To this, we must add the usually unacknowledged bane of all natural history: boredom. You don't see your animals most of the time; so you wait and wait and wait (not always pleasant on the boggy banks of a stream in rainy season). Somehow, though, such plagues seem appropriate enough, given the subject. Frogs, after all, stand among the ten Mosaic originals: "I will smite all thy borders with frogs: And the river shall bring forth frogs abundantly, which shall go up and come into thine house, and into thy bedchambers, and upon thy bed . . . and into thine ovens, and into thy kneading troughs" (Exod. 8:2-3).

The biblical author of Exodus was, unfortunately, not describing *Rheobatrachus,* a rare animal indeed. Not a single *Rheobatrachus silus* has been seen in its natural habitat since 1981. A series of dry summers and late rains has restricted the range of this aquatic frog—and five years of no sitings must raise fears about extinction. Fortunately, a second species, named *R. xutellinus,* was discovered in January 1984, living in shallow sections of fast-flowing streams, about 500 miles north of the range of *R. silus.* This slightly larger version (up to three inches in length) also broods in its stomach; twenty-two baby frogs inhabited a pregnant female.

When discussed as a disembodied oddity (the problem with traditional writing in natural history), *Rheobatrachus* may pique our interest but not our intellect. Placed into a proper context among other objects of nature's diversity—the "comparative approach" so characteristic of evolutionary biology—gastric brooding in *Rheobatrachus* embodies a message of great theoretical interest. *Rheobatrachus,* in one sense, stands alone. No other vertebrate swallows its own fertilized eggs, converts its stomach into a brood pouch, and gives birth through its mouth. But in another sense, *Rheobatrachus* represents just one solution to a common problem among frogs.

In his review of parental care, R. W. McDiarmid argues that frogs display "the greatest array of reproductive modes found in any vertebrates" (see his article in G. M. Burghardt and M. Bekoff, 1978). Much inconclusive speculation has been devoted to reasons for the frequent and independent evolution of brooding (and other forms of parental care) in frogs—a profound departure, after all, from the usual amphibian habit of laying eggs in water and permitting the young to pass their early lives as unattended aquatic tadpoles. Several authors have suggested the following common denominator: In many habitats, and for a variety of reasons, life as a free-swimming tadpole may become sufficiently uninviting to impose strong evolutionary pressure for bypassing this stage and undergoing "direct development" from egg to completed frog. Brooding is an excellent strategy for direct development—since tadpole life may be spent in a brood pouch, and the bad old world need not be faced directly before froghood.

In any case, brooding has evolved often in frogs, and in an astonishing variety of modes. As a minimal encumbrance and modification, some frogs simply attach eggs to their exteriors. Males of the midwife toad *Alytes obstetricans* wrap strings of eggs about their legs and carry them in tow.

At the other extreme of modification, some frogs have evolved special brood pouches in unconventional places. The female *Gastrotheca riobambae,* an Ecuadorean frog from Andean valleys, develops a pouch on her back, with an opening near the rear and an internal extension nearly to her head. The male places fertilized eggs in her pouch, where they develop under the skin of her back for five to six weeks before emerging as late-stage tadpoles.

In another Australian frog, *Assa darlingtoni,* males develop pouches on their undersides, opening near their hind legs but extending forward to the front legs (see article by G.J. Ingram, M. Anstis, and C.J. Corben, 1975). Females lay their eggs among leaves. When they hatch, the male places himself in the middle of the mass and either coats himself with jelly from the spawn or, perhaps, secretes a slippery substance himself. The emerging tadpoles then perform a unique act of acrobatics among amphibians: they move in an ungainly fashion by bending their bodies, head toward tail, and then springing sideways and forward. In this inefficient manner, they migrate over the slippery body of their father and enter the brood pouch under their own steam. (I am almost tempted to say, given the Australian venue, that these creatures have been emboldened to perform in such unfroglike ways by watching too many surrounding marsupials, for the kangaroo's undeveloped, almost larval joey also must endure a slow and tortuous crawl to the parental pouch!)

In a kind of intermediate mode, some frogs brood their young internally but use structures already available for other purposes. I have already discussed *Rhinoderma,* the vocal-pouch brooder of Chile. Evolution seizes its opportunities. The male vocal pouch is roomy and available; in a context of strong pressure for brooding, some lineage will eventually overcome the behavioral obstacles and grasp this ready possibility. The eggs of *R. danvini* develop for twenty-three days before the tadpoles hatch. For the first twenty days, tadpoles grow within eggs exposed to the external environment. But tadpoles then begin to move, and this behavior apparently triggers a response from the male parent. He then takes the advanced eggs into his vocal pouch. They hatch there three days later and remain for fifty-two days until the end of metamorphosis, when the young emerge through their father's mouth as perfectly formed little froglets. In the related species *R. rufum,* muscular activity begins after eight days within the egg, and males keep the tadpoles in their vocal sacs for much shorter periods, finally expelling them, still in the tadpole stage, into water (see article by K. Busse, 1970).

In this context, *Rheobatrachus* is less an oddity than a fulfillment. Stomachs provide the only other large internal pouch with an egress of sufficient size. Some lineage of frogs was bound to exploit this possibility. But stomachs present a special problem not faced by vocal sacs or novel pouches of special construction—and we now encounter the key dilemma that will bring us back to mimicry in butterflies and the evolutionary problem of incipient stages. Stomachs are already doing something else—and that something is profoundly inimical to the care and protection of fragile young. Stomachs secrete acid and digest food—and eggs and tadpoles are, as they say down under, mighty good tucker.

In short, to turn a stomach into a brood pouch, something must turn off the secretion of hydrochloric acid and suppress the passage of eggs into the intestine. At a minimum, the brooding mother cannot eat during the weeks that she carries young in her stomach. This inhibition may arise automatically and present no special problem. Stomachs contain "stretch receptors" that tell an organism when to stop eating by imposing a feeling of satiety as the mechanical consequence of a full stomach. A batch of swallowed eggs will surely set off this reaction and suppress further eating.

But this fact scarcely solves our problem—for why doesn't the mother simply secrete her usual acid, digest the eggs, and relieve her feeling of satiety? What turns off the secretion of hydrochloric acid and the passage of eggs into the intestine?

Tyler and his colleagues immediately realized, when they discovered gastric brooding in *Rheobatrachus,* that suppression of stomach function formed the crux of their problem. "Clearly," they wrote, "the intact amphibian stomach is likely to be an alien environment for brooding." They began by studying the changes induced by brooding in the architecture of the stomach. They found that the secretory mucosa (the lining that produces acid) regresses while the musculature strengthens, thus converting the stomach into a strong and chemically inert pouch. Moreover, these changes are not "preparatory"—that is, they do not occur before a female swallows her eggs. Probably, then, something in the eggs or tadpoles themselves acts to suppress their own destruction and make a congenial place of their new home. The Australian researchers then set out to find the substance that suppresses acid secretion in the stomach—and they have apparently succeeded.

P. O'Brien and D. Shearman, in a series of ingenious experiments, concentrated water that had been in contact with developing *Rheobatrachus* embryos to test for a chemical substance that might suppress stomach function in the mothers. They dissected out the gastric mucosa (secreting surface) of the toad *Bufo marinus* *(Rheobatrachus* itself is too rate to sacrifice so main adult females for such an experiment) and kept it alive in vitro. They showed that this isolated mucosa can function normally to secrete stomach acids and that well-known chemical inhibitors will suppress the secretion. They then demonstrated that water in contact with *Rheobatrachus* tadpoles suppresses the mucosa, while water in contact with tadpoles of other species has no effect. Finally, they succeeded in isolating a chemical suppressor from the water—prostaglandin E_2. (The prostaglandins are hormonelike substances, named for their first discovery as secretions of the human prostate gland—though they form throughout the body and serve many functions.)

Thus, we may finally return to mimicry and the problem of incipient stages. I trust that some readers have been bothered by an apparent dilemma of illogic and reversed causality. The eggs of *Rheobatrachus* must contain the prostaglandin that suppresses secretion of gastric acid and allows the stomach to serve as an inert brood pouch. It's nice to know that eggs contain a substance for their own protection in a hostile environment. But in a world of history—not of created perfection—how can such a system arise? The ancestors of *Rheobatrachus* must have been conventional frogs, laying eggs for external development. At some point, a female *Rheobalrachus* must have swallowed its fertilized eggs (presumably taking them for food, not with the foresight of evolutionary innovation)—and the fortuitous presence of prostaglandin suppressed digestion and permitted the eggs to develop in their mother's stomach.

The key word is *fortuitous.* One cannot seriously believe that ancestral eggs actively evolved prostaglandin because they knew that, millions of years in the future, a mother would swallow them and they would then need some inhibitor of gastric secretion. The eggs must have contained prostaglandin for another reason or for no particular reason at all (perhaps just as a metabolic by-product of development). Prostaglandin provided a lucky break with respect to the later evolution of gastric brooding—a historical precondition fortuitously available at the right moment, a sine qua non evolved for other reasons and pressed into service to initiate a new evolutionary direction.

Darwin proposed the same explanation for the initiation of mimicry—as a general solution to the old problem of incipient stages. Mimicry works splendidly as a completed system, but what gets the process started along one potential pathway among many? Darwin argued that a mimicking butterfly must begin with a slight *and fortuitous* resemblance to its model. Without this leg up for initiation, the process of improvement to mimetic perfection cannot begin. But once an accidental, initial resemblance provides some slight edge, natural selection can improve the fit from imperfect beginnings.

Thus, Darwin noted with pleasure Bates's demonstration that mimicry always arose among butterflies more prone to vary than others that never evolve mimetic forms. This tendency to vary must be the precondition that establishes fortuitous initial resemblance to models in some cases. "It is necessary to suppose," Darwin wrote, that ancestral mimics "accidently resembled a member of another and protected group in a sufficient degree to afford some slight protection, this having given the basis for the subsequent acquisition of the most perfect resemblance." Ancestral mimics happened to resemble a model in some slight manner—and the evolutionary process could begin. The eggs of *Rheobalrachus* happened to contain a prostaglandin that inhibited gastric secretion—and their mother's stomach became a temporary home, not an engine of destruction.

New evolutionary directions must have such quirky beginnings based on the fortuitous presence of structures and possibilities evolved for other reasons. After all, in nature, as in human invention, one cannot prepare actively for the utterly unexpected. Gastric brooding must be an either-or, a quantum jump in evolutionary potential. As Tyler argues, what intermediary stage can one imagine? Many fishes (but no frogs) brood young in their mouths—while only males possess throat pouches, but only female *Rheobalrachus* broods in its stomach. Eggs can't develop halfway down the esophagus.

We glimpse in the story *of Rheobalrachus* a model for the introduction of creativity and new directions in evolution (not just a tale of growing bigger or smaller, fiercer or milder, by the everyday action of natural selection). Such new directions, as Darwin argued in resolving the problem of incipient stages, must be initiated by fortuitous prerequisites, thus imparting a quirky and unpredictable character to the history of life. These new directions may involve minimal changes at first—since the fortuitous prerequisites are already present, though not so utilized, in ancestors. A female *Rheobalrachus* swallowed its fertilized eggs, and a striking new behavior and mode of brooding arose at once by virtue of a chemical fortuitously present in eggs, and by the automatic action of stretch receptors in the stomach. Such minimal changes are pregnant with possibilities. Most probably lead nowhere beyond a few oddballs—as with *Rheobalrachus,* probably already well on its way to extinction.

But a few quirky new directions may become seeds of major innovations and floods of diversity in life's history. The first protoamphibian that crawled out of its pond has long been a favorite source of evolutionary cartoon humor. The captions are endless—from "see ya later as alligator" to "because the weather's better out here." But my favorite reads "here goes nothing." It doesn't happen often, but when nothing becomes something, the inherent power of evolution, normally an exquisitely conservative force, can break forth. Or, as Reginald Bunthorne proclaims in Gilbert and Sullivan's *Patience* (which evolution must have above all else): "Nature for restraint too mighty far, has burst the bonds of art—and here we are."

Postscript

It is my sad duty to report a change of state, between writing and republishing this essay, that has made its title eerily prophetic. *Rheobatrachus situs,* the stomach-brooding frog and star of this essay, has apparently become extinct. This species was discovered in 1973, living in fair abundance in a restricted region of southeast Queensland, Australia. In early 1990, the National Research Council (of the United States) convened a conference to discuss "unexplained losses of amphibian populations around the world" (as reported in *Science News,* March 3, 1990). Michael J. Tyler, member of the team that discovered stomach brooding in *Rheobatrachus,* reported that 100 specimens could easily be observed per night when the population maintained fair abundance during the mid-1970s. Naturalists have not found a single individual since 1981, and must now conclude that the species is extinct (for several years they hoped that they were merely observing a sharp and perhaps cyclical reduction in numbers). Even more sadly, this loss forms part of a disturbing and unexplained pattern in amphibian populations throughout the world. In Australia alone, 20 of 194 frog species have suffered serious local drops in population size during the past decade, and at least one other species has become extinct.

Knight Takes Bishop?

I HAVE NOT THE SLIGHTEST doubt that truth possesses inestimable moral value. In addition, as Mr. Nixon once found to his sorrow, truth represents the only way to keep a complex story straight, for no one can remember all the details of when he told what to whom unless his words have an anchor in actual occurrence.

> Oh, what a tangled web we weave,
> When first we practice to deceive!

Yet, for a scholar, there is nothing quite like falsehood. Lies are pinpoints—identifiable historical events that can be traced. Falsehoods also have motivations—points of departure for our ruminations on the human animal. Truth, on the other hand, simply happens. Its accurate report teaches us little beyond the event itself.

In this light, we should note with interest that the most famous story in all the hagiography of evolution is, if not false outright, at least grossly distorted by biased reconstruction long after the fact. I speak of Thomas Henry Huxley's legendary encounter with the bishop of Oxford, "Soapy Sam" Wilberforce, at the 1860 meeting of the British Association for the Advancement of Science, held in His Lordship's own see.

