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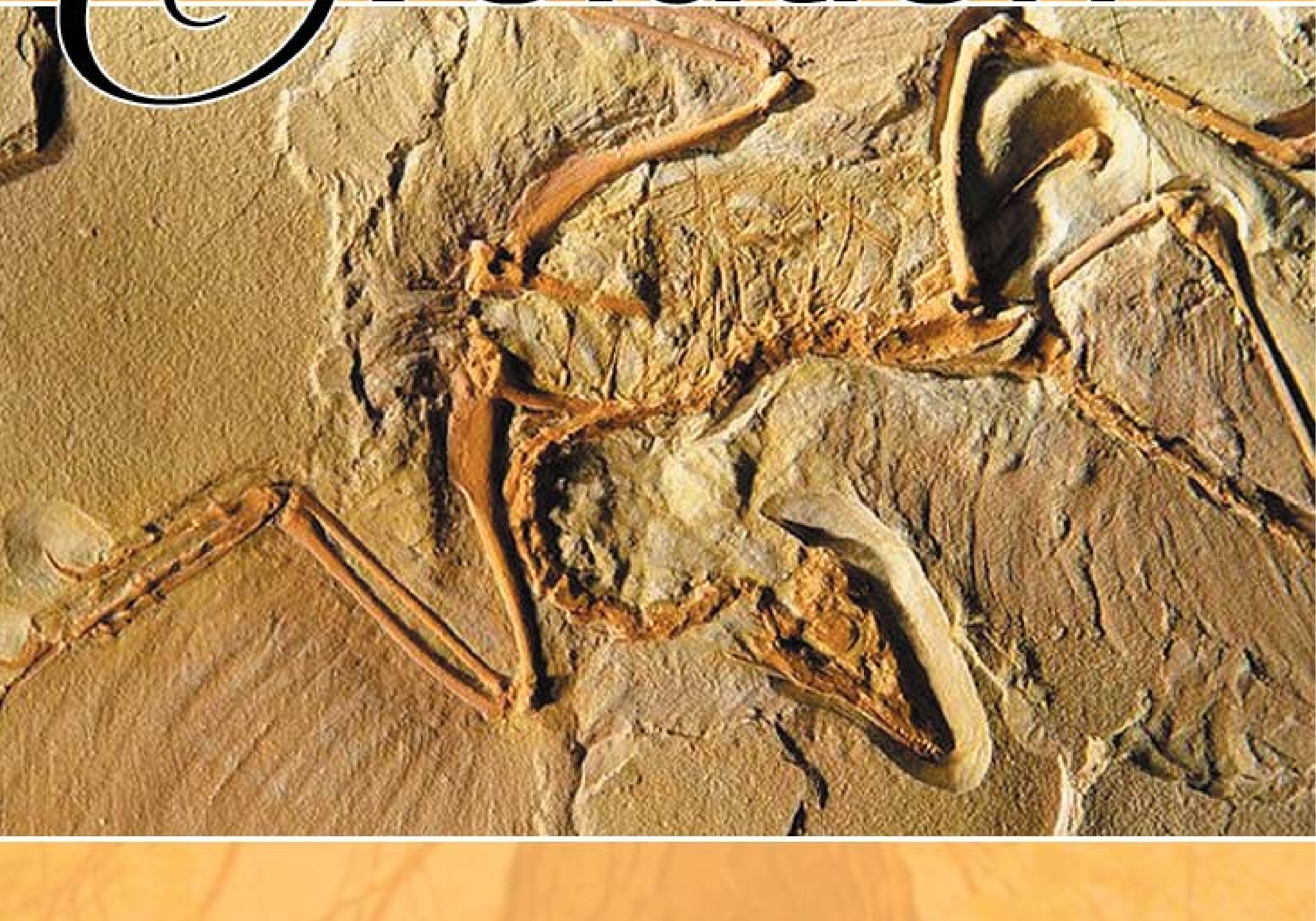
Evolution



EVOLUTION

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“Nothing in biology makes sense except in light of evolution.” So declared geneticist Theodosius Dobzhansky in 1973. Today’s scientists agree: evolution is without a doubt the cornerstone of modern biology. Yet in school districts across the U.S., proponents of creationist ideas such as intelligent design are attempting to introduce their nonscientific alternatives to evolution into curriculums.

Spurred by this worrying state of affairs, we have put together a collection of some of our favorite articles concerning the history of life, starting with a firm refutation of creationist arguments by Scientific American editor-in-chief John Rennie. Riveting accounts of what scientists have pieced together thus far about the evolution of earth’s creatures follow. Learn how four-legged land animals evolved from fish, how birds descended from dinosaurs and where whales come from. Explore the origins of early animals, and retrace the steps of paleontologists hot on the fossil trail of the earliest human ancestor. Also, discover how the application of evolutionary biology to medicine is informing medical research.

We hope you find these articles and the others in this exclusive online issue as thought provoking as we do. --*The Editors*

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originally published in July 2002

15 Answers to Creationist Nonsense

By John Rennie

Opponents of evolution want to make a place for creationism by tearing down real science, but their arguments don't hold up

When Charles Darwin introduced the theory of evolution through natural selection 143 years ago, the scientists of the day argued over it fiercely, but the massing evidence from paleontology, genetics, zoology, molecular biology and other fields gradually established evolution's truth beyond reasonable doubt. Today that battle has been won everywhere—except in the public imagination.

Embarrassingly, in the 21st century, in the most scientifically advanced nation the world has ever known, creationists can still persuade politicians, judges and ordinary citizens that evolution is a flawed, poorly supported fantasy. They lobby for creationist ideas such as "intelligent design" to be taught as alternatives to evolution in science classrooms. As this article goes to press, the Ohio Board of Education is debating whether to mandate such a change. Some antievolutionists, such as Philip E. Johnson, a law professor at the University of California at Berkeley and author of *Darwin on Trial,* admit that they intend for intelligent-design theory to serve as a "wedge" for reopening science classrooms to discussions of God.

Besieged teachers and others may increasingly find themselves on the spot to defend evolution and refute creationism. The arguments that creationists use are typically specious and based on misunderstandings of (or outright lies about) evolution, but the number and diversity of the objections can put even well-informed people at a disadvantage.

To help with answering them, the following list rebuts some of the most common "scientific" arguments raised against evolution. It also directs readers to further sources for information and explains why creation science has no place in the classroom.

when scientists talk about the theory of evolution—or the atomic theory or the theory of relativity, for that matter—they are not expressing reservations about its truth.

1. Evolution is only a theory. It is not a fact or a scientific law.

Many people learned in elementary school that a theory falls in the middle of a hierarchy of certainty—above a mere hypothesis but below a law. Scientists do not use the terms that way, however. According to the National Academy of Sciences (NAS), a scientific theory is "a well-substantiated explanation of some aspect of the natural world that can incorporate facts, laws, inferences, and tested hypotheses." No amount of validation changes a theory into a law, which is a descriptive generalization about nature. So when scientists talk about the theory of evolution—or the atomic theory or the theory of relativity, for that matter—they are not expressing reservations about its truth.

In addition to the *theory* of evolution, meaning the idea of descent with modification, one may also speak of the *fact* of evolution. The NAS defines a fact as "an observation that has been repeatedly confirmed and for all practical purposes is accepted as 'true.'" The fossil record and abundant other evidence testify that organisms have evolved through time. Although no one observed those transformations, the indirect evidence is clear, unambiguous and compelling.

All sciences frequently rely on indirect evidence. Physicists cannot see subatomic particles directly, for instance, so they verify their existence by watching for telltale tracks that the particles leave in cloud chambers. The absence of direct observation does not make physicists' conclusions less certain.

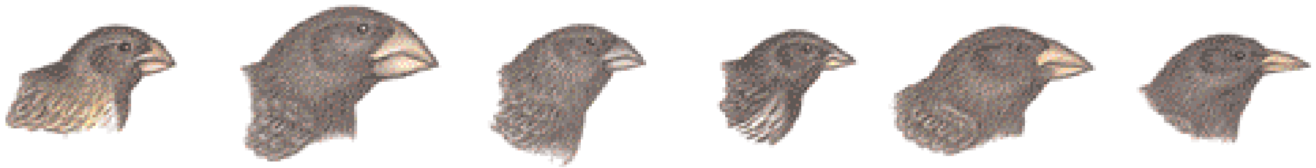
2. Natural selection is based on circular reasoning: the fittest are those who survive, and those who survive are deemed fittest.

"Survival of the fittest" is a conversational way to describe natural selection, but a more technical description speaks of differential rates of survival and reproduction. That is, rather than labeling species as more or less fit, one can describe how many offspring they are likely to leave under given circumstances. Drop a fast-breeding pair of small-beaked finches and a slower-breeding pair of large-beaked finches onto an island full of food seeds. Within a few generations the fast breeders may control more of the food resources. Yet if large beaks more easily crush seeds, the advantage may tip to the slow breeders. In a pioneering study of finches on the Galápagos Islands, Peter R. Grant of Princeton University observed these kinds of population shifts in the wild [see his article "Natural Selection and Darwin's Finches"; Scientific American, October 1991].

The key is that adaptive fitness can be defined without reference to survival: large beaks are better adapted for crushing seeds, irrespective of whether that trait has survival value under the circumstances.

3. Evolution is unscientific, because it is not testable or falsifiable. It makes claims about events that were not observed and can never be re-created.

This blanket dismissal of evolution ignores important



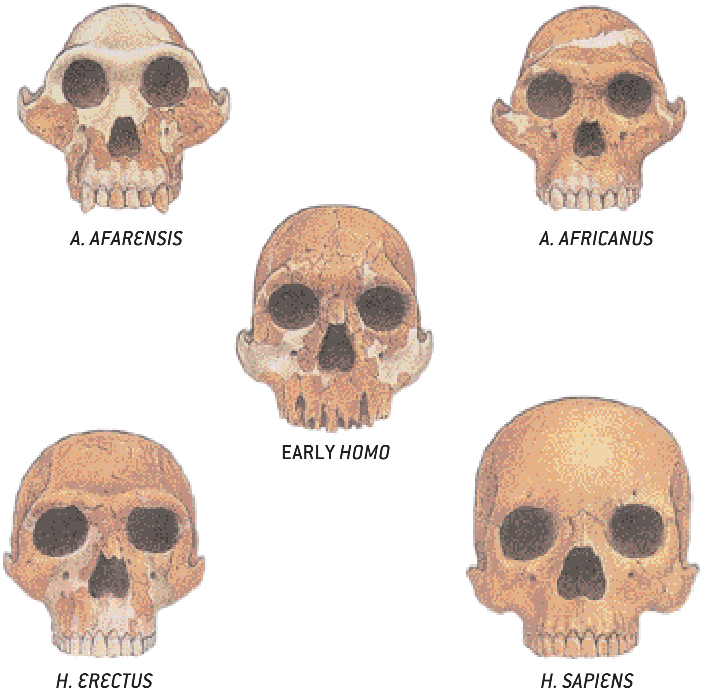
GALÁPAGOS FINCHES show adaptive beak shapes.