Darwin had published the *Origin of Species* in November 1859. Thus, when the British Association for the Advancement of Science met at Oxford in the summer of 1860, this greatest of all debates received its first prominent public airing. On Saturday, June 30, more than 700 people wedged themselves into the largest room of Oxford's Zoological Museum to hear what was, by all accounts, a perfectly dreadful hour-long peroration by an American scholar, Dr. Draper, on the "intellectual development of Europe considered with reference to the views of Mr. Darwin." Leonard Huxley wrote, in *Life and Letters of Thomas Henry Huxley:*

> The room was crowded to suffocation. . . . The very windows by which the room was lighted down the length of its west side were packed with ladies, whose white handkerchiefs, waving and fluttering in the air at the end of the Bishop's speech, were an unforgettable factor in the acclamation of the crowd.

The throng, as Leonard Huxley notes, had not come to hear Dr. Draper drone on about Europe. Word had circulated widely that "Soapy Sam" Wilberforce, the silver-tongued bishop of Oxford, would attend with the avowed purpose of smashing Mr. Darwin in the discussion to follow Draper's paper.

The story of Wilberforce's oration and Huxley's rejoinder has been enshrined among the half-dozen greatest legends of science—surely equal to Newton beaned by an apple or Archimedes jumping from his bath and shouting "Eureka!" through the streets of Syracuse. We have read the tale from comic book to novel to scholarly tome. We have viewed the scene, courtesy of the BBC, in our living rooms. The story has an "official version" codified by Darwin's son Francis, published in his *Life and Letters of Charles Darwin,* and expanded in Leonard Huxley's biography of his father. This reconstruction has become canonical, copied from source to later source hundreds of times, and rarely altered even by jot or tittle. Consider just one of countless retellings, chosen as an average and faithful version (from Ruth Moore's *Charles Darwin,* Hutchinson, 1957):

> For half an hour the Bishop spoke savagely ridiculing Darwin and Huxley, and then he turned to Huxley, who sat with him on the platform. In tones icy with sarcasm he put his famous question: was it through his grandfather or his grandmother that he claimed descent from an ape? . . . At the Bishop's question, Huxley had clapped the knee of the

> surprised scientist beside him and whispered: "The Lord hath delivered him into mine hands." . . . [Huxley] tore into the arguments Wilberforce had used. . . . Working himself up to his climax, he shouted that he would feel no shame in having an ape as an ancestor, but that he would be ashamed of a brilliant man who plunged into scientific questions of which he knew nothing. In effect, Huxley said that he would prefer an ape to the Bishop as an ancestor, and the crowd had no doubt of his meaning.
>
> The room dissolved into an uproar. Men jumped to their feet, shouting at this direct insult to the clergy. Lady Brewster fainted. Admiral Fitzroy, the former Captain of the Beagle, waved a Bible aloft, shouting over the tumult that it, rather than the viper he had harbored in his ship, was the true and unimpeachable authority. . . .
>
> The issue had been joined. From that hour on, the quarrel over the elemental issue that the world believed was involved, science versus religion, was to rage unabated.

We may list as the key, rarely challenged features of this official version the following claims:

1. Wilberforce directly bearded and taunted Huxley by pointedly asking, in sarcastic ridicule, whether he claimed descent from an ape on his grandfather's or grandmother's side.
2. Huxley, before rising to the challenge, mumbled his famous mock-ecclesiastical sarcasm about the Lord's aid in his coming rhetorical victory.
3. Huxley (ban responded to Wilberforce's arguments in loud, clear, and forceful tones.
4. Huxley ended his speech with a devastatingly effective parry to the bishop's taunt.
5. Although Huxley said only that he would prefer an ape to a man who used skills of oratory to obfuscate rather than to seek truth, many took him to mean (and some thought he had said) that he would prefer an ape to a bishop as an ancestor. (Huxley, late in life, disavowed this stronger version about apes and bishops. When Wilberforce's son included it in a biography of his father, Huxley protested and secured a revision.)
6. Huxley's riposte inspired an uproar. The meeting ended forthwith and in tumult.

7. Although Moore, to her credit, does not make this claim, we are usually told that Huxley had scored an unambiguous and decisive victory—a key incident in Darwin's triumph.

8. This debate focused the world's attention on the real and deep issue of Darwin's century—science versus religion. Huxley's victory was a pivotal moment in the battle for science and reason against superstition and dogma.

I have had a strong interest in this story ever since, as an assistant professor on sabbatical leave at Oxford in 1970,1 occupied a dingy office in the back rooms of the Zoological Museum, now crammed with cabinets of fossils and subdivided into cubicles, but then the large and open room where Huxley and Wilberforce fell to blows. For six months, I sat next to a small brass plaque announcing that the great event had occurred on my very spot. I also felt strong discomfort about the official tale for two definite reasons. First, it is all too pat—the victor and the vanquished, good triumphing over evil, reason over superstition. So few heroic tales in the simplistic mode turn out to be true. Huxley was a brilliant orator, but why should Wilberforce have failed so miserably? Much as I dislike the man, he was no fool. He was as gifted an orator as Huxley and a dominant intellectual force among conservative Anglicans.

Second, I knew from preliminary browsings that the official tale was a reconstruction, made by Darwin's champions some quarter century after the fact. Amazingly enough (for all its later fame), no one bothered to record the event in any detail at the time itself. No stenographer was present. The two men exchanged words to be sure, but no one knows what they actually said, and the few sketchy reports of journalists and letter writers contain important gaps and contradictions. Ironically, the official version has been so widely accepted and unchallenged not because we know its truth by copious documentation, but rather because so little data exist for a potential challenge.

For years, this topic has been about number fifty in my list of one hundred or so potential essays (sorry folks, but, the Lord and editors willing, you may have me to kick around for some time to come). Yet for want of new data about my suspicions, it remained well back in my line of processing, until I received a letter from my friend and distinguished Darwin scholar Sam Schweber of Brandeis University. Schweber wrote: "I came across a letter from Balfour Stewart to David Forbes commenting on the BAAS meeting he just attended at which he witnessed the Huxley-Wilberforce debate. It is probably the most accurate statement of what transpired." I read Stewart's letter and sat bolt upright with attention and smiles. Stewart wrote, describing the scene along the usual lines, thus vouching for the basic outline:

> There was an animated discussion in a large room on Saturday last at Oxford on Darwin's theory where the Bishop of Oxford and Prof. Huxley fell to blows. . . . There was one good thing I cannot help mentioning. The Bishop said he had been informed that Prof. Huxley had said he didn't care whether his grandfather was an ape *[sic* for punctuation] now he [the bishop] would not like to go to the Zoological Gardens and find his father's father or his mother's mother in some antiquated ape. To which Prof. Huxley replied that he would rather have for his grandfather an honest ape low in the scale of being than a man of exalted intellect and high attainments who used his power to pervert the truth.

Colorful, though nothing new so far. But I put an ellipsis early in the quotation, and I should now like to restore the missing words. Stewart wrote: "I think the Bishop had the best of it." Score one big point for my long-held suspicions. Balfour Stewart was no benighted cleric, but a distinguished scientist, Fellow of the Royal Society, and director of the Kew Observatory. Balfour Stewart also thought that Wilberforce had won the debate!

This personal discovery sent me to the books (I thank my research assistant, Ned Young, for tracking down all the sources, no mean job for so many obscure bits and pieces). We gathered all the eyewitness accounts (damned few) and found a half dozen or so modern articles, mostly by literary scholars, on aspects of the debate. (See Janet Browne, 1978; Sheridan Gilley, 1981; J. R. Lucas, 1979. I especially commend Browne's detective work on Francis Darwin's construction of the official version, and Gilley's incisive and well-written account of the debate.) I confess disappointment in finding that Stewart's letter was no new discovery. Yet I remain surprised that its key value—the claim by an important scientist that Wilberforce had won—has received so little attention. So far as I know, Stewart's letter has never been quoted *in extenso,* and no reference gives it more than a passing sentence. But I was delighted to find that the falsity of the official version is common knowledge among a small group of scholars. All the more puzzling, then, that the standard, heroic account continues to hold sway.

What is so wrong with the official tale, as epitomized in my eight points above? We should begin by analyzing the very few eyewitness accounts recorded right after the event itself.

Turning to reports by journalists, we must first mark the outstanding negative evidence. In a nation with a lively press, and with traditions for full and detailed reporting (so hard to fathom from our age of television and breathless paragraphs for the least common denominator), the great debate stands out for its nonattention. *Punch,* Wilberforce's frequent and trenchant critic, ignored the exchange but wrote poem and parody aplenty on another famous repartee about evolution from the same meeting—Huxley versus Owen on the brains of humans and gorillas. The *Athenaeum,* in one of but two accounts (the other from *Jackson's Oxford Journal),* presents a straightforward report that, in its barest outline, already belies the standard version in two or three crucial respects. On July 7, the reporter notes Oxford's bucolic charms: "Since Friday, the air has been soft, the sky sunny. A sense of sudden summer has been felt in the meadows of Christ Church and in the gardens of St. John's; many a dreamer of dreams, tempted by the summer warmth . . . and stealing from section A or B [of the meeting] has consulted his ease and taken a boat." But we then learn of a contrast between fireworks inside and punting lazily downstream while taking one's *dolcefar niente.*

> The Bishop of Oxford came out strongly against a theory which holds it possible that man may be descended from an ape. . . . But others—conspicuous among these, Prof. Huxley—have expressed their willingness to accept, for themselves, as well as for their friends and enemies, all actual truths, even the last humiliating truth of a pedigree not registered in the Herald's College. The dispute has at least made Oxford uncommonly lively during the week.

The next issue, July 14, devotes a full page of tiny type to Dr. Draper and his aftermath—the longest eyewitness account ever penned. The summary of Wilberforce's remarks indicates that his half-hour oration was not confined to gibe and rhetoric, but primarily presented a synopsis of the competent (if unoriginal) critique of the *Origin* that he later published in the *Quarterly Review.* The short paragraph allotted to Huxley's reply does not mention the famous repartee—an omission of no great import in a press that, however detailed, could be opaquely discreet. But the account of Huxley's words affirms what all letter writers (see below) also noted—that Huxley spoke briefly and presented no detailed refutation of the bishop's arguments. Instead, he focused his remarks on the logic of Darwin's argument, asserting that evolution was no mere speculation, but a theory supported by copious evidence even if the process of transmutation could not be directly observed.

By the standard account, chaos should now break out, FitzRoy should jump up raving, and Henslow should gavel the meeting closed. No such thing; the meeting went on. FitzRoy took the podium in his turn. Two other speakers followed. And then, the true climax—not entirely omitted in Francis Darwin's "official" version so many years later, but so relegated to a few lines of afterthought that the incident simply dropped out of most later accounts—leading to the popular impression that Huxley's riposte had ended the meeting. Henslow turned tojoseph Hooker, the botanist of Darwin's inner circle, and asked him "to state his view of the botanical aspect of the question."

The *Athenaeum* gave Hooker's remarks four times the coverage awarded to Huxley. It was Hooker who presented a detailed refutation of Wilberforce's specific arguments. It was Hooker who charged directly that the bishop had distorted and misunderstood Darwin's theory. We get some flavor of Hooker's force and effectiveness from a section of ***the*** *Athenaeum's* report:

> In the first place, his Lordship, in his eloquent address, had as it appeared to him [Hooker], completely misunderstood Mr. Darwin's hypothesis: his Lordship intimated that this maintained the doctrine of the transmutation of existing species one into another, and had confounded this with that of the successive development of species by variation and natural selection. The first of these doctrines was so wholly opposed to the facts, reasonings and results of Mr. Darwin's

> work, that he could not conceive how any one who had read it could make such a mistake—the whole book, indeed, being a protest against that doctrine.

Moreover, it was Hooker who presented the single most effective debating point against Wilberforce (according to several eyewitness accounts) by stating publicly that he had long opposed evolution but had been led to the probable truth of Darwin's claim by so many years of direct experience with the form and distribution of plants. The bishop did not respond, and Henslow closed the meeting after Hooker's successful speech.

When we turn to the few letters of eyewitnesses, we find the *Athenaeum* account affirmed, the official story further compromised, and some important information added—particularly on the exchange about apes and ancestors. We must note, first of all, that the three letters most commonly cited—those of Green, Fawcett, and Hooker himself—were all written by participants or strong partisans of Darwin's side. For example, future historian J. R. Green, source of the standard version for Huxley's actual words, began his account (to the geologist W. Boyd Dawkins) with a lovely Egyptian metaphor of fealty to Darwin:

> On Saturday morning I met Jenkins going to the Museum. We joined company, and he proposed going to Section D, the Zoology, etc. "to hear the Bishop of Oxford smash Darwin." "Smash Darwin! Smash the Pyramids," said I in great wrath. . . .

(These one-sided sources make Balfour Stewart's neglected letter all the more important—for he was the only uncommitted scientist who reported his impressions right after the debate.)

We may draw from these letters, I believe, three conclusions that further refute the official version. First, Huxley's words may have rung true, but his oratory was faulty. He was ill at ease (his great career as a public speaker lay in the future). He did not project; many in the audience did not hear what he said. Hooker wrote to Darwin on July 2:

> Well, Sam Oxon [short for *Oxoniensis,* Latin for "of Oxford," Wilberforce's ecclesiastical title] got up and spouted

> for half an hour with inimitable spirit, ugliness and emptiness and unfairness. . . . Huxley answered admirably and turned the tables, but he could not throw his voice over so large an assembly, nor command the audience; and he did not allude to Sam's weak points nor put the matter in a form or way that carried the audience.

The chemist A. G. Vernon-Harcourt could not recall Huxley's famous words many years later because he had not heard them over the din. He wrote to Leonard Huxley: "As the point became clear, there was a great burst of applause, which mostly drowned the end of the sentence."

Second, for all the admitted success of Huxley's great moment, Hooker surely made the more effective rebuttal—and the meeting ended with his upbeat. I hesitate to take Hooker's own account at face value, but he was so scrupulously modest and self-effacing, and so willing to grant Huxley all the credit later on as the official version congealed, that I think we may titrate the adrenaline of his immediate joy with the modesty of his general bearing and regard his account to Darwin as pretty accurate:

> My blood boiled, I felt myself a dastard; now I saw my advantage; I swore to myself that I would smite that Amalekite, Sam, hip and thigh. . . . There and then I smashed him amid rounds of applause. I hit him in the wind and then proceeded to demonstrate in a few words: (1) that he could never have read your book, and (2) that he was absolutely ignorant of the rudiments of Bot [botanical] Science. I said a few more on the subject of my own experience and conversion, . . . Sam was shut up—had not one word to say in reply, and the meeting *was dissolved forthwith* [Hooker's italics].

Third, and most important, we do not really know what either man said in the famous exchange about apes and ancestors. Huxley's retort is not in dispute. The eyewitness versions differ substantially in wording, but all agree in content. We might as well cite Green's version, if only because it became canonical when Huxley himself "approved" it for Francis Darwin's biography of his father:

> I asserted, and I repeat—that a man has no reason to be ashamed of having an ape for his grandfather. If there were an ancestor whom I should feel shame in recalling, it would rather be a *man,* a man of restless and versatile intellect, who, not content with an equivocal success in his own sphere of activity, plunges into scientific questions with which he has no real acquaintance, only to obscure them by an aimless rhetoric, and distract the attention of his hearers from the real points at issue by eloquent digressions and skilled appeals to religious prejudice.

Huxley later demurred only about the word "equivocal," asserting that he would not have besmirched the bishop's competence in matters of religion.

Huxley's own, though lesser-known version (in a brief letter written to his friend Dyster on September 9, 1860) puts the issue more succinctly, but to the same effect:

> If then, said I, the question is put to me would I rather have a miserable ape for a grandfather or a man highly endowed by nature and possessed of great means of influence and yet who employs those faculties and that influence for the mere purpose of introducing ridicule into a grave scientific discussion—I unhesitatingly affirm my preference for the ape.

But what had Wilberforce said to incur Huxley's wrath? Quite astonishingly, on this pivotal point of the entire legend, we have nothing but a flurry of contradictory reports. No two accounts coincide. All mention apes and grandfathers, but beyond this anchor of agreement, we find almost every possible permutation of meaning.

We don't know, first of all, whether or not Wilberforce committed that most dubious imposition upon Victorian sensibilities by daring to mention *female* ancestry from apes—that is, did he add grandmothers or speak only of grandfathers? Several versions cite only the male parent, as in Green's letter: "He [Wilberforce] had been told that Professor Huxley had said that he didn't see that it mattered much to a man whether his grandfather was an ape or not. Let the learned professor speak for himself." Yet, I am inclined to the conclusion that Wilberforce must have said something about grandmothers. The distaff side of descent occurs in several versions, Balfour Stewart's neglected letter in particular (see earlier citation), by disinterested observers or partisans of Wilberforce. I can understand why opponents might have delighted in such an addition ("merely corroborative detail, intended to give artistic verisimilitude to an otherwise bald and unconvincing narrative," as Pooh-Bah liked to say). But why should sympathetic listeners remember such a detail if the bishop had not included it himself?

But, far more important, it seems most unlikely that the central claim of the official version can be true—namely, that Wilberforce taunted Huxley by asking him pointedly whether he could trace his personal ancestry from grandparents back to apes (made all the worse if the bishop really asked whether he could trace it on his. mother's side). No contemporary account puts the taunt quite so baldly. The official version cites a letter from Lyell (who was not there) since the anonymous eyewitness (more on him later) who supplied Francis Darwin's account could not remember the exact words. Lyell wrote: "The Bishop asked whether Huxley was related by his grandfather's or grandmother's side to an ape." The other common version of this taunt was remembered by Isabel Sidgwick in 1898: "Then, turning to his antagonist with a smiling insolence, he begged to know, was it through his grandfather or his grandmother that he claimed his descent from a monkey?"

We will never know for sure, but the memories of Canon Farrar seem so firm and detailed, and ring so true to me, that I shall place my money on his version. Farrar was a liberal clergyman who once organized a meeting for Huxley to explain Darwinism to fellow men of the cloth. His memories, written in 1899 to Leonard Huxley, are admittedly forty years old, but his version makes sense of many puzzles and should be weighted well on that account—especially since he regarded Huxley as the victor and did not write to reconstruct history in the bishop's cause. Farrar wrote, taking the official version of Wilberforce's taunt to task:

> His words are quite misquoted by you (which your father refuted). They did not appear vulgar, nor insolent nor per-

> sonal, but flippant. He had been talking of the perpetuity of species in birds [a correct memory since all agree that Wilberforce criticized Darwin on the breeds of pigeons in exactly this light]: and then denying *a fortiori* the derivation of the species Man from Ape, he rhetorically invoked the help of feeling: and said (I swear to the sense and form of the sentence, if not to the words) "If anyone were to be willing to trace his descent through an ape as his grandfather, would he be willing to trace his descent similarly on the side of his grandmother." It was (you see) the arousing of antipathy about degrading women to the Quadrumana [four-footed apes]. It was not to the point, but it was the purpose. It did not sound insolent, but unscientific and unworthy of the zoological argument which he had been sustaining. It was a bathos. Your father's reply . . . showed that there was a vulgarity as well as a folly in the Bishop's words; and the impression distinctly was, that the Bishop's party as they left the room, felt abashed; and recognized that the Bishop had forgotten to behave like a gentleman.

Farrar's analysis of Huxley's victory includes an interesting comment on Victorian sensibilities:

> The victory of your father, was not the ironical dexterity shown by him, but the fact that he had got a victory in respect of manners and good breeding. You must remember that the whole audience was made up of gentlefolk, who were not prepared to endorse anything vulgar.

Finally, Farrar affirms the other major falsity of the official version by acknowledging the superiority of Hooker's reply:

> The speech which really left its mark scientifically on the meeting, was the short one of Hooker. . . . I should say that to fair minds, the intellectual impression left by the discussion was that the Bishop had staled some facts about the perpetuity of species, but that no one had really contributed any valuable point to the opposite side except Hooker . . . but that your father had scored a victory over Bishop Wilberforce in the question of good manners.

And so, in summary, we may conclude that the heroic legend of the official version fails badly in two crucial points—our ignorance of Wilberforce's actual words and the near certainty that the forgotten Hooker made a better argument than Huxley. What, then, can we conclude, based on such poor evidence, about such a key event in the hagiography of science? Huxley did not debate Wilberforce at Oxford in 1860; rather, they both spoke, one after the other, in a prolonged discussion of Draper's paper. They had one short and wonderful exchange of rhetorical barbs on a totally nonintellectual point prompted by a whimsical remark, perhaps even a taunt, that Wilberforce made about apes and ancestry, though no one remembered precisely what he said. Huxley made a sharp and effective retort. Everyone enjoyed the incident immensely and recalled it in a variety of versions. Some thought Huxley had won the exchange; others credit Wilberforce. Huxley hardly dealt with Wilberforce's case against Darwin. Hooker, however, made an effective reply in Darwin's behalf, and the meeting ended.

All events before the codification of the official version support this ambiguous and unheroic account. In particular, Wilberforce seemed not a bit embarrassed by the incident. Disraeli spoke about it in his presence. Wilberforce reprinted his review of Darwin's *Origin,* the basis of his remarks that fateful day, in an 1874 collection of his works. His son recounted the tale with credit in Wilberforce's biography. Moreover, Darwin and Wilberforce remained on good terms. The ever genial Darwin wrote to Asa Gray that he found Wilberforce's review "uncommonly clever, not worth anything scientifically, but quizzes me in splendid style. I chuckled with laughter at myself." Wilberforce, told by the vicar of Downe about Darwin's reaction, said: "I am glad he takes it in this way. He is such a capital fellow."

Moreover, though I don't believe that self-justification provides much evidence for anything, we do have a short testimony from Wilberforce himself. He wrote to Sir Charles Anderson just three days after the event: "On Saturday Professor Henslow who presided over the Zoological Section called on me by name to address the Section on Darwin's Theory. So I could not escape and had quite a long fight with Huxley. I think I thoroughly beat him." This letter, now housed in the Bodleian Library of Oxford University, escaped all notice until 1978, when Josef L. Altholz cited it in the *Journal of the History of Medicine.* I would not exaggerate the importance of this document because it smacks of insincerity at least once—so why not in its last line as well? We know that 700 people crammed the Museum's largest room to witness the proceedings. They didn't come to hear Dr. Draper on the intellectual development of Europe. Wilberforce was on the dais, and if he didn't know that he would speak, how come everyone else did?

Why then, and how, did the official version so color this event as a primal victory for evolution? The answer largely lies with Huxley himself, who successfully promoted, in retrospect, a version that suited his purposes (and had probably, by then, displaced the actual event in his memory). Huxley, though not antireligious, was uncompromisingly and pugnaciously anticlerical. Moreover, he despised Wilberforce and his mellifluous sophistries. When Wilberforce died in 1873, from head injuries sustained in a fall from his horse, Huxley remarked (as the story goes): "For once, reality and his brains came into contact and the result was fatal."

Janet Browne has traced the construction of the official version in Francis Darwin's biography of his father. The story is told through an anonymous eyewitness, but Browne proves that Hooker himself wrote the account, volunteering for the task with direct purpose (writing to Francis): "Have you any account of the Oxford meeting? If not, I will, if you like, see what I can do towards vivifying it (and vivisecting the Bishop) for you." Hooker dredged his memory with pain and uncertainty. He had forgotten his letter to Darwin and admitted, "It is impossible to be sure of what one heard, or of impressions formed, after nearly thirty years of active life." And further, "I have been driven wild formulating it from memory." Huxley then vetted Hooker's account and the official story was set.

The tale was then twice embellished—first, in 1892, when Francis published a shorter biography of Charles Darwin, and Huxley contributed a letter, now remembering for the first time (more than thirty years later) his *solto voce* crack, "The Lord hath delivered him into mine hands"; second, in 1900, when Leonard Huxley wrote the life of his father. Thus, dutiful sons presented the official version as constructed by a committee of two—the chief participants Huxley and Hooker—from memories colored by thirty years of battle. We can only agree with Sheridan Gilley, who writes:

> The standard account is a wholly one-sided effusion from the winning side, put together long after the event, uncritically copied from book to book, and shaped by the hagiographic conventions of the Victorian life and letters.

So much for correcting a moment of history. But why should we care today? Does the heroic version do any harm? And does its rectification have any meaning beyond our general preference for accuracy? Stories do not become primary legends simply because they tell rip-roaring narratives; they must stand as exemplars, particular representations of something deeper and far more general. The official version of Huxley versus Wilberforce is an archetype for a common belief about the nature of science and its history. The fame and meaning of the official version lie in this wider context. Yet this common belief is not only wrong (or at least seriously oversimplified) but ultimately harmful to science. Thus, in debunking the official version of Huxley versus Wilberforce, we might make a helpful correction for science itself.

Ruth Moore captured the general theme in her version of the standard account: "From that hour on, the quarrel over the elemental issue that the world believed was involved, science versus religion, was to rage unabated." The story has archetypal power because Huxley and Wilberforce, in the official version, are not mere men but symbols, or synecdoches, for a primal struggle: religion versus science, reaction versus enlightenment, dogma versus truth, darkness versus light.

All men have blind spots, however broad their vision. Thomas Henry Huxley was the most eloquent spokesman that evolution has ever known. But his extreme anticlericalism led him to an uncompromising view of organized religion as the enemy of science. Huxley could envision no allies among the official clergy. Conservatives like Wilberforce were enemies pure and simple; liberals lacked the guts to renounce what fact and logic had falsified, as they struggled to marry the irreconcilable findings of science with their supernatural vision. He wrote in 1887 of those "whose business seems to be to mix the black of dogma and the white of science into the neutral tint of what they call liberal theology." Huxley did view his century as a battleground between science and organized religion—and he took great pride in the many notches on his own gun.

This cardboard dichotomy seems favorable for science at first (and superficial) glance. It enshrines science as something pure and apart from the little quirks and dogmas of daily life. It exalts science as a disembodied method for discovering truth at all costs, while social institutions—religion in particular—hold fast to antiquated superstition. Comfort and social stability resist truth, and science must therefore fight a lonely battle for enlightenment. Its heroes, in bad times, are true martyrs—Bruno at the stake, Galileo before the Inquisition—or, in better times, merely irritated, as Huxley was, by ecclesiastical stupidity.

But no battle exists between science and religion—the two most separate spheres of human need. A titanic struggle occurs, always has, always will, between questioning and authority, free inquiry and frozen dogma—but the institutions representing these poles are not science and religion. These struggles occur *within* each field, not primarily across disciplines. The general ethic of science leads to greater openness, but we have our fossils, often in positions of great power. Organized religion, as an arm of state power so frequently in history, has tended to rigidity—but theologies have also spearheaded social revolution. Official religion has not opposed evolution as a monolith. Many prominent evolutionists have been devout, and many churchmen have placed evolution at the center of their personal theologies. Henry Ward Beecher, America's premier pulpiteer during Darwin's century, defended evolution as God's way in a striking commercial metaphor: "Design by wholesale is grander than design by retail"—better, that is, to ordain general laws of change than to make each species by separate fiat.

The struggle of free inquiry against authority is so central, so pervasive that we need all the help we can get from every side. Inquiring scientists must join hands with questioning theologians if we wish to preserve that most fragile of all reeds, liberty itself. If scientists lose their natural allies by casting entire institutions as enemies, and not seeking bonds with soul mates on other paths, then we only make a difficult struggle that much harder.

Huxley had not planned to enter that famous Oxford meeting.

He was still inexperienced in public debate, not yet Darwin's bulldog. He wrote: "I did not mean to attend it—did not see the good of giving up peace and quietness to be episcopally pounded." But his friends prevailed upon him, and Huxley, savoring victory, left the meeting with pleasure and resolution:

> Hooker and I walked away from the meeting together, and I remember saying to him that this experience had changed my opinion as to the practical value of the art of public speaking, and that from that time forth I should carefully cultivate it, and try to leave off hating it.