PATRICIA J. WYNNE

distinctions that divide the field into at least two broad areas: microevolution and macroevolution. Microevolution looks at changes within species over time—changes that may be preludes to speciation, the origin of new species. Macroevolution studies how taxonomic groups above the level of species change. Its evidence draws frequently from the fossil record and DNA comparisons to reconstruct how various organisms may be related.

These days even most creationists acknowledge that microevolution has been upheld by tests in the laboratory (as in studies of cells, plants and fruit flies) and in the field (as in Grant's studies of evolving beak shapes among Galápagos finches). Natural selection and other mechanisms—such as chromosomal changes, symbiosis and hybridization—can drive profound changes in populations over time.

The historical nature of macroevolutionary study involves inference from fossils and DNA rather than direct observation. Yet in the historical sciences (which include astronomy, geology and archaeology, as well as evolutionary biology), hypotheses can still be tested by checking whether they accord with physical evidence and whether they lead to verifiable predictions about future discoveries. For instance, evolution implies that between the earliest-known ancestors of humans (roughly five million years old) and the appearance of anatomically modern humans (about 100,000 years ago), one should find a succession of hominid creatures with features progressively less apelike and more modern, which is indeed what the fossil record shows. But one should not—and does not—find modern human fossils embedded in strata from the Jurassic period (65 million years ago). Evolutionary biology routinely makes predictions far more refined and precise than this, and researchers test them constantly.



SKULLS of some hominids predating modern humans (*Homo sapiens*).

REPRINTED BY PERMISSION OF WADSWORTH/THOMSON LEARNING FROM *BIOLOGY: CONCEPTS AND APPLICATIONS*, BY CECIE STARR, © 1991

Evolution could be disproved in other ways, too. If we could document the spontaneous generation of just one complex life-form from inanimate matter, then at least a few creatures seen in the fossil record might have originated this way. If superintelligent aliens appeared and claimed credit for creating life on earth (or even particular species), the purely evolutionary explanation would be cast in doubt. But no one has yet produced such evidence.

It should be noted that the idea of falsifiability as the defining characteristic of science originated with philosopher Karl Popper in the 1930s. More recent elaborations on his thinking have expanded the narrowest interpretation of his principle precisely because it would eliminate too many branches of clearly scientific endeavor.

4. Increasingly, scientists doubt the truth of evolution.

No evidence suggests that evolution is losing adherents. Pick up any issue of a peer-reviewed biological journal, and you will find articles that support and extend evolutionary studies or that embrace evolution as a fundamental concept.

Conversely, serious scientific publications disputing evolution are all but nonexistent. In the mid-1990s George W. Gilchrist of the University of Washington surveyed thousands of journals in the primary literature, seeking articles on intelligent design or creation science. Among those hundreds of thousands of scientific reports, he found none. In the past two years, surveys done independently by Barbara Forrest of Southeastern Louisiana University and Lawrence M. Krauss of Case Western Reserve University have been similarly fruitless.

Creationists retort that a closed-minded scientific community rejects their evidence. Yet according to the editors of *Nature, Science* and other leading journals, few antievolution manuscripts are even submitted. Some antievolution authors have published papers in serious journals. Those papers, however, rarely attack evolution directly or advance creationist arguments; at best, they identify certain evolutionary problems as unsolved and difficult (which no one disputes). In short, creationists are not giving the scientific world good reason to take them seriously.

5. The disagreements among even evolutionary biologists show how little solid science supports evolution.

Evolutionary biologists passionately debate diverse topics: how speciation happens, the rates of evolutionary change, the ancestral relationships of birds and dinosaurs, whether Neandertals were a species apart from modern humans, and much more. These disputes are like those found in all other branches of science. Acceptance of evolution as a factual occurrence and a guiding principle is nonetheless universal in biology.

Unfortunately, dishonest creationists have shown a willingness to take scientists' comments out of context to exaggerate and distort the disagreements. Anyone acquainted with the works of paleontologist Stephen Jay Gould of Harvard University knows that in addition to co-authoring the punctuated-equilibrium model, Gould was one of the most eloquent defenders and articulators of evolution. (Punctuated equilibrium explains patterns in the fossil record by suggesting that most evolutionary changes occur within geologically brief intervals—which may nonetheless amount to hundreds of generations.) Yet creationists delight in dissecting out phrases from Gould's voluminous prose to make him sound as though he had doubted evolution, and they present punctuated equilibrium as though it allows new species to materialize overnight or birds to be born from reptile eggs.

When confronted with a quotation from a scientific authority that seems to question evolution, insist on seeing the statement in context. Almost invariably, the attack on evolution will prove illusory.

6. If humans descended from monkeys, why are there still monkeys?

This surprisingly common argument reflects several levels of ignorance about evolution. The first mistake is that evolution does not teach that humans descended from monkeys; it states that both have a common ancestor.

The deeper error is that this objection is tantamount to asking, "If children descended from adults, why are there still adults?" New species evolve by splintering off from established ones, when populations of organisms become isolated from the main branch of their family and acquire sufficient differences to remain forever distinct. The parent species may survive indefinitely thereafter, or it may become extinct.

7. Evolution cannot explain how life first appeared on earth.

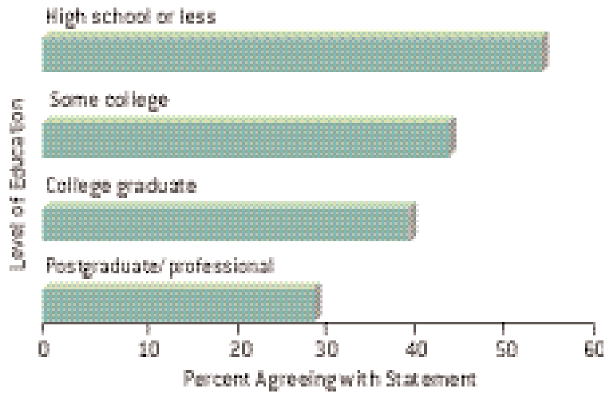
The origin of life remains very much a mystery, but biochemists have learned about how primitive nucleic acids, amino acids and other building blocks of life could have formed and organized themselves into self-replicating, self-sustaining units, laying the foundation for cellular biochemistry. Astrochemical analyses hint that quantities of these compounds might have originated in space and fallen to earth in comets, a scenario that may solve the problem of how those constituents arose under the conditions that prevailed when our planet was young.

Creationists sometimes try to invalidate all of evolution by pointing to science's current inability to explain the origin of life. But even if life on earth turned out to have a nonevolutionary origin (for instance, if aliens introduced the first cells billions of years ago), evolution since then would be robustly confirmed by countless microevolutionary and macroevolutionary studies.

8. Mathematically, it is inconceivable that anything as complex as a protein, let alone a living cell or a human, could spring up by chance.

Chance plays a part in evolution (for example, in the random mutations that can give rise to new traits), but evolution does not depend on chance to create organisms, proteins or other entities. Quite the opposite: natural selection, the principal known mechanism of evolution, harnesses nonrandom change by preserving "desirable" (adaptive) features and eliminating "undesirable" (nonadaptive) ones. As long as the forces of selection stay constant, natural selection can push evolution in one direction and produce sophisticated structures in surprisingly short times.

"GOD CREATED HUMANS IN THEIR PRESENT FORM WITHIN THE PAST 10,000 YEARS OR SO."



SOURCE: The Gallup Organization, 1999

As an analogy, consider the 13-letter sequence "TOBEORNOTTOBE." Those hypothetical million monkeys, each pecking out one phrase a second, could take as long as 78,800 years to find it among the 26^{13} sequences of that length. But in the 1980s Richard Hardison of Glendale College wrote a computer program that generated phrases randomly while preserving the positions of individual letters that happened to be correctly placed (in effect, selecting for phrases more like Hamlet's). On average, the program re-created the phrase in just 336 iterations, less than 90 seconds. Even more amazing, it could reconstruct Shakespeare's entire play in just four and a half days.

CLEO VILETT

9. The Second Law of Thermodynamics says that systems must become more disordered over time. Living cells therefore could not have evolved from inanimate chemicals, and multicellular life could not have evolved from protozoa.

This argument derives from a misunderstanding of the Second Law. If it were valid, mineral crystals and snowflakes would also be impossible, because they, too, are complex structures that form spontaneously from disordered parts.

The Second Law actually states that the total entropy of a closed system (one that no energy or matter leaves or enters) cannot decrease. Entropy is a physical concept often casually described as disorder, but it differs significantly from the conversational use of the word.

More important, however, the Second Law permits parts of a system to decrease in entropy as long as other parts experience an offsetting increase. Thus, our planet as a whole can grow more complex because the sun pours heat and light onto it, and the greater entropy associated with the sun's nuclear fusion more than rebalances the scales. Simple organisms can fuel their rise toward complexity by consuming other forms of life and nonliving materials.

10. Mutations are essential to evolution theory, but mutations can only eliminate traits. They cannot produce new features.

On the contrary, biology has catalogued many traits produced by point mutations (changes at precise positions in an organism's DNA)—bacterial resistance to antibiotics, for example.

Mutations that arise in the homeobox (*Hox*) family of development-regulating genes in animals can also have complex effects. *Hox* genes direct where legs, wings, antennae and body segments should grow. In fruit flies, for instance, the mutation called *Antennapedia* causes legs to sprout where antennae should grow. These abnormal limbs are not functional, but their existence demonstrates that genetic mistakes can produce complex structures, which natural selection can then test for possible uses.

Moreover, molecular biology has discovered mechanisms for genetic change that go beyond point mutations, and these expand the ways in which new traits can appear. Functional modules within genes can be spliced together in novel ways. Whole genes can be accidentally duplicated in an organism's DNA, and the duplicates are free to mutate into genes for new, complex features. Comparisons of the DNA from a wide variety of organisms indicate that this is how the globin family of blood proteins evolved over millions of years.

11. Natural selection might explain microevolution, but it cannot explain the origin of new species and higher orders of life.