So Huxley became the greatest popular spokesman for science in his century—as a direct result of his famous encounter with Wilberforce. He waded into the public arena and struggled for three decades to breach the boundaries between science and the daily life of ordinary people. And yet, ironically, his Manichean view of science and religion—abetted so strongly by the official version, his own construction in part, of the debate with Wilberforce.—harmed his greatest hope by establishing boundaries to exclude natural allies and, ultimately, by encircling science as something apart from other human passions. We may, perhaps, read one last document of the great Oxford debate in a larger metaphorical context as a plea, above all, for solidarity among people of like minds and institutions of like purposes. Darwin to Hooker upon receiving his account of the debate: "Talk of fame, honor, pleasure, wealth, all are dirt compared with affection."

William Jennings Bryan's Last Campaign

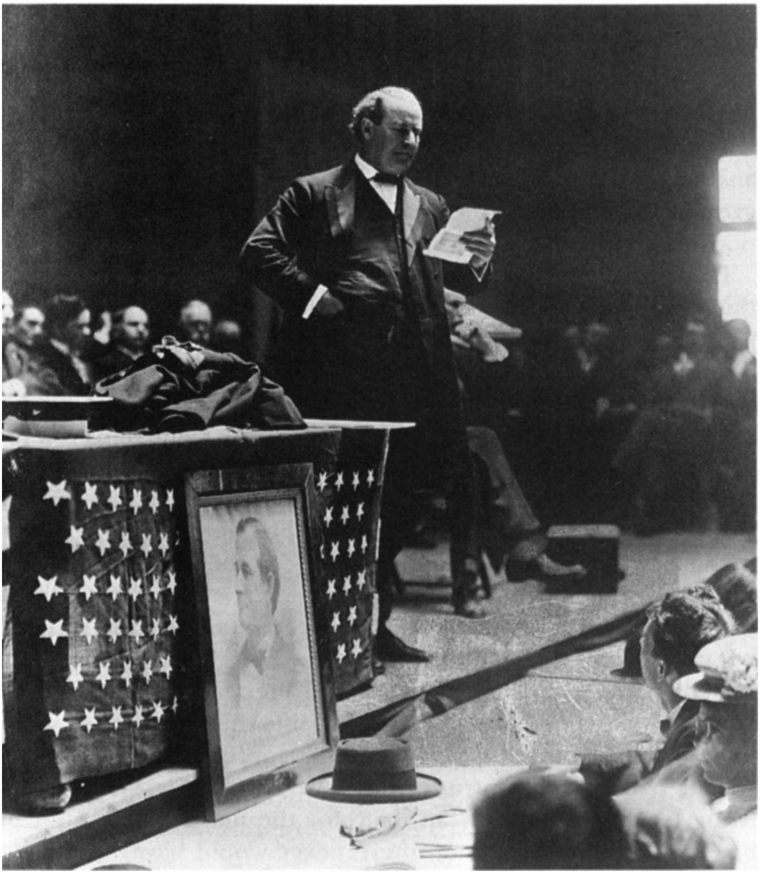
I HAVE SEVERAL REASONS for choosing to celebrate our legal victory over "creation science" by trying to understand with sympathy the man who forged this long and painful episode in American history—William Jennings Bryan. In June 1987, the Supreme Court voided the last creationist statute by a decisive 7-2 vote, and then wrote their decision in a manner so clear, so strong, and so general that even the most ardent fundamentalists must admit the defeat of their legislative strategy against evolution. In so doing, the Court ended William Jennings Bryan's last campaign, the cause that he began just after World War I as his final legacy, and the battle that took both his glory and his life in Dayton, Tennessee, when, humiliated by Clarence Darrow, he died just a few days after the Scopes trial in 1925.

My reasons range across the domain of Bryan's own character. I could invoke rhetorical and epigrammatic expressions, the kind that Bryan, as America's greatest orator, laced so abundantly into his speeches—Churchill's motto for World War II, for example: "In victory: magnanimity." But I know that my main reason is personal, even folksy, the kind of one-to-one motivation that Bryan, in his persona as the Great Commoner, would have applauded. Two years ago, a colleague sent me an ancient tape of Bryan's voice. I expected to hear the pious and polished shoutings of an old stump master, all snake oil and orotund sophistry. Instead, I heard the most uncanny and friendly sweetness, high pitched, direct, and apparently sincere. Surely this man could not simply be dismissed, as by H. L. Mencken, reporting the Scopes trial for the Baltimore *Sun:* as "a tinpot Pope in the Coca-Cola belt."

I wanted to understand a man who could speak with such warmth, yet talk such yahoo nonsense about evolution. I wanted, above all, to resolve a paradox that has always cried out for some answer rooted in Bryan's psyche. How could this man, America's greatest populist reformer, become, late in life, her arch reactionary?

For it was Bryan who, just one year beyond the minimum age of thirty-five, won the Democratic presidential nomination in 1896 with his populist rallying cry for abolition of the gold standard: "You shall not press down upon the brow of labor this crown of thorns. You shall not crucify mankind upon a cross of gold." Bryan who ran twice more, and lost in noble campaigns for reform, particularly for Philippine independence and against American imperialism. Bryan, the pacifist who resigned as Wilson's secretary of state because he sought a more rigid neutrality in the First World War. Bryan who stood at the forefront of most progressive victories in his time: women's suffrage, the direct election of senators, the graduated income tax (no one loves it, but can you think of a fairer way?). How could this man have then joined forces with the cult of biblical literalism in an effort to purge religion of all liberality, and to stifle the same free thought that he had advocated in so many other contexts?

This paradox still intrudes upon us because Bryan forged a living legacy, not merely an issue for the mists and niceties of history. For without Bryan, there never would have been antievolution laws, never a Scopes trial, never a resurgence in our day, never a decade of frustration and essays for yours truly, never a Supreme Court decision to end the issue. Every one of Bryan's progressive triumphs would have occurred without him. He fought mightily and helped powerfully, but women would be voting today and we would be paying income tax if he had never been born. But the legislative attempt to curb evolution was his baby, and he pursued it with all his legendary demoniac fury. No one else in the ill-organized fundamentalist movement had the inclination, and surely no one else had the legal skill or political clout. Ironically, fundamentalist legislation against evolution is the only truly distinctive and enduring brand that Bryan placed



William Jennings Bryan on the stump. Taken during the presidential campaign of 1896. THE BETTMANN ARCHIVE.

upon American history. It was Bryan's movement that finally hit the dust in Washington in June of 1987.

The paradox of shifting allegiance is a recurring theme in literature about Bryan. His biography in the *Encyclopaedia Britannica* holds that the Scopes trial "proved to be inconsistent with many progressive causes he had championed for so long." One prominent biographer located his own motivation in trying to discover "what had transformed Bryan from a crusader for social and economic reform to a champion of anachronistic rural evangelism, cheap moral panaceas, and Florida real estate" (L. W. Levine, 1965).

Two major resolutions have been proposed. The first, clearly the majority view, holds that Bryan's last battle was inconsistent with, even a nullification of, all the populist campaigning that had gone before. Who ever said that a man must maintain an unchanging ideology throughout adulthood; and what tale of human psychology could be more familiar than the transition from crusading firebrand to diehard reactionary. Most biographies treat the Scopes trial as an inconsistent embarrassment, a sad and unsettling end. The title to the last chapter of almost every book about Bryan features the word "retreat" or "decline."

The minority view, gaining ground in recent biographies and clearly correct in my judgment, holds that Bryan never transformed or retreated, and that he viewed his last battle against evolution as an extension of the populist thinking that had inspired his life's work (in addition to Levine, cited previously, see Paolo E. Coletta, 1969, and W. H. Smith, 1975).

Bryan always insisted that his campaign against evolution meshed with his other struggles. I believe that we should take him at his word. He once told a cartoonist how to depict the harmony of his life's work: "If you would be entirely accurate you should represent me as using a double-barreled shotgun, firing one barrel at the elephant as he tries to enter the treasury and another at Darwinism—the monkey—as he tries to enter the schoolroom." And he said to the Presbyterian General Assembly in 1923: "There has not been a reform for 25 years that I did not support. And I am now engaged in the biggest reform of my life. I am trying to save the Christian Church from those who are trying to destroy her faith."

But how can a move to ban the teaching of evolution in public schools be deemed progressive? How did Bryan link his previous efforts to this new strategy? The answers lie in the history of Bryan's changing attitudes toward evolution.

Bryan had passed through a period of skepticism in college. (According to one story, more than slightly embroidered no doubt, he wrote to Robert G. Ingersoll for ammunition but, upon receiving only a pat reply from his secretary, reverted immediately to orthodoxy.) Still, though Bryan never supported evoludon, he did not place opposition high on his agenda; in fact, he evinced a positive generosity and pluralism toward Darwin. In "The Prince of Peace," a speech that ranked second only to the "Cross of Gold" for popularity and frequency of repetition, Bryan said:

> I do not carry the doctrine of evolution as far as some do; I am not yet convinced that man is a lineal descendant of the lower animals. I do not mean to find fault with you if you want to accept the theory. . . . While I do not accept the Darwinian theory I shall not quarrel with you about it.

(Bryan, who certainly got around, first delivered this speech in 1904, and described it in his collected writings as "a lecture delivered at many Chautauqua and religious gatherings in America, also in Canada, Mexico, Tokyo, Manila, Bombay, Cairo, and Jerusalem.")

He persisted in this attitude of laissez-faire until World War I, when a series of events and conclusions prompted his transition from toleration to a burning zeal for expurgation. His arguments did not form a logical sequence, and were dead wrong in key particulars; but who can doubt the passion of his feelings?

We must acknowledge, before explicating the reasons for his shift, that Bryan was no intellectual. Please don't misconstrue this statement. I am not trying to snipe from the depth of Harvard elitism, but to understand. Bryan's dearest friends said as much. Bryan used his first-rate mind in ways that are intensely puzzling to trained scholars—and we cannot grasp his reasons without mentioning this point. The "Prince of Peace" displays a profound ignorance in places, as when Bryan defended the idea of miracles by stating that we continually break the law of gravity: "Do we not suspend or overcome the law of gravitation every day? Every time we move a foot or lift a weight we temporarily overcome one of the most universal of natural laws and yet the world is not disturbed." (Since Bryan gave this address hundreds of times, I assume that people tried to explain to him the difference between laws and events, or reminded him that without gravity, our raised foot would go off into space. I must conclude that he didn't care because the line conveyed a certain rhetorical oomph.) He also explicitly defended the suppression of understanding in the service of moral good:

> If you ask me if I understand everything in the Bible, I answer no, but if we will try to live up to what we do understand, we will be kept so busy doing good that we will not have time to worry about the passages which we do not understand.

This attitude continually puzzled his friends and provided fodder for his enemies. One detractor wrote: "By much talking and little thinking his mentality ran dry." To the same effect, but with kindness, a friend and supporter wrote that Bryan was "almost unable to think in the sense in which you and I use that word. Vague ideas floated through his mind but did not unite to form any system or crystallize into a definite practical position."

Bryan's long-standing approach to evolution rested upon a threefold error. First, he made the common mistake of confusing the fact of evolution with the Darwinian explanation of its mechanism. He then misinterpreted natural selection as a martial theory of survival by battle and destruction of enemies. Finally, he made the logical error of arguing that Darwinism implied the moral virtuousness of such deathly struggle. He wrote in the *Prince of Peace* (1904):

> The Darwinian theory represents man as reaching his present perfection by the operation of the law of hate—the merciless law by which the strong crowd out and kill off the weak. If this is the law of our development then, if there is any logic that can bind the human mind, we shall turn backward toward the beast in proportion as we substitute the law of love. I prefer to believe that love rather than hatred is the law of development.

And to the sociologist F. A. Ross, he said in 1906 that "such a conception of man's origin would weaken the cause of democracy and strengthen class pride and the power of wealth." He persisted in this uneasiness until World War I, when two events galvanized him into frenzied action. First, he learned that the martial view of Darwinism had been invoked by most German intellectuals and military leaders as a justification for war and future domination. Second, he feared the growth of skepticism at home, particularly as a source of possible moral weakness in the face of German militarism.

Bryan united his previous doubts with these new fears into a campaign against evolution in the classroom. We may question the quality of his argument, but we cannot deny that he rooted his own justifications in his lifelong zeal for progressive causes. In this crucial sense, his last hurrah does not nullify, but rather continues, all the applause that came before. Consider the three principal foci of his campaign, and their links to his populist past:

1. For peace and compassion against militarism and murder. "I learned," Bryan wrote, "that it was Darwinism that was at the basis of that damnable doctrine that might makes right that had spread over Germany."

2. For fairness and justice toward farmers and workers and against exploitation for monopoly and profit. Darwinism, Bryan argued, had convinced so many entrepreneurs about the virtue of personal gain that government now had to protect the weak and poor from an explosion of anti-Christian moral decay: "In the United Slates," he wrote,

> pure-food laws have become necessary to keep manufacturers from poisoning their customers; child labor laws have become necessary to keep employers from dwarfing the bodies, minds and souls of children; anti-trust laws have become necessary to keep overgrown corporations from strangling smaller competitors, and we are still in a death grapple with profiteers and gamblers in farm products.

3. For absolute rule of majority opinion against imposing elites. Christian belief still enjoyed widespread majority support in America, but college education was eroding a consensus that once ensured compassion within democracy. Bryan cited studies showing that only 15 percent of college male freshmen harbored doubts about God, but that 40 percent of graduates had become skeptics. Darwinism, and its immoral principle of domination by a selfish elite, had fueled this skepticism. Bryan railed against this

insidious undermining of morality by a minority of intellectuals, and he vowed to fight fire with fire. If they worked through the classroom, he would respond in kind and ban their doctrine from the public schools. The majority of Americans did not accept human evolution, and had a democratic right to proscribe its teaching.

Let me pass on this third point. Bryan's contention strikes at the heart of academic freedom, and I have often treated this subject in previous essays. Scientific questions cannot be decided by majority vote. I merely record that Bryan embedded his curious argument in his own concept of populism. "The taxpayers," he wrote,

> have a right to say what shall be taught . . . to direct or dismiss those whom they employ as teachers and school authorities. . . . The hand that writes the paycheck rules the school, and a teacher has no right to teach that which his employers object to.

But what of Bryan's first two arguments about the influence of Darwinism on militarism and domestic exploitation? We detect the touch of the Philistine in Bryan's claims, but I think we must also admit that he had identified something deeply troubling—and that the fault does lie partly with scientists and their acolytes.