Evolutionary biologists have written extensively about how natural selection could produce new species. For instance, in the model called allopatry, developed by Ernst Mayr of Harvard University, if a population of organisms were isolated from the rest of its species by geographical boundaries, it might be subjected to different selective pressures. Changes would accumulate in the isolated population. If those changes became so significant that the splinter group could not or routinely would not breed with the original stock, then the splinter group would be *reproductively isolated* and on its way toward becoming a new species.

Natural selection is the best studied of the evolutionary mechanisms, but biologists are open to other possibilities as well. Biologists are constantly assessing the potential of unusual genetic mechanisms for causing speciation or for producing complex features in organisms. Lynn Margulis of the University of Massachusetts at Amherst and others have persuasively argued that some cellular organelles, such as the energy-generating mitochondria, evolved through the symbiotic merger of ancient organisms. Thus, science welcomes the possibility of evolution resulting from forces beyond natural selection. Yet those forces must be natural; they cannot be attributed to the actions of mysterious creative intelligences whose existence, in scientific terms, is unproved.

12. Nobody has ever seen a new species evolve.

Speciation is probably fairly rare and in many cases might take centuries. Furthermore, recognizing a new species during a formative stage can be difficult, because biologists sometimes disagree about how best to define a species. The most widely used definition, Mayr's Biological Species Concept, recognizes a species as a distinct community of reproductively isolated populations—sets of organisms that normally do not or cannot breed outside their community. In practice, this standard can be difficult to apply to organisms isolated by distance or terrain or to plants (and, of course, fossils do not breed). Biologists therefore usually use organisms' physical and behavioral traits as clues to their species membership.

Nevertheless, the scientific literature does contain reports of apparent speciation events in plants, insects and worms. In most of these experiments, researchers subjected organisms to various types of selection—for anatomical differences, mating behaviors, habitat preferences and other traits—and found that they had created populations of organisms that did not breed with outsiders. For example, William R. Rice of the University of New Mexico and George W. Salt of the University of California at Davis demonstrated that if they sorted a group of fruit flies by their preference for certain environments and bred those flies separately over 35 generations, the resulting flies would refuse to breed with those from a very different environment.

13. Evolutionists cannot point to any transitional fossils—creatures that are half reptile and half bird, for instance.

Actually, paleontologists know of many detailed examples of fossils intermediate in form between various taxonomic groups. One of the most famous fossils of all time is *Archaeopteryx,* which combines feathers and skeletal structures peculiar to birds with features of dinosaurs. A flock's worth of other feathered fossil species, some more avian and some less, has also been found. A sequence of fossils spans the evolution of modern horses from the tiny *Eohippus*. Whales had four-legged ancestors that walked on land, and creatures known as *Ambulocetus* and *Rodhocetus* helped to make that transition [see "The Mammals That Conquered the Seas," by Kate Wong; Scientific American, May 2002]. Fossil seashells trace the evolution of various mollusks through millions of years. Perhaps 20 or more hominids (not all of them our ancestors) fill the gap between Lucy the australopithecine and modern humans.

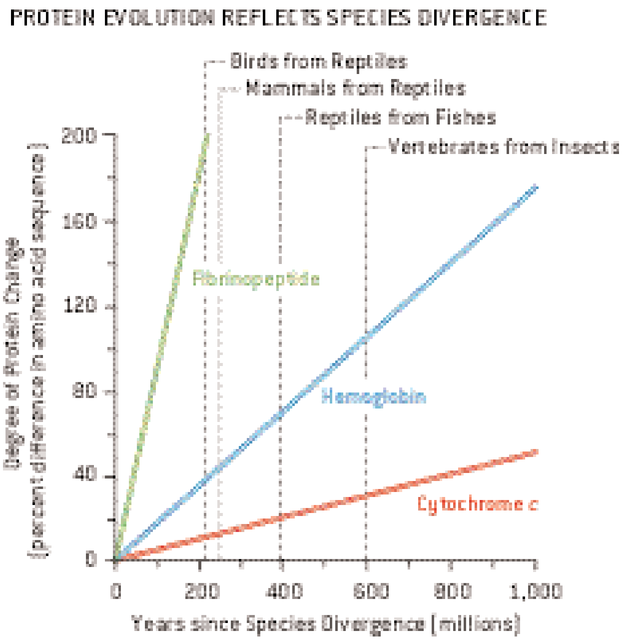
Creationists, though, dismiss these fossil studies. They argue that *Archaeopteryx* is not a missing link between reptiles and birds—it is just an extinct bird with reptilian features. They want evolutionists to produce a weird, chimeric monster that cannot be classified as belonging to any known group. Even if a creationist does accept a fossil as transitional between two species, he or she may then insist on seeing other fossils intermediate between it and the first two. These frustrating requests can proceed ad infinitum and place an unreasonable burden on the always incomplete fossil record.

Nevertheless, evolutionists can cite further supportive evidence from molecular biology. All organisms share most of the same genes, but as evolution predicts, the structures of these genes and their products diverge among species, in keeping with their evolutionary relationships. Geneticists speak of the "molecular clock" that records the passage of time. These molecular data also show how various organisms are transitional within evolution.

14. Living things have fantastically intricate features—at the anatomical, cellular and molecular levels—that could not function if they were any less complex or sophisticated. The only prudent conclusion is that they are the products of intelligent design, not evolution.

This "argument from design" is the backbone of most recent attacks on evolution, but it is also one of the oldest. In 1802 theologian William Paley wrote that if one finds a pocket watch in a field, the most reasonable conclusion is that someone dropped it, not that natural forces created it there. By analogy, Paley argued, the complex structures of living things must be the handiwork of direct, divine invention. Darwin wrote *On the Origin of Species* as an answer to Paley: he explained how natural forces of selection, acting on inherited features, could gradually shape the evolution of ornate organic structures.

Generations of creationists have tried to counter Darwin by citing the example of the eye as a structure that could not have evolved. The eye's ability to provide vision depends on the perfect arrangement of its parts, these critics say. Natural selection could thus never favor the transitional forms needed during the eye's evolution—what good is half an eye? Anticipating this criticism, Darwin suggested that even "incomplete" eyes might confer benefits (such as helping creatures orient toward light) and thereby survive for further evolutionary refinement. Biology has vindicated Darwin: researchers have identified primitive eyes and light-sensing organs throughout the animal kingdom and have even tracked the evolutionary history of eyes through comparative genetics. (It now appears that in various families of organisms, eyes have evolved independently.)

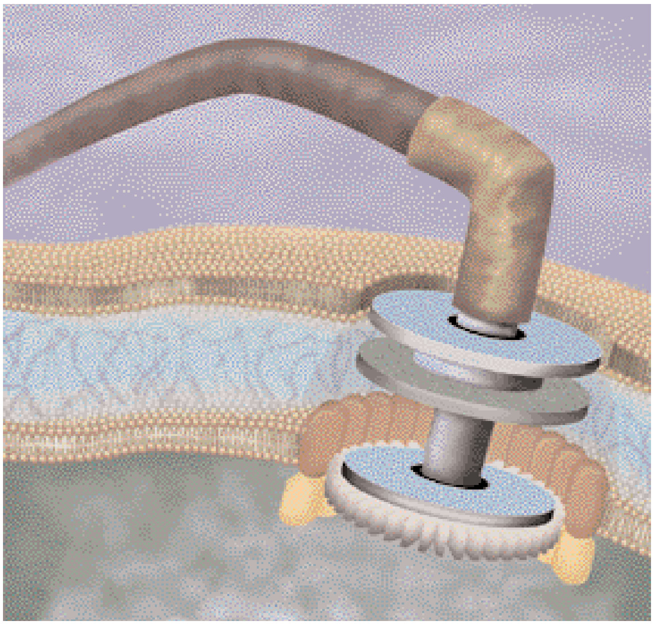

PROTEIN EVOLUTION REFLECTS SPECIES DIVERGENCE

Today's intelligent-design advocates are more sophisticated than their predecessors, but their arguments and goals are not fundamentally different. They criticize evolution by trying to demonstrate that it could not account for life as we know it and then insist that the only tenable alternative is that life was designed by an unidentified intelligence.

CLEO VILETT

15. Recent discoveries prove that even at the microscopic level, life has a quality of complexity that could not have come about through evolution.

"Irreducible complexity" is the battle cry of Michael J. Behe of Lehigh University, author of *Darwin's Black Box: The Biochemical Challenge to Evolution.* As a household example of irreducible complexity, Behe chooses the mousetrap—a machine that could not function if any of its pieces were missing and whose pieces have no value except as parts of the whole. What is true of the mousetrap, he says, is even truer of the bacterial flagellum, a whiplike cellular organelle used for propulsion that operates like an outboard motor. The proteins that make up a flagellum are uncannily arranged into motor components, a universal joint and other structures like those that a human engineer might specify. The possibility that this intricate array could have arisen through evolutionary modification is virtually nil, Behe argues, and that bespeaks intelligent design. He makes similar points about the blood's clotting mechanism and other molecular systems.



CLOSE-UP of a bacterial flagellum.

CLEO VILETT

Yet evolutionary biologists have answers to these objections. First, there exist flagellae with forms simpler than the one that Behe cites, so it is not necessary for all those components to be present for a flagellum to work. The sophisticated components of this flagellum all have precedents elsewhere in nature, as described by Kenneth R. Miller of Brown University and others. In fact, the entire flagellum assembly is extremely similar to an organelle that *Yersinia pestis,* the bubonic plague bacterium, uses to inject toxins into cells.

The key is that the flagellum's component structures, which Behe suggests have no value apart from their role in propulsion, can serve multiple functions that would have helped favor their evolution. The final evolution of the flagellum might then have involved only the novel recombination of sophisticated parts that initially evolved for other purposes. Similarly, the blood-clotting system seems to involve the modification and elaboration of proteins that were originally used in digestion, according to studies by Russell F. Doolittle of the University of California at San Diego. So some of the complexity that Behe calls proof of intelligent design is not irreducible at all.

Complexity of a different kind—"specified complexity"—is the cornerstone of the intelligent-design arguments of William A. Dembski of Baylor University in his books *The Design Inference* and *No Free Lunch.* Essentially his argument is that living things are complex in a way that undirected, random processes could never produce. The only logical conclusion, Dembski asserts, in an echo of Paley 200 years ago, is that some superhuman intelligence created and shaped life.

Dembski's argument contains several holes. It is wrong to insinuate that the field of explanations consists only of random processes or designing intelligences. Researchers into nonlinear systems and cellular automata at the Santa Fe Institute and elsewhere have demonstrated that simple, undirected processes can yield extraordinarily complex patterns. Some of the complexity seen in organisms may therefore emerge through natural phenomena that we as yet barely understand. But that is far different from saying that the complexity could not have arisen naturally.

"Creation science" is a contradiction in terms. A central tenet of modern science is methodological naturalism—it seeks to explain the universe purely in terms of observed or testable natural mechanisms. Thus, physics describes the atomic nucleus with specific concepts governing matter and energy, and it tests those descriptions experimentally. Physicists introduce new particles, such as quarks, to flesh out their theories only when data show that the previous descriptions cannot adequately explain observed phenomena. The new particles do not have arbitrary properties, moreover—their definitions are tightly constrained, because the new particles must fit within the existing framework of physics.

In contrast, intelligent-design theorists invoke shadowy entities that conveniently have whatever unconstrained abilities are needed to solve the mystery at hand. Rather than expanding scientific inquiry, such answers shut it down. (How does one disprove the existence of omnipotent intelligences?)

Intelligent design offers few answers. For instance, when and how did a designing intelligence intervene in life's history? By creating the first DNA? The first cell? The first human? Was every species designed, or just a few early ones? Proponents of intelligent-design theory frequently decline to be pinned down on these points. They do not even make real attempts to reconcile their disparate ideas about intelligent design. Instead they pursue argument by exclusion—that is, they belittle evolutionary explanations as far-fetched or incomplete and then imply that only design-based alternatives remain.

Logically, this is misleading: even if one naturalistic explanation is flawed, it does not mean that all are. Moreover, it does not make one intelligent-design theory more reasonable than another. Listeners are essentially left to fill in the blanks for themselves, and some will undoubtedly do so by substituting their religious beliefs for scientific ideas.

Time and again, science has shown that methodological naturalism can push back ignorance, finding increasingly detailed and informative answers to mysteries that once seemed impenetrable: the nature of light, the causes of disease, how the brain works. Evolution is doing the same with the riddle of how the living world took shape. Creationism, by any name, adds nothing of intellectual value to the effort.

John Rennie is editor in chief of Scientific American.

OTHER RESOURCES FOR DEFENDING EVOLUTION

How to Debate a Creationist: 25 Creationists' Arguments and 25 Evolutionists' Answers. Michael Shermer. Skeptics Society, 1997. This well-researched refutation of creationist claims deals in more depth with many of the same scientific arguments raised here, as well as other philosophical problems. *Skeptic* magazine routinely covers creation/evolution debates and is a solid, thoughtful source on the subject: **www.skeptic.com**

Defending Evolution in the Classroom: A Guide to the Creation/Evolution Controversy. Brian J. Alters and Sandra M. Alters. Jones and Bartlett Publishers, 2001. This up-to-date overview of the creation/evolution controversy explores the issues clearly and readably, with a full appreciation of the cultural and religious influences that create resistance to teaching evolution. It, too, uses a question-and-answer format that should be particularly valuable for teachers.

Science and Creationism: A View from the National Academy of Sciences. Second edition. National Academy Press, 1999. This concise booklet has the backing of the country's top scientific authorities. Although its goal of making a clear, brief statement necessarily limits the detail with which it can pursue its arguments, the publication serves as handy proof that the scientific establishment unwaveringly supports evolution. It is also available at **www7.nationalacademies.org/evolution/**

The Triumph of Evolution and the Failure of Creationism. Niles Eldredge. W. H. Freeman and Company, 2000. The author, a leading contributor to evolution theory and a curator at the American Museum of Natural History in New York City, offers a scathing critique of evolution's opponents.

Intelligent Design Creationism and Its Critics. Edited by Robert T. Pennock. Bradford Books/MIT Press, 2001. For anyone who wishes to understand the "intelligent design" controversy in detail, this book is a terrific one-volume summary of the scientific, philosophical and theological issues. Philip E. Johnson, Michael J. Behe and William A. Dembski make the case for intelligent design in their chapters and are rebutted by evolutionists, including Pennock, Stephen Jay Gould and Richard Dawkins.

Talk.Origins archive (www.talkorigins.org). This wonderfully thorough online resource compiles useful essays and commentaries that have appeared in Usenet discussions about creationism and evolution. It offers detailed discussions (some of which may be too sophisticated for casual readers) and bibliographies relating to virtually any objection to evolution that creationists might raise.

National Center for Science Education Web site (www.ncseweb.org). The center is the only national organization that specializes in defending the teaching of evolution against creationist attacks. Offering resources for combating misinformation and monitoring antievolution legislation, it is ideal for staying current with the ongoing public debate.

PBS Web site for evolution (www.pbs.org/wgbh/evolution/). Produced as a companion to the seven-part television series *Evolution,* this site is an enjoyable guide to evolutionary science. It features multimedia tools for teaching evolution. The accompanying book, *Evolution,* by Carl Zimmer (HarperCollins, 2001), is also useful for explaining evolution to doubters.

originally published in October 1994

the evolution of life on earth

By Stephen Jay Gould

The history of life is not necessarily progressive; it is certainly not predictable. The earth's creatures have evolved through a series of contingent and fortuitous events

Some creators announce their inventions with grand éclat. God proclaimed, "*Fiat lux,*" and then flooded his new universe with brightness. Others bring forth great discoveries in a modest guise, as did Charles Darwin in defining his new mechanism of evolutionary causality in 1859: "I have called this principle, by which each slight variation, if useful, is preserved, by the term Natural Selection."

Natural selection is an immensely powerful yet beautifully simple theory that has held up remarkably well, under intense and unrelenting scrutiny and testing, for 135 years. In essence, natural selection locates the mechanism of evolutionary change in a "struggle" among organisms for reproductive success, leading to improved fit of populations to changing environments. (Struggle is often a metaphorical description and need not be viewed as overt combat, guns blazing. Tactics for reproductive success include a variety of nonmartial activities such as earlier and more frequent mating or better cooperation with partners in raising offspring.) Natural selection is therefore a principle of local adaptation, not of general advance or progress.

Yet powerful though the principle may be, natural selection is not the only cause of evolutionary change (and may, in many cases, be overshadowed by other forces). This point needs emphasis because the standard misapplication of evolutionary theory assumes that biological explanation may be equated with devising accounts, often speculative and conjectural in practice, about the adaptive value of any given feature in its original environment (human aggression as good for hunting, music and religion as good for tribal cohesion, for example). Darwin himself strongly emphasized the multifactorial nature of evolutionary change and warned against too exclusive a reliance on natural selection, by placing the following statement in a maximally conspicuous place at the very end of his introduction: "I am convinced that Natural Selection has been the most important, but not the exclusive, means of modification."

Reality versus Conceit

NATURAL SELECTION is not fully sufficient to explain evolutionary change for two major reasons. First, many other causes are powerful, particularly at levels of biological organization both above and below the traditional Darwinian focus on organisms and their struggles for reproductive success. At the lowest level of substitution in individual base pairs of DNA, change is often effectively neutral and therefore random. At higher levels, involving entire species or faunas, punctuated equilibrium can produce evolutionary trends by selection of species based on their rates of origin and extirpation, whereas mass extinctions wipe out substantial parts of biotas for reasons unrelated to adaptive struggles of constituent species in "normal" times between such events.

Second, and the focus of this article, no matter how adequate our general theory of evolutionary change, we also yearn to document and understand the actual pathway of life's history. Theory, of course, is relevant to explaining the pathway (nothing about the pathway can be inconsistent with good theory, and theory can predict certain general aspects of life's geologic pattern). But the actual pathway is strongly *underdetermined* by our general theory of life's evolution. This point needs some belaboring as a central yet widely misunderstood aspect of the world's complexity. Webs and chains of historical events are so intricate, so imbued with random and chaotic elements, so unrepeatable in encompassing such a multitude of unique (and uniquely interacting) objects, that standard models of simple prediction and replication do not apply.

History can be explained, with satisfying rigor if evidence be adequate, after a sequence of events unfolds, but it cannot be predicted with any precision beforehand. Pierre-Simon Laplace, echoing the growing and confident determinism of the late 18th century, once said that he could specify all future states if he could know the position and motion of all particles in the cosmos at any moment, but the nature of universal complexity shatters this chimerical dream. History includes too much chaos, or extremely sensitive dependence on minute and unmeasurable differences in initial conditions, leading to massively divergent outcomes based on tiny and unknowable disparities in starting points. And history includes too much contingency, or shaping of present results by long chains of unpredictable antecedent states, rather than immediate determination by timeless laws of nature.

Homo sapiens did not appear on the earth, just a geologic second ago, because evolutionary theory predicts such an outcome based on themes of progress and increasing neural complexity. Humans arose, rather, as a fortuitous and contingent outcome of thousands of linked events, any one of which could have occurred differently and sent history on an alternative pathway that would not have led to consciousness. To cite just four among a multitude: (1) If our inconspicuous and fragile lineage had not been among the few survivors of the initial radiation of multicellular animal life in the Cambrian explosion 530 million years ago, then no vertebrates would have inhabited the earth at all. (Only one member of our chordate phylum, the genus *Pikaia,* has been found among these earliest fossils. This small and simple swimming creature, showing its allegiance to us by possessing a notochord, or dorsal stiffening rod, is among the rarest fossils of the Burgess Shale, our best preserved Cambrian fauna.) (2) If a small and unpromising group of lobe-finned fishes had not evolved fin bones with a strong central axis capable of bearing weight on land, then vertebrates might never have become terrestrial. (3) If a large extraterrestrial body had not struck the earth 65 million years ago, then dinosaurs would still be dominant and mammals insignificant (the situation that had prevailed for 100 million years previously). (4) If a small lineage of primates had not evolved upright posture on the drying African savannas just two to four million years ago, then our ancestry might have ended in a line of apes that, like the chimpanzee and gorilla today, would have become ecologically marginal and probably doomed to extinction despite their remarkable behavioral complexity.

Therefore, to understand the events and generalities of life's pathway, we must go beyond principles of evolutionary theory to a paleontological examination of the contingent pattern of life's history on our planet—the single actualized version among millions of plausible alternatives that happened not to occur. Such a view of life's history is highly contrary both to conventional deterministic models of Western science and to the deepest social traditions and psychological hopes of Western culture for a history culminating in humans as life's highest expression and intended planetary steward.