Bryan often stated that two books had fueled his transition from laissez-faire to vigorous action: *Headquarters Nights,* by Vernon L. Kellogg (1917), and *The Science of Power,* by Benjamin Kidd (1918). I fault Harvard University for many things, but all are overbalanced by its greatest glory—its unparalleled resources. Half an hour after I needed these obscure books if I ever hoped to hold the key to Bryan's activities, I had extracted them from the depths of Widener Library. I found them every bit as riveting as Bryan had, and I came to understand his fears, even to agree in part (though not, of course, with his analysis or his remedies).

Vernon Kellogg was an entomologist and perhaps the leading teacher of evolution in America (he held a professorship at Stanford and wrote a major textbook, *Evolution and Animal Life,* with his mentor and Darwin's leading disciple in America, David Starr Jordan, ichthyologist and president of Stanford University). During the First World War, while America maintained official neutrality, Kellogg became a high official in the international, nonpartisan effort for Belgian relief, a cause officially "tolerated" by Germany. In this capacity, he was posted at the headquarters of the German Great General Staff, the only American on the premises. Night after night, he listened to dinner discussions and arguments, sometimes in the presence of the Kaiser himself, among Germany's highest military officers. *Headquarters Mights* is Kellogg's account of these exchanges. He arrived in Europe as a pacifist, but left committed to the destruction of German militarism by force.

Kellogg was appalled, above all, at the justification for war and German supremacy advanced by these officers, many of whom had been university professors before the war. They not only proposed an evolutionary rationale but advocated a particularly crude form of natural selection, defined as inexorable, bloody battle:

> Professor von Flussen is Neo-Darwinian, as are most German biologists and natural philosophers. The creed of the *Allmachl* ["all might" or omnipotence! of a natural selection based on violent and competitive struggle is the gospel of the German intellectuals; all else is illusion and anathema. . . . This struggle not only must go on, for that is the natural law, but it should go on so that this natural law may work out in its cruel, inevitable way the salvation of the human species. . . . That human group which is in the most advanced evolutionary stage . . . should win in the struggle for existence, and this struggle should occur precisely that the various types may be tested, and the best not only preserved, but put in position to impose its kind of social organization—its *Kultur*—on the others, or, alternatively, to destroy and replace them. This is the disheartening kind of argument that I faced at Headquarters. . . . Add the additional assumption that the Germans are the chosen race, and that German social and political organization the chosen type of human community life, and you have a wall of logic and conviction that you can break your head against but can never shatter—by headwork. You long for the muscles of Samson.

Kellogg, of course, found in this argument only "horrible academic casuistry and . . . conviction that the individual is nothing, the state everything." Bryan conflated a perverse interpretation with the thing itself and affirmed his worst fears about the polluting power of evolution.

Benjamin Kidd was an English commentator highly respected in both academic and lay circles. His book *Social Evolution* (1894) was translated into a dozen languages and as widely read as anything ever published on the implications of evolution. In *The Science of Power* (1918), his posthumous work, Kidd constructs a curious argument that, in a very different way from Kellogg's, also fueled Bryan's dread. Kidd, a philosophical idealist, believed that life must move toward progress by rejecting material struggle and individual benefit. Like the German militarists, but to excoriate rather than to praise, Kidd identified Darwinism with these impediments to progress. In a chapter entitled "The Great Pagan Retrogression," Kidd presented a summary of his entire thesis:

1. Darwin's doctrine of force rekindled the most dangerous of human tendencies—our pagan soul, previously (but imperfectly) suppressed for centuries by Christianity and its doctrines of love and renunciation:

> The hold which the theories of the *Origin of Species* obtained on the popular mind in the West is one of the most remarkable incidents in the history of human thought. . . . Everywhere throughout civilization an almost inconceivable influence was given to the doctrine of force as the basis of legal authority. . . .
>
> For centuries the Western pagan had struggled with the ideals of a religion of subordination and renunciation coming to him from the past. For centuries he had been bored almost beyond endurance with ideals of the world presented to him by the Churches of Christendom. .. . But here was a conception of life which stirred to its depths the inheritance in him from past epochs of time. . . . This was the world which the masters of force comprehended. The pagan heart of the West sang within itself again in atavistic-joy-

2. In England and America, Darwinism's worst influence lay in its justification for industrial exploitation as an expression of natural selection ("social Darwinism" in its pure form):

> The prevailing social system, born as it had been in struggle, and resting as it did in the last resort on war and on the toil of an excluded proletariat, appeared to have become clothed with a new and final kind of authority.

3. In Germany, Darwin's doctrine became a justification for war:

> Darwin's theories came to be openly set out in political and military textbooks as the full justification for war and highly organized schemes of national policy in which the doctrine of force became the doctrine of Right.

4. Civilization can only advance by integration: The essence of Darwinism is division by force for individual advantage. Social progress demands the "subordination of the individual to the universal" via "the iron ethic of Renunciation."

5. Civilization can only be victorious by suppressing our pagan soul and its Darwinian justification:

> It is the psychic and spiritual forces governing the social integration in which the individual is being subordinated to the universal which have become the winning forces in evolution.

This characterization of evolution has been asserted in many contexts for nearly 150 years—by German militarists, by Kidd, by hosts of the vicious and the duped, the self-serving and the well-meaning. But it remains deeply and appallingly wrong for three basic reasons.

1. Evolution means only that all organisms are united by ties of genealogical descent. This definition says nothing about the mechanism of evolutionary change: In principle, externally directed upward striving might work as well as the caricatured straw man of bloody Darwinian battle to the death. The objections, then, are to Darwin's theory of natural selection, not to evolution itself.

2. Darwin's theory of natural selection is an abstract argument about a metaphorical "struggle" to leave more offspring in subsequent generations, not a statement about murder and mayhem. Direct elimination of competitors is one pathway to Darwinian advantage, but another might reside in cooperation through social ties within a species or by symbiosis between species. For every act of killing and division, natural selection can also favor cooperation and integration in other circumstances. Nineteenth-century interpreters did generally favor a martial view of selection, but to every militarist, we may counterpose a Prince Kropotkin (see Essay 22), urging that the "real" Darwinism be recognized as a doctrine of integration and "mutual aid."

3. Whatever Darwinism represents on the playing fields of nature (and by representing both murder and cooperation at different times, it upholds neither as nature's principal way), Darwinism implies nothing about moral conduct. We do not find our moral values in the actions of nature. One might argue, as Thomas Hcnn Huxlev did in his famous essay "Evolution and Ethics," that Darwinism embodies a law of battle, and that human morality must be defined as the discovery of an opposite path. Or one might argue, as grandson Julian did, that Darwinism is a law of cooperation and that moral conduct should follow nature. If two such brilliant and committed Darwinians could come to such opposite opinions about evolution and ethics, I can only conclude that Darwinism offers no moral guidance.

But Bryan made this common threefold error and continually characterized evolution as a doctrine of battle and destruction of the weak, a dogma that undermined any decent morality and deserved banishment from the classroom. In a rhetorical flourish near the end of his "Last Evolution Argument," the final speech that he prepared with great energy, but never had an opportunity to present at the Scopes trial, Bryan proclaimed:

> Again force and love meet face to face, and the question "What shall I do with Jesus?" must be answered. A bloody, brutal doctrine—Evolution—demands, as the rabble did nineteen hundred years ago, that He be crucified.

I wish I could stop here with a snide comment on Bryan as yahoo and a ringing defense for science's proper interpretation of Darwinism. But I cannot, for Bryan was right in one crucial way. Lord only knows, he understood precious little about science, and he wins no medals for logic of argument. But when he said that Darwinism had been widely protrayed as a defense of war, domination, and domestic exploitation, he was right. Scientists would not be to blame for this if we had always maintained proper caution in interpretation and proper humility in resisting the extension of our findings into inappropriate domains. But many of these insidious and harmful misinterpretations had been promoted by scientists. Several of the German generals who traded arguments with Kellogg had been university professors of biology.

Just one example from a striking source. In his "Last Evolution Argument," Bryan charged that evolutionists had misused science to present moral opinions about the social order as though they represented facts of nature.

> By paralyzing the hope of reform, it discourages those who labor for the improvement of man's condition. . . . Its only program for man is scientific breeding, a system under which a few supposedly superior intellects, self-appointed, would direct the mating and the movements of the mass of mankind—an impossible system!

I cannot fault Bryan here. One of the saddest chapters in all the history of science involves the extensive misuse of data to support biological determinism, the claim that social inequalities based on race, sex, or class cannot be altered because they reflect the innate and inferior genetic endowments of the disadvantaged (see my book *The Mnmeasure of Man).* It is bad enough when scientists misidentify their own social preferences as facts of nature in their technical writings and even worse when writers of textbooks, particularly for elementary- and high-school students, promulgate these (or any) social doctrines as the objective findings of science.

Two years ago, I obtained a copy of the book that John Scopes used to teach evolution to the children of Dayton, Tennessee—*A Civic Biology,* by George William Hunter (1914). Many writers have looked into this book to read the section on evolution that Scopes taught and Bryan quoted. But I found something disturbing in another chapter that has eluded previous commentators—an egregious claim that science holds the moral answer to questions about mental retardation, or social poverty so misinterpreted. Hunter discusses the infamous Jukes and Kallikaks, the "classic," and false, cases once offered as canonical examples of how bad heredity runs in families. Under the heading "Parasitism and Its Cost to Society—the Remedy," he writes:

> Hundreds of families such as those described above exist today, spreading disease, immorality and crime to all parts of this country. The cost to society of such families is very severe. Just as certain animals or plants become parasitic on other plants or animals, these families have become parasitic on society. They not only do harm to others by corrupting, stealing or spreading disease, but they are actually protected and cared for by the state out of public money. Largely for them the poorhouse and the asylum exist. They take from society, but they give nothing in return. They are true parasites.
>
> If such people were lower animals, we would probably kill them off to prevent them from spreading. Humanity will not allow this, but we do have the remedy of separating the sexes in asylums or other places and in various ways preventing intermarriage and the possibilities of perpetuating such a low and degenerate race.

Bryan had the wrong solution, but he had correctly identified a problem!

Science is a discipline, and disciplines are exacting. All maintain rules of conduct and self-policing. All gain strength, respect, and acceptance by working honorably within their bounds and knowing when transgression upon other realms counts as hubris or folly. Science, as a discipline, tries to understand the factual state of nature and to explain and coordinate these data into general theories. Science teaches us many wonderful and disturbing things—facts that need weighing when we try to develop standards of conduct and ponder the great questions of morals and aesthetics. But science cannot answer these questions alone and cannot dictate social policy.

Scientists have power by virtue of the respect commanded by the discipline. We may therefore be sorely tempted to misuse that power in furthering a personal prejudice or social goal—why not provide that extra oomph by extending the umbrella of science over a personal preference in ethics or politics? But we cannot, lest we lose the very respect that tempted us in the first place.

If this plea sounds like the conservative and pessimistic retrenching of a man on the verge of middle age, I reply that I advocate this care and restraint in order to demonstrate the enormous power of science. We live with poets and politicians, preachers and philosophers. All have their ways of knowing, and all are valid in their proper domains. The world is too complex and interesting for one way to hold all the answers. Besides, highfalutin morality aside, if we continue to overextend the boundaries of science, folks like Bryan will nail us properly for their own insidious purposes.

We should give the last word to Vernon Kellogg, the great teacher who understood the principle of strength in limits, and who listened with horror to the ugliest misuses of Darwinism. Kellogg properly taught in his textbook (with David Starr Jordan) that Darwinism cannot provide moral answers:

> Some men who call themselves pessimists because they cannot read good into the operations of nature forget that they cannot read evil. In morals the law of competition no more justifies personal, official, or national selfishness or brutality than the law of gravitation justifies the shooting of a bird.

Kellogg also possessed the cardinal trait lacked both by Bryan and by many of his evolutionary adversaries: humility in the face of our profound ignorance about nature's ways, combined with that greatest of all scientific privileges, the joy of the struggle to know. In his greatest book, *Darwinism Today* (1907), Kellogg wrote:

> We are ignorant, terribly, immensely ignorant. And our work is, to learn. To observe, to experiment, to tabulate, to induce, to deduce. Biology was never a clearer or more inviting field for fascinating, joyful, hopeful work.

Amen, brother!

Postscript

As I was writing this essay, I learned of the untimely death from cancer (at age forty-seven) of Federal Judge William R. Overton of Arkansas. Judge Overton presided and wrote the decision in *McLean* v. *Arkansas* (January 5, 1982), the key episode that led to our final victory in the Supreme Court in June 1987. In this decision, he struck down the Arkansas law mandating equal time for "creation science." This precedent encouraged Judge Duplantier to strike down the similar Louisiana law by summary judgment (without trial). The Supreme Court then affirmed this summary judgment in their 1987 decision. (Since Arkansas and Louisiana had passed the only anti-evolution statutes in the country, these decisions close the issue.) Judge Overton's brilliant and beautifully crafted decision is the finest legal document ever written about this question—far surpassing anything that the Scopes trial generated, or any document arising from the two Supreme Court cases *(Epperson* v. *Arkansas* of 1968, striking down Scopes-era laws that banned evolution outright, and the 1987 decision banning the "equal time" strategy). Judge Overton's definitions of science are so cogent and clearly expressed that we can use his words as a model for our own proceedings. *Science,* the leading journal of American professional science, published Judge Overton's decision verbatim as a major article.

I was a witness in *McLean* v. *Arkansas* (see Essay 21 in *Hen's Teeth and Horse's Toes).* I never spoke to Judge Overton personally, and I spent only part of a day in his courtroom. Yet, when I fell ill with cancer the next year, I learned from several sources that Judge Overton had heard and had inquired about my health from mutual acquaintances, asking that his best wishes be conveyed to me. I mourn the passing of this brilliant and compassionate man, and I dedicate this essay to his memory.

An Essay on a Pig Roast

ON INDEPENDENCE DAY, 1919, in Toledo, Ohio, Jack Dempsey won the heavyweight crown by knocking out Jess Willard in round three. (Willard, the six-foot six-inch wheat farmer from Kansas, was "the great white hope" who, four years earlier in Havana, had finally KO'd Jack Johnson, the first black heavyweight champ, and primary thorn in the side of racist America.) Dempsey ruled the ring for seven years, until Gene Tunney whipped him in 1926.