Science can, and does, strive to grasp nature's factuality, but all science is socially embedded, and all scientists record prevailing "certainties," however hard they may be aiming for pure objectivity. Darwin himself, in the closing lines of *On the Origin of Species,* expressed Victorian social preference more than nature's record in writing: "As natural selection works solely by and for the good of each being, all corporeal and mental endowments will tend to progress towards perfection."

Life's pathway certainly includes many features predictable from laws of nature, but these aspects are too broad and general to provide the "rightness" that we seek for validating evolution's particular results—roses, mushrooms, people and so forth. Organisms adapt to, and are constrained by, physical principles. It is, for example, scarcely surprising, given laws of gravity, that the largest vertebrates in the sea (whales) exceed the heaviest animals on land (elephants today, dinosaurs in the past), which, in turn, are far bulkier than the largest vertebrate that ever flew (extinct pterosaurs of the Mesozoic era).

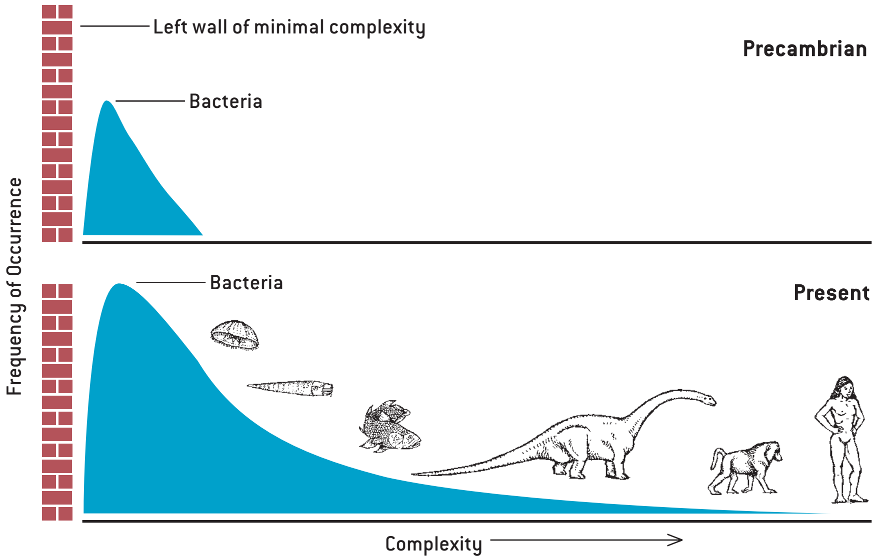
Predictable ecological rules govern the structuring of communities by principles of energy flow and thermodynamics (more biomass in prey than in predators, for example). Evolutionary trends, once started, may have local predictability ("arms races," in which both predators and prey hone their defenses and weapons, for example—a pattern that Geerat J. Vermeij of the University of California at Davis has called "escalation" and documented in increasing strength of both crab claws and shells of their gastropod prey through time). But laws of nature do not tell us why we have crabs and snails at all, why insects rule the multicellular world and why vertebrates rather than persistent algal mats exist as the most complex forms of life on the earth.

Relative to the conventional view of life's history as an at least broadly predictable process of gradually advancing complexity through time, three features of the paleontological record stand out in opposition and shall therefore serve as organizing themes for the rest of this article: the constancy of modal complexity throughout life's history; the concentration of major events in short bursts interspersed with long periods of relative stability; and the role of external impositions, primarily mass extinctions, in disrupting patterns of "normal" times. These three features, combined with more general themes of chaos and contingency, require a new framework for conceptualizing and drawing life's history, and this article therefore closes with suggestions for a different iconography of evolution.

The Lie of "Progress"

THE PRIMARY paleontological fact about life's beginnings points to predictability for the onset and very little for the particular pathways thereafter. The earth is 4.6 billion years old, but the oldest rocks date to about 3.9 billion years because the earth's surface became molten early in its history, a result of bombardment by large amounts of cosmic debris during the solar system's coalescence and of heat generated by radioactive decay of short-lived isotopes. These oldest rocks are too metamorphosed by subsequent heat and pressure to preserve fossils (although some scientists interpret the proportions of carbon isotopes in these rocks as signs of organic production). The oldest rocks sufficiently unaltered to retain cellular fossils—African and Australian sediments dated to 3.5 billion years old—do preserve prokaryotic cells (bacteria and cyanophytes) and stromatolites (mats of sediment trapped and bound by these cells in shallow marine waters). Thus, life on the earth evolved quickly and is as old as it could be. This fact alone seems to indicate an inevitability, or at least a predictability, for life's origin from the original chemical constituents of atmosphere and ocean.

No one can doubt that more complex creatures arose sequentially after this prokaryotic beginning—first eukaryotic cells, perhaps about two billion years ago, then multicellular an-



PROGRESS DOES NOT RULE (and is not even a primary thrust of) the evolutionary process. For reasons of chemistry and physics, life arises next to the "left wall" of its simplest conceivable and preservable complexity. This style of life (bacterial) has remained most common and most successful. A few creatures occasionally move to the right, thus extending the right tail in the distribution of complexity. Many always move to the left, but they are absorbed within space already occupied. Note that the bacterial mode has never changed in position, but just grown higher.

imals about 600 million years ago, with a relay of highest complexity among animals passing from invertebrates, to marine vertebrates and, finally (if we wish, albeit parochially, to honor neural architecture as a primary criterion), to reptiles, mammals and humans. This is the conventional sequence represented in the old charts and texts as an "age of invertebrates," followed by an "age of fishes," "age of reptiles," "age of mammals," and "age of man" (to add the old gender bias to all the other prejudices implied by this sequence).

I do not deny the facts of the preceding paragraph but wish to argue that our conventional desire to view history as progressive, and to see humans as predictably dominant, has grossly distorted our interpretation of life's pathway by falsely placing in the center of things a relatively minor phenomenon that arises only as a side consequence of a physically constrained starting point. The most salient feature of life has been the stability of its bacterial mode from the beginning of the fossil record until today and, with little doubt, into all future time so long as the earth endures. This is truly the "age of bacteria"—as it was in the beginning, is now and ever shall be.

For reasons related to the chemistry of life's origin and the physics of self-organization, the first living things arose at the lower limit of life's conceivable, preservable complexity. Call this lower limit the "left wall" for an architecture of complexity. Because so little space exists between the left wall and life's initial bacterial mode in the fossil record, only one direction for future increment exists—toward greater complexity at the right. Thus, every once in a while, a more complex creature evolves and extends the range of life's diversity in the only available direction. In technical terms, the distribution of complexity becomes more strongly right skewed through these occasional additions.

But the additions are rare and episodic. They do not even constitute an evolutionary series but form a motley sequence of distantly related taxa, usually depicted as eukaryotic cell, jellyfish, trilobite, nautiloid, eurypterid (a large relative of horseshoe crabs), fish, an amphibian such as *Eryops*, a dinosaur, a mammal and a human being. This sequence cannot be construed as the major thrust or trend of life's history. Think rather of an occasional creature tumbling into the empty right region of complexity's space. Throughout this entire time, the bacterial mode has grown in height and remained constant in position. Bacteria represent the great success story of life's pathway. They occupy a wider domain of environments and span a broader range of biochemistries than any other group. They are adaptable, indestructible and astoundingly diverse. We cannot even imagine how anthropogenic intervention might threaten their extinction, although we worry about our impact on nearly every other form of life. The number of *Escherichia coli* cells in the gut of each human being exceeds the number of humans that has ever lived on this planet.

One might grant that complexification for life as a whole represents a pseudotrend based on constraint at the left wall but still hold that evolution within particular groups differentially favors complexity when the founding lineage begins far enough from the left wall to permit movement in both directions. Empirical tests of this interesting hypothesis are just beginning (as concern for the subject mounts among paleontologists), and we do not yet have enough cases to advance a generality. But the first two studies—by Daniel W. McShea of the University of Michigan on mammalian vertebrae and by George F. Boyajian of the University of Pennsylvania on ammonite suture lines—show no evolutionary tendencies to favor increased complexity.

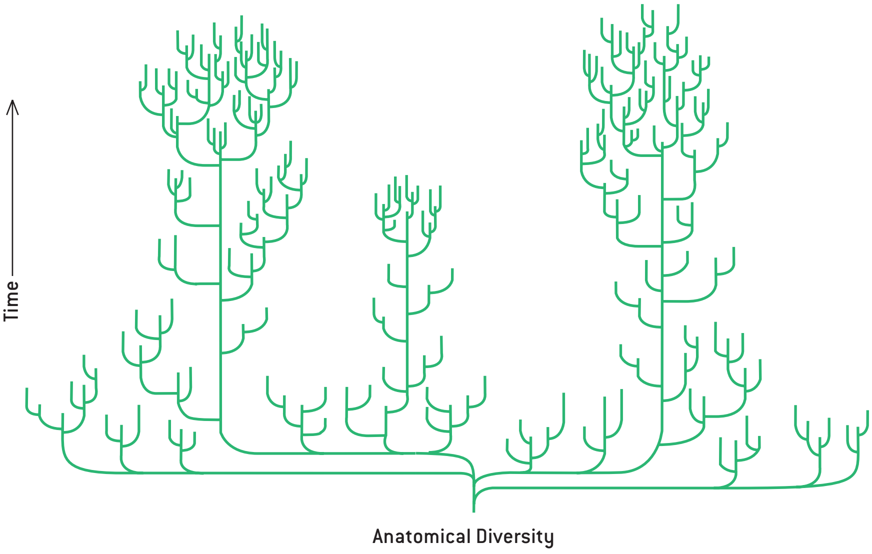
Moreover, when we consider that for each mode of life involving greater complexity, there probably exists an equally advantageous style based on greater simplicity of form (as often found in parasites, for example), then preferential evolution toward complexity seems unlikely a priori. Our impression that life evolves toward greater complexity is probably only a bias inspired by parochial focus on ourselves, and consequent overattention to complexifying creatures, while we ignore just as many lineages adapting equally well by becoming simpler in form. The morphologically degenerate parasite, safe within its host, has just as much prospect for evolutionary success as its gorgeously elaborate relative coping with the slings and arrows of outrageous fortune in a tough external world.

Steps, Not Inclines

EVEN IF COMPLEXITY is only a drift away from a constraining left wall, we might view trends in this direction as more predictable and characteristic of

DAVID STARWOOD

life's pathway as a whole if increments of complexity accrued in a persistent and gradually accumulating manner through time. But nothing about life's history is more peculiar with respect to this common (and false) expectation than the actual pattern of extended stability and rapid episodic movement, as revealed by the fossil record.



NEW ICONOGRAPHY OF LIFE'S TREE shows that maximal diversity in anatomical forms (not in number of species) is reached very early in life's multicellular history. Later times feature extinction of most of these initial experiments and enormous success within surviving lines. This success is measured in the proliferation of species but not in the development of new anatomies. Today we have more species than ever before, although they are restricted to fewer basic anatomies.

DAVID STARWOOD

Life remained almost exclusively unicellular for the first five sixths of its history—from the first recorded fossils at 3.5 billion years to the first well-documented multicellular animals less than 600 million years ago. (Some simple multicellular algae evolved more than a billion years ago, but these organisms belong to the plant kingdom and have no genealogical connection with animals.) This long period of unicellular life does include, to be sure, the vitally important transition from simple prokaryotic cells without organelles to eukaryotic cells with nuclei, mitochondria and other complexities of intracellular architecture—but no recorded attainment of multicellular animal organization for a full three billion years. If complexity is such a good thing, and multicellularity represents its initial phase in our usual view, then life certainly took its time in making this crucial step. Such delays speak strongly against general progress as the major theme of life's history, even if they can be plausibly explained by lack of sufficient atmospheric oxygen for most of Precambrian time or by failure of unicellular life to achieve some structural threshold acting as a prerequisite to multicellularity.

More curiously, all major stages in organizing animal life's multicellular architecture then occurred in a short period beginning less than 600 million years ago and ending by about 530 million years ago—and the steps within this sequence are also discontinuous and episodic, not gradually accumulative. The first fauna, called Ediacaran to honor the Australian locality of its initial discovery but now known from rocks on all continents, consists of highly flattened fronds, sheets and circlets composed of numerous slender segments quilted together. The nature of the Ediacaran fauna is now a subject of intense discussion. These creatures do not seem to be simple precursors of later forms. They may constitute a separate and failed experiment in animal life, or they may represent a full range of diploblastic (two-layered) organization, of which the modern phylum Cnidaria (corals, jellyfishes and their allies) remains as a small and much altered remnant.

In any case, they apparently died out well before the Cambrian biota evolved. The Cambrian then began with an assemblage of bits and pieces, frustratingly difficult to interpret, called the "small shelly fauna." The subsequent main pulse, starting about 530 million years ago, constitutes the famous Cambrian explosion, during which all but one modern phylum of animal life made a first appearance in the fossil record. (Geologists had previously allowed up to 40 million years for this event, but an elegant study, published in 1993, clearly restricts this period of phyletic flowering to a mere five million years.) The Bryozoa, a group of sessile and colonial marine organisms, do not arise until the beginning of the subsequent, Ordovician period, but this apparent delay may be an artifact of failure to discover Cambrian representatives.

Although interesting and portentous events have occurred since, from the flowering of dinosaurs to the origin of human consciousness, we do not exaggerate greatly in stating that the subsequent history of animal life amounts to little more than variations on anatomical themes established during the Cambrian explosion within five million years. Three billion years of unicellularity, followed by five million years of intense creativity and then capped by more than 500 million years of variation on set anatomical themes can scarcely be read as a predictable, inexorable or continuous trend toward progress or increasing complexity.

We do not know why the Cambrian explosion could establish all major anatomical designs so quickly. An "external" explanation based on ecology seems attractive: the Cambrian explosion represents an initial filling of the "ecological barrel" of niches for multicellular organisms, and any experiment found a space. The barrel has never emptied since; even the great mass extinctions left a few species in each principal role, and their oc-

THE AUTHOR

STEPHEN JAY GOULD taught biology, geology and the history of science at Harvard University from 1967 until his death in 2002 at age 60. The influential and provocative evolutionary biologist had a Ph.D. in paleontology from Columbia University. Well known for his popular writings, in particular a monthly column in *Natural History* magazine, he was the author of more than a dozen books, including *Full House: The Spread of Excellence from Plato to Darwin* and *The Mismeasure of Man.*

cupation of ecological space forecloses opportunity for fundamental novelties. But an "internal" explanation based on genetics and development also seems necessary as a complement: the earliest multicellular animals may have maintained a flexibility for genetic change and embryological transformation that became greatly reduced as organisms "locked in" to a set of stable and successful designs.

Either way, this initial period of both internal and external flexibility yielded a range of invertebrate anatomies that may have exceeded (in just a few million years of production) the full scope of animal form in all the earth's environments today (after more than 500 million years of additional time for further expansion). Scientists are divided on this question. Some claim that the anatomical range of this initial explosion exceeded that of modern life, as many early experiments died out and no new phyla have ever arisen. But scientists most strongly opposed to this view allow that Cambrian diversity at least equaled the modern range—so even the most cautious opinion holds that 500 million subsequent years of opportunity have not expanded the Cambrian range, achieved in just five million years. The Cambrian explosion was the most remarkable and puzzling event in the history of life.

Dumb Luck

MOREOVER, WE DO NOT know why most of the early experiments died, while a few survived to become our modern phyla. It is tempting to say that the victors won by virtue of greater anatomical complexity, better ecological fit or some other predictable feature of conventional Darwinian struggle. But no recognized traits unite the victors, and the radical al-

1. *Vauxia* (gracile)
2. *Branchiocaris*
3. *Opabinia*
4. *Amiskwia*
5. *Vauxia* (robust)
6. *Molaria*
7. *Aysheaia*
8. *Sarotrocercus*
9. *Nectocaris*
10. *Pikaia*
11. *Micromitra*
12. *Echmatocrinus*
13. *Chancelloria*
14. *Pirania*
15. *Choia*
16. *Leptomitus*
17. *Dinomischus*
18. *Wiwaxia*
19. *Naraoia*
20. *Hyolithes*
21. *Habelia*
22. *Emeraldella*
23. *Burgessia*
24. *Leanchoilia*
25. *Sanctacaris*
26. *Ottoia*
27. *Louisella*
28. *Actaeus*
29. *Yohoia*
30. *Peronochaeta*
31. *Selkirkia*
32. *Ancalagon*
33. *Burgessochaeta*
34. *Sidneyia*
35. *Odaraia*
36. *Eiffelia*
37. *Mackenzia*
38. *Odontogriphus*
39. *Hallucigenia*
40. *Elrathia*
41. *Anomalocaris*
42. *Lingulella*
43. *Scenella*
44. *Canadaspis*
45. *Marrella*
46. *Olenoides*

PATRICIA J. WYNNE

ternative must be entertained that each early experiment received little more than the equivalent of a ticket in the largest lottery ever played out on our planet—and that each surviving lineage, including our own phylum of vertebrates, inhabits the earth today more by the luck of the draw than by any predictable struggle for existence. The history of multicellular animal life may be more a story of great reduction in initial possibilities, with stabilization of lucky survivors, than a conventional tale of steady ecological expansion and morphological progress in complexity.

Finally, this pattern of long stasis, with change concentrated in rapid episodes that establish new equilibria, may be quite general at several scales of time and magnitude, forming a kind of fractal pattern in self-similarity. According to the punctuated equilibrium model of speciation, trends within lineages occur by accumulated episodes of geologically instantaneous speciation, rather than by gradual change within continuous populations (like climbing a staircase rather than rolling a ball up an inclined plane).

Even if evolutionary theory implied a potential internal direction for life's pathway (although previous facts and arguments in this article cast doubt on such a claim), the occasional imposition of a rapid and substantial, perhaps even truly catastrophic, change in environment would have intervened to stymie the pattern. These environmental changes trigger mass extinction of a high percentage of the earth's species and may so derail any internal direction and so reset the pathway that the net pattern of life's history looks more capricious and concentrated in episodes than steady and directional.

Mass extinctions have been recognized since the dawn of paleontology; the major divisions of the geologic time scale were established at boundaries marked by such events. But until the revival of interest that began in the late 1970s, most paleontologists treated mass extinctions only as intensifications of ordinary events, leading (at most) to a speeding up of tendencies that pervaded normal times. In this gradualistic theory of mass extinction, these events really took a few million years to unfold (with the appearance of suddenness interpreted as an artifact of an imperfect fossil record), and they only made the ordinary occur faster (more intense Darwinian competition in tough times, for example, leading to even more efficient replacement of less adapted by superior forms).

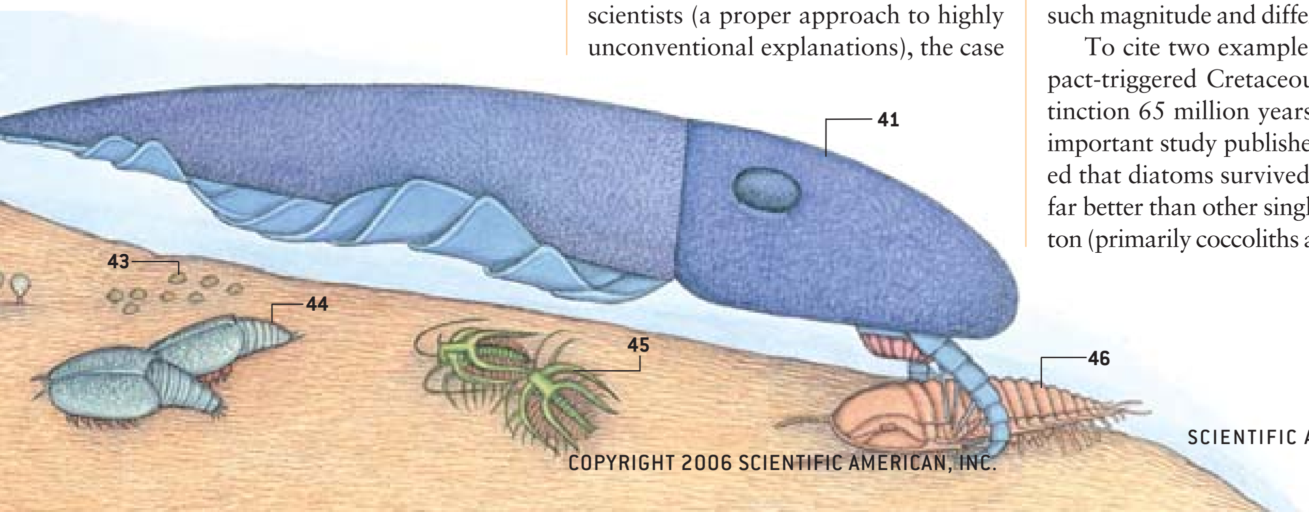
The reinterpretation of mass extinctions as central to life's pathway and radically different in effect began with the presentation of data by Luis and Walter Alvarez in 1979, indicating that the impact of a large extraterrestrial object (they suggested an asteroid seven to 10 kilometers in diameter) set off the last great extinction at the Cretaceous-Tertiary boundary 65 million years ago. Although the Alvarez hypothesis initially received very skeptical treatment from scientists (a proper approach to highly unconventional explanations), the case now seems virtually proved by discovery of the "smoking gun," a crater of appropriate size and age located off the Yucatán peninsula in Mexico.