Yet during Dempsey's domination of pugilism in its active mode, some mighty impressive fighters were squaring away on other, less physical but equally contentious turfs. One prominent battle occurred entirely within Dempsey's reign, beginning with William Jennings Bryan's decision in 1920 to launch a nationwide legislative campaign against the teaching of evolution and culminating in the Scopes trial of 1925. The main bout may have pitted Bryan against Clarence Darrow at the trial itself, but a preliminary skirmish in 1922, before any state legislature had passed an anti-evolution law, had brought two equally formidable foes together—Bryan again, but this time against Henry Fairfield Osborn, head of the American Museum of Natural History. In some respects, the Bryan-Osborn confrontation was more dramatic than the famous main event three years later. One can hardly imagine two more powerful but more different men: the arrogant, patrician, archconservative Osborn versus the folksy "Great Commoner" from Nebraska. Moreover, while Darrow maintained a certain respect based on genuine affection for

Bryan (or al least for his earlier greatness), I detect nothing but pure venom and contempt from Osborn.

The enemy within, as the old saying goes, is always more dangerous than the enemy without. An atheist might have laughed at Bryan or merely felt bewildered. But Osborn was a dedicated theist and a great paleontologist who viewed evolution as the finest expression of God's intent. For Osborn, Bryan was perverting both science and the highest notion of divinity. (Darrow later selected Osborn as one of his potential witnesses in the Scopes trial not only because Osborn was so prominent, socially as well as scientifically, but primarily because trial strategy dictated that religiously devout evolutionists could blunt Bryan's attack on science as intrinsically godless.)

On February 26, 1922, Bryan published an article in the Sunday *New York Tunes* to further his legislative campaign against the teaching of evolution. Bryan, showing some grasp of the traditional parries against Darwin, but constantly confusing doubts about the mechanism of natural selection with arguments against the fact of evolution itself, rested his case upon a supposed lack of direct evidence for the claims of science:

> The real question is, Did God use evolution as His plan? If it could be shown that man, instead of being made in the image of God, is a development of beasts we would have to accept it, regardless of its effect, for truth is truth and must prevail. But when there is no proof we have a right to consider the effect of the acceptance of an unsupported hypothesis.

The *Times,* having performed its civic duty by granting Bryan a platform, promptly invited Osborn to prepare a reply for the following Sunday. Osborn's answer, published on March 5 and reissued as a slim volume by Charles Scribner's Sons under the title *Evolution and Religion,* integrated two arguments into a single thesis: The direct, primarily geological evidence for evolution is overwhelming, and evolution is not incompatible with religion in any case. As a motto for his approach, and a challenge to Bryan from a source accepted by both men as unimpeachable, Osborn cited a passage from Job (12:8): ". . . speak to the earth, and it shall teach thee." When, on the eve of the Scopes trial, Osborn expanded his essay into a longer attack on Bryan, he dedicated the new book to John Scopes and chose a biting parody of Job for his title—*The Earth Speaks to Bryan* (Charles Scribner's Sons, 1925).

When a man poses such a direct challenge to an adversary, nothing could possibly be more satisfying than a quick confirmation from an unanticipated source. On February 25, 1922, just the day before Bryan's *Times* article, Harold J. Cook, a rancher and consulting geologist, had written to Osborn:

> I have had here, for some little time, a molar tooth from the Upper, or Hipparion phase of the Snake Creek Beds, that very closely approaches the human type. . . . Inasmuch as you are particularly interested in this problem and, in collaboration with Dr. Gregory and others, are in the best position of anyone to accurately determine the relationships of this tooth, if it can be done, I will be glad to send it on to you, should you care to examine and study it.

In those bygone days of an efficient two-penny post, Osborn probably received this letter on the very morning following Bryan's diatribe or, at most, a day or two later. Osborn obtained the tooth itself on March 14, and, with his usual precision (and precisely within the ten-word limit for the basic rate), promptly telegraphed Cook: "Tooth just arrived safely. Looks very promising. Will report immediately." Later that day, Osborn wrote to Cook:

> The instant your package arrived, I sat down with the tooth, in my window, and I said to myself: "It looks one hundred per cent anthropoid." I then took the tooth into Dr. Matthew's room and we have been comparing it with all the books, all the casts and all the drawings, with the conclusion that it is the last right upper molar tooth of some higher Primate. . . . We may cool down tomorrow, but it looks to me as if the first anthropoid ape of America has been found.

But Osborn's enthusiasm only warmed as he studied the tooth and considered the implications. The human fossil record had improved sufficiently to become a source of strength, rather than an embarrassment, to evolutionists, with Cro-Magnon and Neanderthal in Europe (not to mention the fraudulent Piltdown, then considered genuine and strongly supported by Osborn) and *Pithecanthropus* (now called *Homo erectus)* in East Asia. But no fossils of higher apes or human ancestors had ever been found anywhere in the Americas. This absence, in itself, posed no special problem to evolutionists. Humans had evolved in Asia or Africa, and the Americas were an isolated world, accessible primarily by a difficult route of migration over the Bering land bridge. Indeed, to this day, ancient humans are unknown in the New World, and most anthropologists accept a date of 20,000 years or considerably less (probably more like 11,000) for the first peopling of our hemisphere. Moreover, since these first immigrants were members of our stock, *Homo sapiens,* no ancestral species have ever been found—and none probably ever will—in the Americas.

Still, an American anthropoid would certainly be a coup for Osborn's argument that the earth spoke to Bryan in the language of evolution, not to mention the salutary value of a local product for the enduring themes of hoopla, chauvinism, and flag-waving.

Therefore, Osborn's delight—and his confidence—in this highly worn and eroded molar tooth only increased. Within a week or two, he was ready to proclaim the first momentous discovery of a fossil higher primate, perhaps even a direct human ancestor, in America. He honored our hemisphere in choosing the name *Hesperopithecus,* or "ape of the western world." On April 25, less than two months after Bryan's attack, Osborn presented *Hesperopithecus* in two simultaneous papers with the same title and different content: one in the prestigious *Proceedings of the National Academy of Sciences;* the other, containing figures and technical descriptions, in the *Novitates of the American Museum of Natural History—"Hesperopithecus,* the First Anthropoid Primate Found in America."

Hesperopithecus was good enough news in the abstract, but Osborn particularly exulted in the uncannily happy coincidences of both time and place. Cook had probably written his letter at the very moment that the compositors were setting Bryan's oratory in type. Moreover, for the crowning irony, *Hesperopithecus* had been found in Nebraska—home state of the Great Commoner! If God had permitted a paleontologist to invent a fossil with maximal potential to embarrass Bryan, no one could have bettered *Hesperopithecus* for rhetorical impact. Needless to say, this preciously ironical situation was not lost on Osborn, who inserted the following gloat of triumph into his article for the staid *Proceedings*—about as incongruous in this forum as the erotic poetry of the Song of Songs between Ecclesiastes and Isaiah.

> It has been suggested humorously that the animal should be named *Bryopithecus* after the most distinguished Primate which the State of Nebraska has thus far produced. It is certainly singular that this discovery is announced within six weeks of the day (March 5, 1922) that the author advised William Jennings Bryan to consult a certain passage in the Book of Job, "Speak to the earth and it shall teach thee," and it is a remarkable coincidence that the first earth to speak on this subject is the sandy earth of the Middle Pliocene Snake Creek deposits of western Nebraska.

Old Robert Burns certainly knew his stuff when he lamented the frequent unraveling of the best laid plans of mice and men. Unless you browse in the marginal genre of creationist tracts, you will probably not have encountered *Hesperopithecus* in anything written during the past fifty years (except, perhaps, as a cautionary sentence in a textbook or a paragraph on abandoned hopes in a treatise on the history of science). The reign of *Hesperopithecus* was brief and contentious. In 1927, Osborn's colleague William King Gregory, the man identified in Cook's original letter as the best-qualified expert on primate teeth, threw in the towel with an article in *Science: "Hesperopithecus* Apparently not an Ape nor a Man." Expeditions sent out by Osborn in the summers of 1925 and 1926 to collect more material of *Hesperopithecus,* and to test the hypothesis of primate affinity, had amassed a large series to complement the original tooth. But this abundance also doomed Osborn's interpretation—for the worn and eroded *Hesperopithecus* tooth, when compared with others in better and more diagnostic condition, clearly belonged not to a primate but to the extinct peccary *Prosthennops.*

One can hardly blame modern creationists for making hay of this brief but interesting episode in paleontology. After all, they're only getting their fair licks at Osborn, who used the original interpretation to ridicule and lambaste their erstwhile champion Bryan. I don't think I have ever read a modern creationist tract that doesn't feature the tale of "Nebraska Man" in a feint from our remarkable record of genuine human fossils, and an attempted KO of evolution with the one-two punch of Piltdown and *Hesperopithecus.* I write this essay to argue that Nebraska man tells a precisely opposite tale, one that should give creationists pause (though I do admit the purely rhetorical value of a proclaimed primate ancestor later exposed as a fossil pig).

The story of *Hesperopithecus* was certainly embarrassing to Osborn and Gregory in a personal sense, but the sequence of discovery, announcement, testing, and refutation—all done with admirable dispatch, clarity, and honesty—shows science working at its very best. Science is a method for testing claims about the natural world, not an immutable compendium of absolute truths. The fundamentalists, by "knowing" the answers before they start, and then forcing nature into the straitjacket of their discredited preconceptions, lie outside the domain of science—or of any honest intellectual inquiry. The actual story *of Hesperopithecus* could teach creationists a great deal about science as properly practiced if they chose to listen, rather than to scan the surface for cheap shots in the service of debate pursued for immediate advantage, rather than interest in truth.

When we seek a textbook case for the proper operation of science, the correction of certain error offers far more promise than the establishment of probable truth. Confirmed hunches, of course, are more upbeat than discredited hypotheses. Since the worst traditions of "popular" writing falsely equate instruction with sweetness and light, our promotional literature abounds with insipid tales in the heroic mode, although tough stories of disappointment and loss give deeper insight into a methodology that the celebrated philosopher of science Karl Popper once labeled as "conjecture and refutation."

Therefore, I propose that we reexamine the case of Nebraska Man, not as an embarrassment to avoid in polite company, but as an exemplar complete with lessons and ample scope for the primary ingredient of catharsis and popular appeal—the opportunity to laugh at one's self. Consider the story as a chronological sequence of live episodes:

1. *Proposal.* Harold Cook's fossil tooth came from a deposit

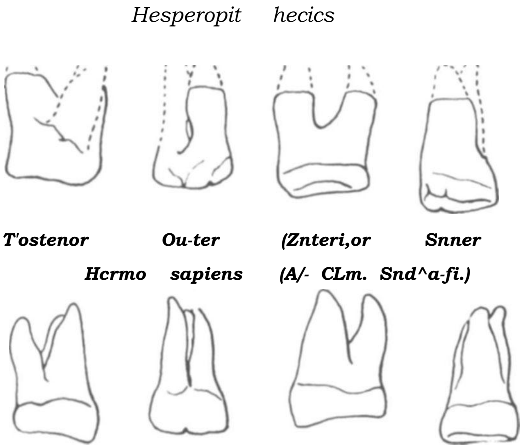
about 10 million years old and filled with mammals of Asiatic ancestry. Since paleontologists of Osborn's generation believed that humans and most other higher primates had evolved in Asia, the inclusion of a fossil ape in a fauna filled with Asian migrants seemed entirely reasonable. Osborn wrote to Cook a month before publication:

> The animal is certainly a new genus of anthropoid ape, probably an animal which wandered over here from Asia with the large south Asiatic element which has recently been discovered in our fauna. . . . It is one of the greatest surprises in the history of American paleontology.

Osborn then announced the discovery of *Hesperopithecus* in three publications—technical accounts in the *American Museum Novitates* (April 25, 1922) and in the British journal *Nature* (August 26, 1922), and a shorter notice in the *Proceedings of the National Academy of Sciences* (August 1922, based on an oral report delivered in April).

2. *Proper doubt and statement of alternatives.* Despite all the hoopla and later recrimination, Osborn never identified *Hesperopithecus* as a human ancestor. The tooth had been heavily worn during life, obliterating the distinctive pattern of cusps and crown. Considering both this extensive wear and the further geological erosion of the tooth following the death of its bearer, Osborn knew that he could make no certain identification. He did not cast his net of uncertainty widely enough, however, for he labeled *Hesperopithecus* as an undoubted higher primate. But he remained agnostic about the crucial issue of closer affinity with the various ape branches or the human twig of the primate evolutionary tree.

Osborn described the tooth of *Hesperopithecus* as "a second or third upper molar of the right side of a new genus and species of anthropoid." Osborn did lean toward human affinity, based both on the advice of his colleague Gregory (see point three below) and, no doubt, on personal hope and preference: "On the whole, we think its nearest resemblances are with . . . men rather than with apes." But his formal description left this crucial question entirely open:



An illustration from Osborn's article of 1922, showing the strong similarity between worn teeth of *Hesperopithecus* and modern humans, **NEC** NO. 2A**17804.** COURTESY DEPARTMENT OF LIBRARY SERVICES, AMERICAN MUSEUM OF NATURAL HISTORY.

> The *Hesperopithecus* molar cannot be said to resemble any known type of human molar very closely. It is certainly not closely related to *Pithecanthropus erectus* in the structure of the molar crown. . . . It is therefore a new and independent type of Primate, and we must seek more material before we can determine its relationships.

3. *Encouragement of further study.* If Osborn had been grandstanding with evidence known to be worthless or indecipherable, he would have made his public point and then shut up after locking his useless or incriminating evidence away in a dark drawer in the back room of a large museum collection. Osborn proceeded in exactly the opposite way. He did everything possible to encourage further study and debate, hoping to resolve his own strong uncertainties. (Osborn, by the way, was probably the most pompous, self-assured S.O.B. in the history of American paleontology, a regal patrician secure in his birthright, rather than a scrappy, self-made man. He once published a book devoted en-

tirely to photographs of his medals and awards and to a list of his publications; as an excuse for such vanity, he claimed that he harbored only a selfless desire to inspire young scientists by illustrating the potential rewards of a fine profession. "Osborn stories" are still told by the score wherever vertebrate paleontologists congregate. And when a man's anecdotes outlive him by more than half a century, you know that he was larger than life. Thus, the real news about *Hesperopithecus* must be that, for once, Osborn was expressing genuine puzzlement and uncertainty.)

In any case, Osborn reached out to colleagues throughout the world. He made numerous casts of *Hesperopitlurus* and sent them to twenty-six universities and museums in Europe and North America. As a result, he was flooded with alternative interpretations from the world's leading paleoanthropologists. He received sharp criticisms from both sides: from Arthur Smith Woodward, describer of Piltdown, who thought that *Hesperopithecus* was a bear (and I don't mean metaphorically), and from G. Elliot Smith, another "hero" of Piltdown, who became too enthusiastic about the humanity of Osborn's tooth, causing considerable later embarrassment and providing creationists with their "hook." Osborn tried to rein both sides in, beginning his *Xatiire* article with these words:

> Every discovery directly or indirectly relating to the prehistory of man attracts world-wide attention and is apt to be received either with too great optimism or with too great incredulity. One of my friends, Prof. G. Elliot Smith, has perhaps shown too great optimism in his most interesting newspaper and magazine articles on *Hesperopithecus,* while another of my friends, Dr. A. Smith Woodward, has shown too much incredulity.

Moreover, Osborn immediately enlisted his colleague W. K. Gregory, the acknowledged local expert on primate teeth, to prepare a more extensive study of *Hesperopithecus,* including a formal comparison of the tooth with molars of all great apes and human fossils. Gregory responded with two detailed, technical articles, both published in 1923 with the collaboration of Milo Hellman.

Gregory followed Osborn in caution and legitimate expression of doubt. He began his first article by dividing the characters of the tooth into three categories: those due to wear, to subsequent erosion, and to the genuine taxonomic uniqueness of *Hesperopithecus.* Since the first two categories, representing information lost, tended to overwhelm the last domain of diagnostic biology, Gregory could reach no conclusion beyond a basic placement among the higher primates:

> The type of *Hesperopithecm haroldcookn* represents a hitherto unknown form of higher primates. It combines characters seen in the molars of the chimpanzee, of *Pithecanthropus,* and of man, but, in view of the extremely worn and eroded state of the crown, it is hardly safe to affirm more than that *Hesperopithecm* was structurally related to all three.

In the second and longer article, Gregory and Hellman stuck their necks out a bit more—but in opposite directions. Hellman opted for the human side; Gregory for affinity with "the gorilla-chimpanzee group."

4. *Gathering of additional data.* Osborn knew, of course, that a worn and eroded tooth would never resolve the dilemma of *Hesperopithecm,* no matter how many casts were made or how many paleontologists peered down their microscopes. The answers lay in more data buried in the sands of Nebraska, and Osborn pledged, in his diatribe against Bryan, to make the earth speak further:

> What shall we do with the Nebraska tooth? Shall we destroy it because it jars our long preconceived notion that the family of manlike apes never reached the Western world, or shall we endeavor to interpret it, to discover its real relationship to the apes of Asia and of the more remote Africa. Or shall we continue our excavations, difficult and baffling as they are, in the confident hope, inspired by the admonition of Job, that if we keep on speaking to the earth we shall in time have a more audible and distinct reply [from *The Earth Speaks to Bryan,* p. 43).

To his professional audiences in *Nature,* Osborn made the same pledge with more detail: "We are this season renewing the search with great vigor and expect to run every shovelful of loose river sand which comprises the deposit through a sieve of mesh fine enough to arrest such small objects as these teeth."

Thus, in the summers of 1925 and 1926, Osborn sent a collecting expedition, led by Albert Thomson, to the Snake Creek beds of Nebraska. Several famous paleontologists visited the site and pitched in, including Barnum Brown, the great dinosaur collector; Othenio Abel of Vienna (a dark figure who vitiated the memory of his fine paleontological work by later activity in the Austrian Nazi party); and Osborn himself. They found abundant material to answer their doubts. The earth spoke both audibly and distinctly, but not in the tones that Osborn had anticipated.

5. *Retraction.* After all this buildup and detail, the denouement can only be described as brief, simple, and conclusive. The further expeditions were blessed with success. Abundant new specimens destroyed Osborn's dream for two reasons that could scarcely be challenged. First, the new specimens formed a series from teeth worn as profoundly as *Hesperopithecus* to others of the same species with crown and cusps intact. The diagnostic pattern of the unworn teeth proclaimed pig rather than primate. Second, the unworn teeth could not be distinguished from premolars firmly residing in a peccary's palate found during a previous expedition. Osborn, who was never praised for a charitable nature, simply shut up and never mentioned *Hesperopithecus* again in his numerous succeeding articles on human ancestry. He had enjoyed the glory, but he let Gregory take the heat in a forthright retraction published in *Science* (December 16, 1927):

> Among other material the expedition secured a series of specimens which have led the writer to doubt his former identification of the type as the upper molar of an extinct primate, and to suspect that the type specimen of *Hesperopithecus haroldcookii* may be an upper premolar of a species of *Prosthennops,* an extinct genus related to modern peccaries.

Why should the detractors of science still be drawing such mileage from this simple story of a hypothesis swiftly refuted by science working well? I would divide the reasons into red herrings and a smaller number of allowable points. The red herrings all center on rhetorical peculiarities that anyone skilled in debate could use to advantage. (Debate, remember, is an art form dedicated to the winning of arguments. Truth is one possible weapon, rarely the best, in such an enterprise.) Consider three good lines:

1. "How can you believe those evolutionists if they can make monkeys out of themselves by calling a pig a monkey?" As a trope of rhetoric, given the metaphorical status of pigs in our culture, the true affinity of *Hesperopithecus* became a blessing for creationists. What could possibly sound more foolish than the misidentification of a pig as a primate. My side might have been better off if *Hesperopithecus* had been, say, a deer or an antelope (both members of the order Artiodactyla, along with pigs, and therefore equally far from primates).

Yet anyone who has studied the dental anatomy of mammals knows immediately that this seemingly implausible mix-up of pig for primate is not only easy to understand but represents one of the classic and recurring confusions of the profession. The cheek teeth of pigs and humans are astonishingly and uncannily similar. (I well remember mixing them up more than once in my course on mammalian paleontology, long before I had ever heard the story of *Hesperopithecus.)* Unworn teeth can be told apart by details of the cusps, but isolated and abraded teeth of older animals are very difficult to distinguish. The *Hesperopithecus* tooth, worn so flat and nearly to the roots, was a prime candidate for just such a misidentification.

A wonderfully ironic footnote to this point was unearthed by John Wolf and James S. Mellett in an excellent article on Nebraska Man that served as the basis for my researches (see bibliography). In 1909, the genus *Prosthennops* was described by W. D. Matthew, Osborn's other paleontological colleague at the American Museum of Natural History, and—guess who—the same Harold Cook who would find *Hesperopithecus* ten years later. 'They explicitly warned their colleagues about the possible confusion of these peccary teeth with the dentition of primates:

> The anterior molars and premolars of this genus of peccaries show a startling resemblance to the teeth of Anthropoidea, and might well be mistaken for them by anyone not familiar with the dentition of Miocene peccaries.

2. "How can you believe those evolutionists if they can base an identification on a single worn tooth?" William Jennings Bryan,

the wily old lawyer, remarked: "These men would destroy the Bible on evidence that would not convict a habitual criminal of a misdemeanor."

My rejoinder may seem like a cavil, but it really isn't. Harold Cook did send but a single tooth to Osborn. (I do not know why he had not heeded his own previous warning of 1909. My guess would be that Cook played no part in writing the manuscript and that Matthew had been sole author of the statement. An old and admirable tradition grants joint authorship to amateur collectors who often find the material that professionals then exploit and describe. Matthew was the pro, Cook the experienced and sharp-eyed local collector.) Osborn sought comparative material in the Museum's collection of fossil mammals and located a very similar tooth found in the same geological strata in 1908. He added this second tooth to the sample and based the genus *Hesperopithecus* on both specimens. (This second tooth had been found by W. D. Matthew, and we must again raise the question of why Matthew didn't heed his own warning of 1909 about mixing up primates and peccaries. For Osborn showed both teeth to Matthew and won his assent for a probable primate identification. In his original description, Osborn wrote of this second tooth: "The specimen belonged to an aged animal and is so water-worn that Doctor Matthew, while inclined to regard it as a primate, did not venture to describe it.")

Thus the old canard about basing a human reconstruction on a single tooth is false. The sample of *Hesperopithecus* included two teeth from the start. You might say that two is only minimally better than one, and still so far from a whole animal that any conclusion must be risible. Not so. One of anything can be a mistake, an oddball, an isolated peculiarity; two, on the other hand, is the beginning of a pattern. Second specimens always provide a great increment of respect. The Piltdown fraud, for example, did not take hold until the forgers concocted a second specimen.

3. "How can you believe those evolutionists if they reconstruct an entire man—hair, skin, and all—from a single tooth?" On this issue, Osborn and Gregory were unjustly sandbagged by an overzealous colleague. In England, G. Elliot Smith collaborated with the well-known scientific artist Amedee Forestier to produce a graphic reconstruction of a *Hesperopithecus* couple in a forest sur-

The infamous restoration of *Hesperopithecus* published in the *Illustrated London News* in 1922. NEG. NO. 2A17487. COURTESY DEPARTMENT OF LIBRARY SERVICES, AMERICAN MUSEUM OF NATURAL HISTORY.

rounded by other members of the Snake Creek fauna. Forestier, of course, could learn nothing from the tooth and actually based his reconstruction on the conventional rendering of *Pithecanthropus,* or Java man.

Forestier's figure is the one ridiculed and reproduced by creationists, and who can blame them? The attempt to reconstruct an entire creature from a single tooth is absolute folly—especially in this case when the authors of *Hesperopithecus* had declined to decide whether their creature was ape or human. Osborn had explicitly warned against such an attempt by pointing out how organs evolve at different rates, and how teeth of one type can be found in bodies of a different form. (Ironically, he cited Piltdown as an example of this phenomenon, arguing that, by teeth alone, the "man" would have been called an ape. How prescient in retrospect, since Piltdown is a fraud made of orangutan teeth and a human skull.)

Thus, Osborn explicitly repudiated the major debating point continually raised by modern creationists—the nonsense of reconstructing an entire creature from a single tooth. He said so obliquely and with gentle satire in his technical article for *Nature,* complaining that G. E. Smith had shown "too great optimism in his most interesting newspaper and magazine articles on *Hesperopithecus."* The *New York Times* reported a more direct quotation: "Such a drawing or 'reconstruction' would doubtless be only a figment of the imagination of no scientific value, and undoubtedly inaccurate."

Among the smaller number of allowable points, I can hardly blame creationists for gloating over the propaganda value of this story, especially since Osborn had so shamelessly used the original report to tweak Bryan. Tit for tat.

I can specify only one possibly legitimate point of criticism against Osborn and Gregory. Perhaps they were hasty. Perhaps they should have waited and not published so quickly. Perhaps they should have sent out their later expedition before committing anything to writing, for then the teeth would have been officially identified as peccaries first, last, and always. Perhaps they proceeded too rapidly because they couldn't resist such a nifty opportunity to score a rhetorical point at Bryan's expense. I am not bothered by the small sample of only two teeth. Single teeth, when well preserved, can be absolutely diagnostic of a broad taxonomic group. The argument for caution lay in the worn and eroded character of both premolars. Matthew had left the second tooth of 1908 in a museum drawer; why hadn't Osborn shown similar restraint?

But look at the case from a different angle. The resolution of *Hespeiopithecus* may have been personally embarrassing for Osborn and Gregory, but the denouement was only invigorating and positive for the institution of science. A puzzle had been noted and swiftly solved, though not in the manner anticipated by the original authors. In fact, I would argue that Osborn's decision to publish, however poor his evidence and tentative his conclusions, was the most positive step he could have taken to secure a resolution. The published descriptions were properly cautious and noncommittal. They focused attention on the specimens, provided a series of good illustrations and measurements, provoked a rash of hypotheses for interpretation, and inspired the subsequent study and collection that soon resolved the issue. If Osborn had left the molar in a museum drawer, as Matthew had for the second tooth found in 1908, persistent anomaly would have been the only outcome. Conjecture and refutation is a chancy game with more losers than winners.

I have used the word *irony* too may times in this essay, for the story of *Hesperopithecus* is awash in this quintessential consequence of human foibles. But I must beg your indulgence for one last round. As their major pitch, modern fundamentalists argue that their brand of biblical literalism represents a genuine discipline called "scientific creationism." They use the case of Nebraska Man, in their rhetorical version, to bolster this claim, by arguing that conventional science is too foolish to merit the name and that the torch should pass to them.

As the greatest irony of all, they could use the story of *Hesperopithecus,* if they understood it properly, to advance their general argument. Instead, they focus on their usual ridicule and rhetoric, thereby showing their true stripes even more clearly. The real message of *Hesperopithecus* proclaims that science moves forward by admitting and correcting its errors. If creationists really wanted to ape the procedures of science, they would take this theme to heart. They would hold up their most ballyhooed, and now most thoroughly discredited, empirical claim—the coexistence of dinosaur and human footprints in the Paluxy Creek beds near Dallas—and publicly announce their error and its welcome correction. (The supposed human footprints turn out to be either random depressions in the hummocky limestone surface or partial dinosaur heel prints that vaguely resemble a human foot when the dinosaur toe strikes are not preserved.) But the world of creationists is too imbued with irrefutable dogma, and they don't seem able even to grasp enough about science to put up a good show in imitation.

I can hardly expect them to seek advice from me. May they, therefore, learn the virtue of admitting error from their favorite source of authority, a work so full of moral wisdom and intellectual value that such a theme of basic honesty must win special prominence. I remind my adversaries, in the wonderful mixed metaphors of Proverbs (25:11,14), that "a word fitly spoken is like apples of gold in pictures of silver. . . . Whoso boasteth himself of a false gift is like clouds and wind without rain."