This reawakening of interest also inspired paleontologists to tabulate the data of mass extinction more rigorously. Work by David M. Raup, J. J. Sepkoski, Jr., and David Jablonski of the University of Chicago has established that multicellular animal life experienced five major (end of Ordovician, late Devonian, end of Permian, end of Triassic and end of Cretaceous) and many minor mass extinctions during its 530-million-year history. We have no clear evidence that any but the last of these events was triggered by catastrophic impact, but such careful study leads to the general conclusion that mass extinctions were more frequent, more rapid, more extensive in magnitude and more different in effect than paleontologists had previously realized. These four properties encompass the radical implications of mass extinction for understanding life's pathway as more contingent and chancy than predictable and directional.

Mass extinctions are not random in their impact on life. Some lineages succumb and others survive as sensible outcomes based on presence or absence of evolved features. But especially if the triggering cause of extinction be sudden and catastrophic, the reasons for life or death may be random with respect to the original value of key features when first evolved in Darwinian struggles of normal times. This "different rules" model of mass extinction imparts a quirky and unpredictable character to life's pathway based on the evident claim that lineages cannot anticipate future contingencies of such magnitude and different operation.

To cite two examples from the impact-triggered Cretaceous-Tertiary extinction 65 million years ago: First, an important study published in 1986 noted that diatoms survived the extinction far better than other single-celled plankton (primarily coccoliths and radiolaria).

GREAT DIVERSITY quickly evolved at the dawn of multicellular animal life during the Cambrian period (530 million years ago). The creatures shown here are all found in the Middle Cambrian Burgess Shale fauna of Canada. They include some familiar forms (sponges, brachiopods) that have survived. But many creatures (such as the giant *Anomalocaris,* at the lower right, largest of all the Cambrian animals) did not live for long and were so anatomically peculiar (relative to survivors) that we cannot classify them among known phyla.



This study found that many diatoms had evolved a strategy of dormancy by encystment, perhaps to survive through seasonal periods of unfavorable conditions (months of darkness in polar species as otherwise fatal to these photosynthesizing cells; sporadic availability of silica needed to construct their skeletons). Other planktonic cells had not evolved any mechanisms for dormancy. If the terminal Cretaceous impact produced a dust cloud that blocked light for several months or longer (one popular idea for a "killing scenario" in the extinction), then diatoms may have survived as a fortuitous result of dormancy mechanisms evolved for the entirely different function of weathering seasonal droughts in ordinary times. Diatoms are not superior to radiolaria or other plankton that succumbed in far greater numbers; they were simply fortunate to possess a favorable feature, evolved for other reasons, that fostered passage through the impact and its sequelae.

Second, we all know that dinosaurs perished in the end Cretaceous event and that mammals therefore rule the vertebrate world today. Most people assume that mammals prevailed in these tough times for some reason of general superiority over dinosaurs. But such a conclusion seems most unlikely. Mammals and dinosaurs had coexisted for 100 million years, and mammals had remained rat-sized or smaller, making no evolutionary "move" to oust dinosaurs. No good argument for mammalian prevalence by general superiority has ever been advanced, and fortuity seems far more likely. As one plausible argument, mammals may have survived partly as a result of their small size (with much larger, and therefore extinction-resistant, populations as a consequence, and less ecological specialization with more places to hide, so to speak). Small size may not have been a positive mammalian adaptation at all, but more a sign of inability ever to penetrate the dominant domain of dinosaurs. Yet this "negative" feature of normal times may be the key reason for mammalian survival and a prerequisite to my writing and your reading this article today.

Sigmund Freud often remarked that great revolutions in the history of science have but one common, and ironic, feature: they knock human arrogance off one pedestal after another of our previous conviction about our own self-importance. In Freud's three examples, Copernicus moved our home from center to periphery; Darwin then relegated us to "descent from an animal world"; and, finally (in one of the least modest statements of intellectual history), Freud himself discovered the unconscious and exploded the myth of a fully rational mind.

In this wise and crucial sense, the Darwinian revolution remains woefully incomplete because, even though thinking humanity accepts the fact of evolution, most of us are still unwilling to abandon the comforting view that evolution means (or at least embodies a central principle of) progress defined to render the appearance of something like human consciousness either virtually inevitable or at least predictable. The pedestal is not smashed until we abandon progress or complexification as a central principle and come to entertain the strong possibility that *H. sapiens* is but a tiny, late-arising twig on life's enormously arborescent bush—a small bud that would almost surely not appear a second time if we could replant the bush from seed and let it grow again.

Parochial Evolution

PRIMATES ARE VISUAL ANIMALS, and the pictures we draw betray our deepest convictions and display our current conceptual limitations. Artists have always painted the history of fossil life as a sequence from invertebrates, to fishes, to early terrestrial amphibians and reptiles, to dinosaurs, to mammals and, finally, to humans. There are no exceptions; all sequences painted since the inception of this genre in the 1850s follow the convention.

Yet we never stop to recognize the almost absurd biases coded into this universal mode. No scene ever shows another invertebrate after fishes evolved, but invertebrates did not go away or stop evolving! After terrestrial reptiles emerge, no subsequent scene ever shows a fish (later oceanic tableaux depict only such returning reptiles as ichthyosaurs and plesiosaurs). But fishes did not stop evolving after one small lineage managed to invade the land. In fact, the major event in the evolution of fishes, the origin and rise to dominance of the teleosts, or modern bony fishes, occurred during the time of the dinosaurs and is therefore never shown at all in any of these sequences—even though teleosts include more than half of all species of vertebrates. Why should humans appear at the end of all sequences? Our order of primates is ancient among mammals, and many other successful lineages arose later than we did.

We will not smash Freud's pedestal and complete Darwin's revolution until we find, grasp and accept another way of drawing life's history. J.B.S. Haldane proclaimed nature "queerer than we can suppose," but these limits may only be socially imposed conceptual locks rather then inherent restrictions of our neurology. New icons might break the locks. Trees—or rather copiously and luxuriantly branching bushes—rather than ladders and sequences hold the key to this conceptual transition.

We must learn to depict the full range of variation, not just our parochial perception of the tiny right tail of most complex creatures. We must recognize that this tree may have contained a maximal number of branches near the beginning of multicellular life and that subsequent history is for the most part a process of elimination and lucky survivorship of a few, rather than continuous flowering, progress and expansion of a growing multitude. We must understand that little twigs are contingent nubbins, not predictable goals of the massive bush beneath. We must remember the greatest of all biblical statements about wisdom: "She is a tree of life to them that lay hold upon her; and happy is every one that retaineth her." SA

MORE TO EXPLORE

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The Early Evolution of Animals

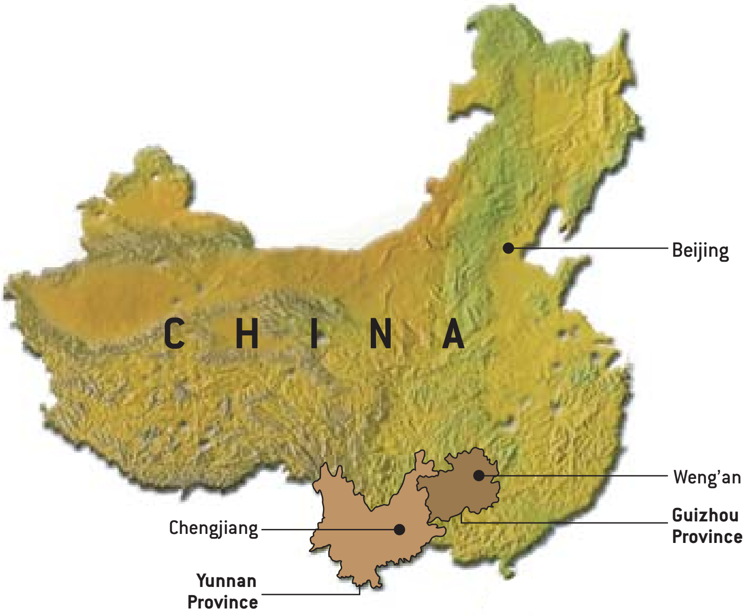
Tiny fossils reveal that complex animal life is older than we thought—by at least as much as 50 million years

By David J. Bottjer originally published in August 2005

"THERE IS A BILATERIAN IN THAT TRUCK," Jun-Yuan Chen said as we watched the vehicle disappear around a bend in the road. Chen, a paleontologist at the Chinese Academy of Sciences in Nanjing, and I, along with Stephen Q. Dornbos, a colleague then at the University of Southern California, had just collected a truckload of black rocks from a 580-million- to 600-million-year-old deposit in Guizhou Province. Chen was sure they held something important.

We had come to Guizhou in 2002 to hunt for microscopic fossils of some of the earliest animals on earth. Specifically, we were hoping to find a bilaterian. The advent of bilateral symmetry—the mirror-image balance of limbs and organs—marks a critical step in the history of life. The first multicelled animals were not bilaterally symmetrical; they were asymmetrical aquatic blobs—sponges—that filtered food particles from currents they generated. Radially symmetrical

OLDEST FOSSIL ANIMAL with a bilateral body plan yet discovered, *Vernanimalcula* lived in the seas some 580 million to 600 million years ago. This reconstruction enlarges the creature to reveal its complexity; in life it was about the size of the period at the end of this sentence.



TWO DEPOSITS IN CHINA have preserved the remains of soft-bodied animals that provide new information about early evolution. In 2004 the author and his colleagues discovered the oldest known bilaterian animal in rocks collected from the 580-million- to 600-million-year-old Doushantuo Formation, near Weng'an. Significantly younger fossils from the approximately 525-million-year-old deposits in the vicinity of Chengjiang have expanded understanding of the Cambrian explosion.

aquatic creatures, the cnidarians, are slightly more complex; they have specialized stinging cells that can immobilize prey. Bilaterians constitute all the rest of us, from worms to human beings. During some stage in their life cycle, all display not only the crucial left-right balance but a multilayered body that typically has a mouth, gut and anus.