The Ant and the Plant

WHY DO WE CARE so much about size and number? My friend Ralph Kcyes, who tips the charts with me at five feet seven and a half inches, wrote an entire book about our obsession with this supposedly irrelevant subject—*The Height of Your Life.* He documented the extraordinary steps that short politicians and film stars often take to avoid discovery of their secret. (Ralph couldn't penetrate the subterfuges of Jimmy Carter's staff to discover the height of our shortest recent president, who is at least an inch or two taller than Ralph and me, and therefore at, or not far from, the American average.) The most amusing item in Ralph's book is an old publicity shot of a short Humphrey Bogart with two of his leading ladies, Lauren Bacall and Katharine Hepburn. They have just emerged from an airplane. Bogie is on the first step of the gangplank; the two women stand on the ground.

Why do we so stupidly equate more with better? Penises and automobiles, two objects frequently graded for size by foolish men, work just as well, and often more efficiently, at smaller than average lengths. Extremes in body size almost always entail tragic consequences (at least off the basketball court). Robert Wadlow, just shy of nine feet and the tallest human ever recorded, died at age twenty-two from infection caused by a faulty ankle brace needed for supplementary support since his legs could not adequately carry his body. Moving beyond the pathology of extreme individuals, entire species of unusually large body size generally have short geological lifetimes. I doubt that their problem lies in biomechanical inefficiency, as earlier theories of lumbering dinosaurs held. Rather, large creatures tend to be anatomically specialized and form relatively small populations (fewer brontosauruses than boll weevils)—perhaps the two strongest detriments to extended survival in a world of large and capricious environmental fluctuation over time.

While most people do understand that large size does not guarantee long-term success, the myth of "more is better" still pervades our interpretations. I have, for example, noted with surprise, as I have monitored the impressions of students and correspondents for **more** (ban twenty years, how **main** people assume, as almost logically necessary a priori, that evolutionary "progress" and complexity should correlate with the amount of DNA in an organism's cell—the ultimate baseline for more is better. Not so. The very simplest creatures, including viruses at the low end, followed by bacteria and other prokaryotic organisms, do have relatively little DNA. But as soon as we reach multicellular life, based on eukaryotic cells with nuclei and chromosomes, the correlation breaks down completely. Mammals stand squarely in the middle of the pack, with 10^9—10^{10} nucleotides per haploid cell. The largest values, ranging to nearly 100 times more DNA than the most richly endowed mammals, belong to salamanders and to some flowering plants.

Many species of plants arise by polyploidy, **or** doubling of chromosome number. These doublings often run through several cycles among a group of closely related species, so the amount of DNA can increase greatly—and the high DNA content of some polyploid plants has never been much of a mystery. On the other hand, the extreme values for amphibians once puzzled zoologists sufficiently that they gave the phenomenon a name—"the C-value paradox." However, since the discovery that so little **of** the total DNA codes actively for enzymes and proteins, this hundredfold difference between some mammals and salamanders seems less troubling. Most DNA consists of repeated copies; much of it codes for nothing and may represent "junk" in terms of an organism's morphology. The hundredfold difference does not mean that salamanders have 100 times more active genes than mammals, for the disparity occurs chiefly in nonessential, **or** noncoding, regions. (We would still, of course, like to know why some groups accumulate more junk and more repetitions, but such differences do not merit special recognition as a formal paradox.)

This essay considers another expression of maximum and minimum, and another test of correlation between quantity and quality—numbers of chromosomes. We have voluminous data on average differences in number of chromosomes among groups of organisms, and some patterns surely emerge. Diptera (flies and their allies) tend to have few per cell; *Drosophila,* the great laboratory stalwart (and largely for this reason), harbors four pairs per diploid cell. Birds tend to have many. Instead of providing a compendium for these well-chronicled differences, I shall focus on the extreme cases of more and less among organisms. Extreme values may titillate our fancy, but they are also unusually instructive for recognizing and specifying generalities. Exceptions do prove rules. (The etymology of that cliche, usually mistaken for a reversed meaning, is not "prove" in the sense of verify, but "probe" in the sense of test or challenge. This definition, from the Latin *probare,* is not entirely archaic in English—consider printer's proof, or a proving ground for testing weapons.)

Until two years ago, the lowest number of chromosomes, a commandingly minimal one pair, had been found for only a single organism—a nematode worm, appropriately honored in its subspecific name as *Parascaris equorum univalent.* This minimal complement had been discovered long ago, in 1887, by Theodor Boveri, the greatest cytologist (student of cellular architecture) of the late nineteenth century. Boveri (1862-1915) was a great intellectual in the European tradition—a complex and fascinating man who lived for the laboratory, but who also played the piano and painted with professional competence. His short life was scarred by lils of depression, and he died in despondency as the First World War enveloped Europe. Of Boveri's many scientific discoveries, the two greatest centered on chromosomes. First, he established their individuality and shifted attention from the nucleus as a whole to chromosomes as the agent of inheritance (in years before the rediscovery of Mendel's laws). Second, he demonstrated the differential value of chromosomes. Before Boveri's experiments, many scientists had conjectured that each chromosome carried all the hereditary information, and that organisms with many chromosomes carried more copies of this totality. Boveri proved that each chromosome carried only part of the hereditary information (some of the genes, as we might say today), and that the full complement built the organism through a complex orchestration of development.

Boveri took great interest in his discovery of an organism that carried but one pair of chromosomes per cell—and therefore did place all its hereditary information into one package. But Boveri quickly discovered that *P. equorum univalent,* though no imposter in its claims to minimalism, was not entirely consistent either. Only the cells of the germ line, those destined to produce eggs and sperm by meiosis, kept all the hereditary material together in a single pair of chromosomes. In cells destined to form body tissues, this chromosome fractured several times during the first cleavage divisions of early embryology, leading to adult cells with up to seventy chromosomes!

Finally, in 1986, Australian zoologists Michael W.J. Crosland and Ross H. Crozier reported a remarkable new species within a closely related group of ants, previously united into the overextended species *Myrniecia pilosula* (see their article of 1988 cited in the bibliography). This name falsely amalgamates several distinct species sharing a similar body form, but carrying different numbers of chromosomes in their cells. Species with nine, ten, sixteen, twenty-four, thirty, thirty-one, and thirty-two pairs of chromosomes have been described. Obviously, this complex of forms has evolved some way of speciating in concert with substantial changes in chromosome number.

On February 24, 1985, on the Tidbinbilla Nature Reserve near Canberra, Crosland and Crozier collected a colony of winged males and females, plus a mated queen with pupae and more than 100 workers. All workers tested from this colony carried but a single pair of chromosomes in their cells—all of them, not just cells of a particular type. An unambiguous example of chromosomal minimalism had finally been discovered, almost exactly 100 years after Boveri found only one pair of chromosomes in the germ line cells of *Parascaris.*

But the story of A/, *pilosula* is even better, deliciously so. If you were out searching for absolute minimalism, you would have to root for finding your single pair of chromosomes in an ant, bee, or wasp—for the following interesting reason: The Hymenoptera, and just a few other creatures, reproduce by an unusual genetic system called haplodiploidy. In most animals, all body cells contain chromosomes in pairs, and sex is determined by maternal and paternal contributions (or noncontributions in some cases) to a single pair. But haplodiploid organisms specify sex by a different route. Reproductive females usually store sperm, often for long periods. Genetic females (including the functionally neuter workers) arise from fertilized eggs, and therefore contain chromosomes in pairs. But males are produced when the queen fails to fertilize a developing egg with stored sperm (in most other animal groups unfertilized eggs are inviable). Thus, the cells of male ants, bees, and wasps do not carry chromosomes in pairs and bear only the single set inherited from their mother. These males have no father, and their cells contain only half the chromosomes of females—a condition called haploid, as opposed to the diploid, or paired, complement of their sisters. (The entire system therefore receives the name haplodiploid, or male-female in this case.)

Haplodiploidy implies, of course, that males of the Tidbinbilla colony of *M. pilosula* have a truly and absolutely minimal number of one chromosome per cell. Not even a single pair—-just one. The only lower possibility is disappearance. Crosland and Crozier checked just to be sure. The males of their colony contained a single chromosome per cell.

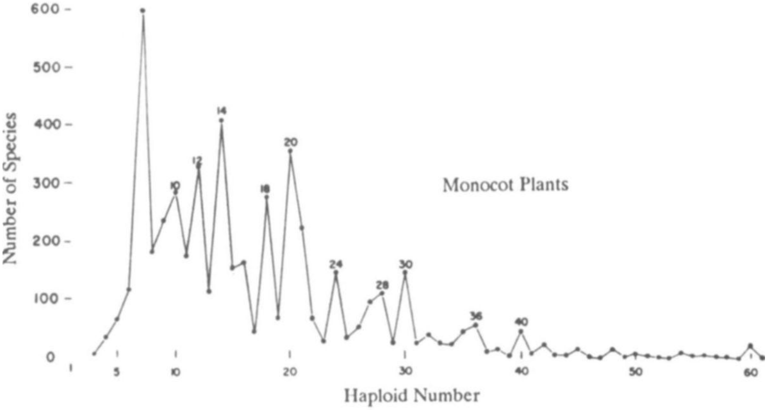
If we have reached a limit in the search for less, the other extreme seems more open-ended. How many chromosomes can a cell contain and still undergo the orderly divisions of mitosis and meiosis? Can hundreds of chromosomes line up neatly along a mitotic spindle and divide precisely to place an equal complement into each daughter cell? At what point do things become so crowded that this most elegant of biological mechanisms breaks down?

Maximal numbers are most easily reached by polyploidy, or doubling of chromosomes. This process occurs in two basic modes with differing evolutionary significances. In autoploidy, a cell doubles its own complement, forming, initially at least, a cell with two sets of identical pairs. Thus, the new autoploid usually looks like its parent. Autoploidy is not a mechanism for rapid evolution of form, though the redundancy introduced by doubling does permit considerable evolutionary divergence afterward—as one member of the duplicated pair becomes free to change. On the other hand, alloploidy, the second mode of doubling, can produce viable hybrids between distant species and can serve as a mechanism for sudden and substantial changes in form. Hybrids, with different forms and numbers of maternal and paternal chromosomes, will usually be sterile because chromosomes have no partners for pairing before meiosis—the "reduction division" that produces sex cells with half the genetic information of body cells. But if the precursors of sex cells undergo polyploidy, then each chromosome will find a partner in the duplicated version of its own form.

Since polyploidy is so much more common in plants than animals, we should search for maximalism in our gardens, not our zoos. The numerical importance of polyploidy in plants can best be appreciated in a wonderful graph that I first encountered, when a graduate student, in Verne Grant's *The Origin of Adaptations.* This graph is a frequency distribution for chromosome pairs in monocot plants. For ten pairs of chromosomes and higher, without exception, all peaks are for even numbers of chromosome pairs.

At first inadequate sight, this pattern doesn't make sense in the deepest possible way. Biology is not numerology; its regularities do not take the form of such abstractions as "cleave to even numbers." Such a graph will not be satisfying until we figure out a biological mechanism that, as a side consequence and not because evens are better than odds per se, produces an imbalance of species with chromosomes in pairs of even numbers. The resolution is elegantly simple in this case. Polyploidy is very common in plants, and every number, odd or even, when doubled, yields an even number. The peaks therefore indicate the prevalence of polyploidy in plants. Estimates range as high as 50 percent for the number of angiosperm species produced by polyploidy.

Since polyploidy can continue in cycles—doubling followed by redoubling—chromosome numbers, like the pot in a poker game with table stakes, can rise alarmingly from small beginnings. The champions among all organisms are ferns in the family Ophioglossaceae. The genus *Ophioglossum* exhibits a basic number of 120 chromosome pairs, the lowest value among living species. (Such a high number must, itself, be derived from earlier incidents of polyploidy among species now extinct. The basic number for the entire family, 15 pairs, may have been the starting



Frequency distribution for the number of chromosome pairs in monocot plants. Note that all peaks are for even numbers of chromosomes. This occurs because so many plant species are produced by polyploidy, or doubling of chromosome number, and a doubling of any number, odd or even, produces an even number, FROM VERNE GRANT, *THE ORIGIN OF ADAPTATIONS,* 1963.

point.) In any case, cycles of polyploidy have proceeded onward from this alt each huge beginning of 120 pairs. The all-time champion, not only in *Ophioglossum,* but among all organisms, is *Ophioglossum reticulatum,* with about 630 pairs of chromosomes, or 1,260 per cell! (The total need not be an exact multiple of 120, because doubling may be imperfect, and secondary gains or losses for individual chromosomes are common.)

The very idea of a nucleus with 1,260 chromosomes, all obeying the rules of precise alignment and division as cells proliferate, inspired G. Ledyard Stebbins, our greatest living evolutionary botanist, to a rare emotion for a scientific paper—rapture (since Ledyard and I share a passion for Gilbert and Sullivan, I will write, for his sake, "modified rapture"—and he will know the reference and meaning): "At meiosis, these chromosomes pair regularly to form about 630 bivalents, a feat which to cytologists is as remarkable a wonder of nature as are the fantastic elaborations of form exhibited by orchids, insectivorous plants, and many animals" (see Stebbins, 1966, in the bibliography).

In fifteen years of writing these monthly essays, I have specialized in trying to draw general messages from particulars. But this time, I am stumped. I don't know what deep truth of nature emerges from the documentation of minimal and maximal chromosome numbers. Oh, I can cite some cliches and platitudes: Quantity is not quality; good things come in small packages. I can also state the obvious conclusion that inheritance and development do not depend primarily upon the number of distinct rods holding hereditary information—but this fact has been featured in textbooks of genetics for more than seventy years.

No, I think that every once in a while, we must simply let a fact stand by itself, for its own absolutely unvarnished fascination. Has your day not been brightened just a bit by learning that a plant can orchestrate the division of its cells by splitting 630 pairs of chromosomes with unerring accuracy—or that an ant, looking much like others, can gallivant about with an absolute minimum of one chromosome per cell? If so, I have earned my keep, and can go cultivate my garden. I think I'll try growing some ferns. Then I might take some colchicine, which often induces polyploidy, and maybe, just maybe. . . .