Until several years ago, consensus held that bilaterian animals first appeared in the fossil record about 555 million years ago, although the vast majority showed up somewhat later in a burst of innovation known as the Cambrian explosion, which began about 542 million years ago. The dearth of earlier fossils made it impossible to test ideas about what triggered the "explosion" or even to say for sure whether it was real or merely seemed so because earlier animals left few detectable traces of themselves. But research over the past half a dozen years—including ours in Guizhou Province—has changed the long-held view, suggesting that complex animals arose at least 50 million years earlier than the Cambrian explosion.

Molecular Clocks and Lagerstätten

MOLECULAR ANALYSIS, in particular a technique called the molecular clock, has been key in the new thinking about when the earliest animals arose. The clock idea is based on the supposition that some evolutionary changes occur at a regular rate. Over millions of years, for example, mutations may be incorporated in the DNA of genes at a steady rate. Differences in the DNA of organisms, then, can act as a "timepiece" for measuring the date at which two lineages split from a common ancestor, each going its separate way and accumulating its own distinctive mutations.

To estimate the timing of the origin of various major animal groups, Gregory Wray of Duke University and his colleagues used a molecular clock rate based on vertebrates (animals that have a backbone). Their results, published in 1996, postulated that bilaterians diverged from more primitive animals deep into the Precambrian era, as much as 1.2 billion years ago.

Follow-up studies using the molecular clock produced estimates for this split that varied significantly, ranging from as old as one billion years ago to as young as just before the Cambrian period. Such discrepancies naturally generated doubts about the technique, and a more recent study by Kevin Peterson of Dartmouth College and his colleagues addressed some of these concerns. In particular, they used a molecular clock rate derived from invertebrates, which is faster than the one based on vertebrates.

This investigation placed the last common ancestor of bilaterian animals at a much younger date, though still older than the Cambrian explosion, somewhere between 573 million and 656 mil-

Overview/*Older Than We Thought*

- The development of bilateral symmetry marks a critical step in the early evolution of animals.
- Genetic analysis has suggested that bilateral symmetry arose 573 million to 656 million years ago, but controversy clouds the date for several reasons. The most telling is that until recently the earliest known bilaterian fossils were dated to only 555 million years ago.
- Now the author and his colleagues have found supporting fossil evidence for the earlier date: microscopic creatures in Chinese deposits 580 million to 600 million years old.
- The minuscule fossils not only support an early date for the beginning of complex animal life but show that internal complexity evolved before large size did.

AMADEO BACHAR (*preceding pages*); ALISON KENDALL (*this page*)

lion years ago. But even this date sparked controversy. It had become clear that only actual fossils would furnish incontrovertible evidence for the time at which bilaterians had emerged. This realization provided a big incentive for paleontologists to get out in the field and find fossils older than the Cambrian. I was among the scientists spurred to search for these elusive specimens.

One huge problem with finding such animals is that they did not have hard skeletons that would mineralize and become fossils. So we must rely on uncovering the rare deposit that, because of the type of rock and the chemical processes involved, preserves intricate details of the remains. These deposits are called *lagerstätten,* a German word that means “lode places” or “mother lode.” A lagerstätte that preserves soft tissue is a spectacular rarity; we know of only several dozen scattered over the earth. One of the best known is the Solnhofen Limestone in Germany, where the 150-million-year-old feathered specimens of what is generally considered to be the earliest fossil bird, *Archaeopteryx,* are preserved. In British Columbia, an older deposit, the Burgess Shale, made famous by the writings of Stephen Jay Gould [see, for example, “The Evolution of Life on Earth,” SCIENTIFIC AMERICAN; October 1994], reveals a cornucopia of curious soft-bodied organisms from the ancient oceans of the Cambrian period.

A lagerstätte older than the Burgess Shale, in the Chengjiang area of China’s Yunnan Province, has yielded many important recent finds of soft-bodied organisms also characteristic of the Cambrian explosion. And, at several spots on the planet, the Ediacaran lagerstätten, named after the Ediacara Hills of Australia where the first example was found, harbor strange Precambrian soft-bodied fossils and animal burrows, including evidence for early bilaterians.

Amazingly, in 1998 two different groups of paleobiologists reported finding fossils with remarkable soft-tissue preservation in another Precambrian lagerstätte—the Doushantuo Formation in Guizhou Province of south China. This deposit contains tiny soft-bodied adult sponges and cnidarians as well as minuscule eggs and embryos. Much of the sediment in which they occur is composed of the mineral calcium phosphate (apatite), which has exquisitely replaced the original soft tissues of these fossils. The latest studies show that these rocks are older than the Ediacara biota, most likely 580 million to 600 million years old, and thus that the microfossils they contain lived 40 million to 55 million years before the Cambrian.

And So to China

THOSE OF US interested in the origin of animals quickly realized that the Doushantuo Formation might be the window through which we would glimpse early bilaterian life. So, in the autumn of 1999, a group of us joined together, at the urging of Eric Davidson, a molecular biologist at the California Institute of Technology, to study the Doushantuo microfossils. The team also included Chen and Chia-Wei Li, who were among the first investigators to report on eggs and embryos in the Doushantuo. Li, a professor at National Tsing Hua University, is an expert on biomineralization, and Chen has extensive experience studying early animal life through his pioneering work on the Lower Cambrian Chengjiang lagerstätte.

Our initial probes suggested that a relatively thin sedimentary layer, which is black in color, would be the most promising for finding a variety of microfossils. Other researchers at the site had applied acid to dissolve the rock matrix in the laboratory, revealing the tiny phosphatized fossils. Unfortunately, the acid dissolution technique was not successful with the layer of black rock that we had targeted. We therefore turned to a different approach: we collected great piles of this black rock and brought it back to Chen’s lab at the Early Life Research Center of the Nanjing Institute of Geology and Palaeontology in adjacent Yunnan Province. That is where our dump truck was headed when Chen made his bilaterian prediction.

Once back in Yunnan with our rocks, we sliced the samples into thousands of sections, so thin that they were translucent and, when mounted on glass slides, could be examined under a microscope. We made more than 10,000 of these slides, a gargantuan task that Chen and his technicians threw themselves into with optimism and energy. Painstaking analysis of the thousands of slides took several years and revealed myriad eggs and embryos; it confirmed the presence of tiny adult sponges and cnidarians that had been reported previously.

But of course what we were really focused on finding was a bilaterian. Did our catch in the dump truck actually include one of these? In the summer of 2003 we began to zero in on one microfossil type whose complex morphological characteristics particularly intrigued us. Among the 10,000 slides, we were able to locate 10 examples of this type, and, early in 2004, after months of analysis, we came to the conclusion that this tiny organism displayed the basic features of a bilaterian. This was what we were looking for!

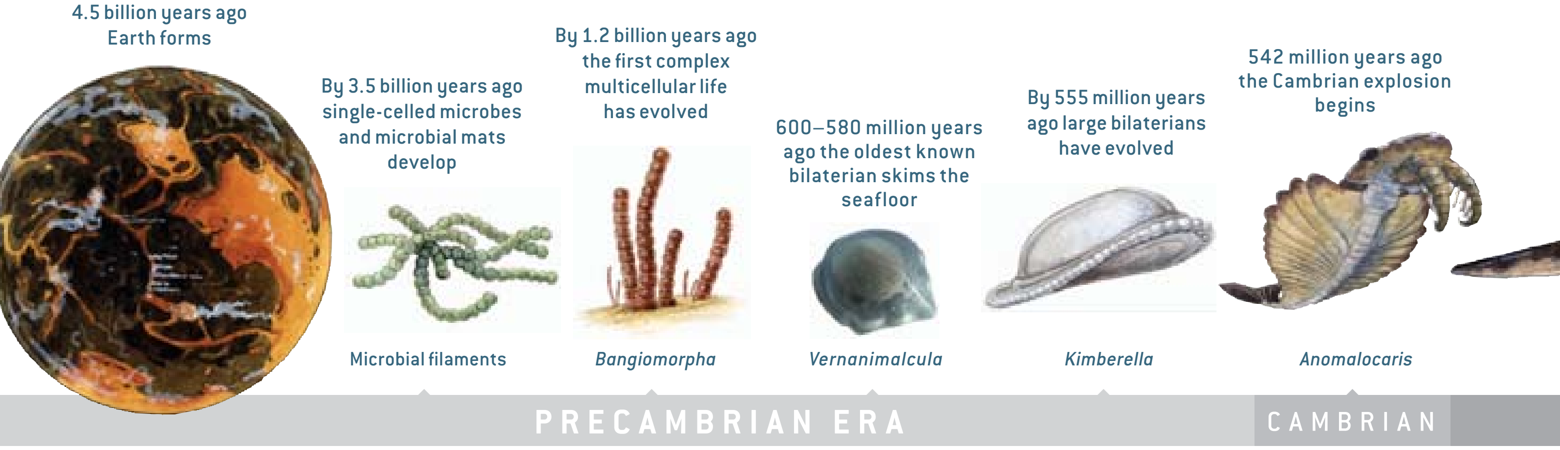
Ranging from 100 to 200 microns across, the width of several human hairs, these microscopic fossils are surprisingly complex and constitute almost a textbook example of a bilaterian, including the three major tissue layers (the endoderm, mesoderm and ectoderm familiar from high school biology texts), the presence of a gut with a mouth and anus, and paired coeloms (body cavities) surrounding the gut. Oval-shaped and looking something like a minute gumdrop,

THE AUTHOR

DAVID J. BOTTJER is a paleobiologist who has focused his research on the origin and subsequent evolutionary history of animals on Earth. He approaches this work in an interdisciplinary fashion, which has led to collaborative ventures with colleagues versed in developmental biology, molecular biology, informatics and geochemistry. He received his Ph.D. in geology from Indiana University and is currently professor of earth and biological sciences at the University of Southern California. He is president of the Paleontological Society (2004–2006) and editor in chief of the journal *Palaeogeography, Palaeoclimatology, Palaeoecology.*

A Tiny Fossil's Place in History

The evolution of complex animal life was formerly thought to have started with a bang during the early Cambrian period, an event often referred to as the Cambrian explosion. The discovery in 2004 of the microscopic *Vernanimalcula* by the author and his colleagues pushes back the origins of complex animal life as much as 50 million years before the Cambrian.



The Real Meaning of the Cambrian Explosion

The Cambrian explosion is generally thought of as a sudden increase in the types of bilaterian animals—those with a right-left balance of limbs and organs. But the story is more complicated, and more interesting, than that. Recent research has shown that a dramatic upsurge in interactions among animals played a large role in this increase in diversity.

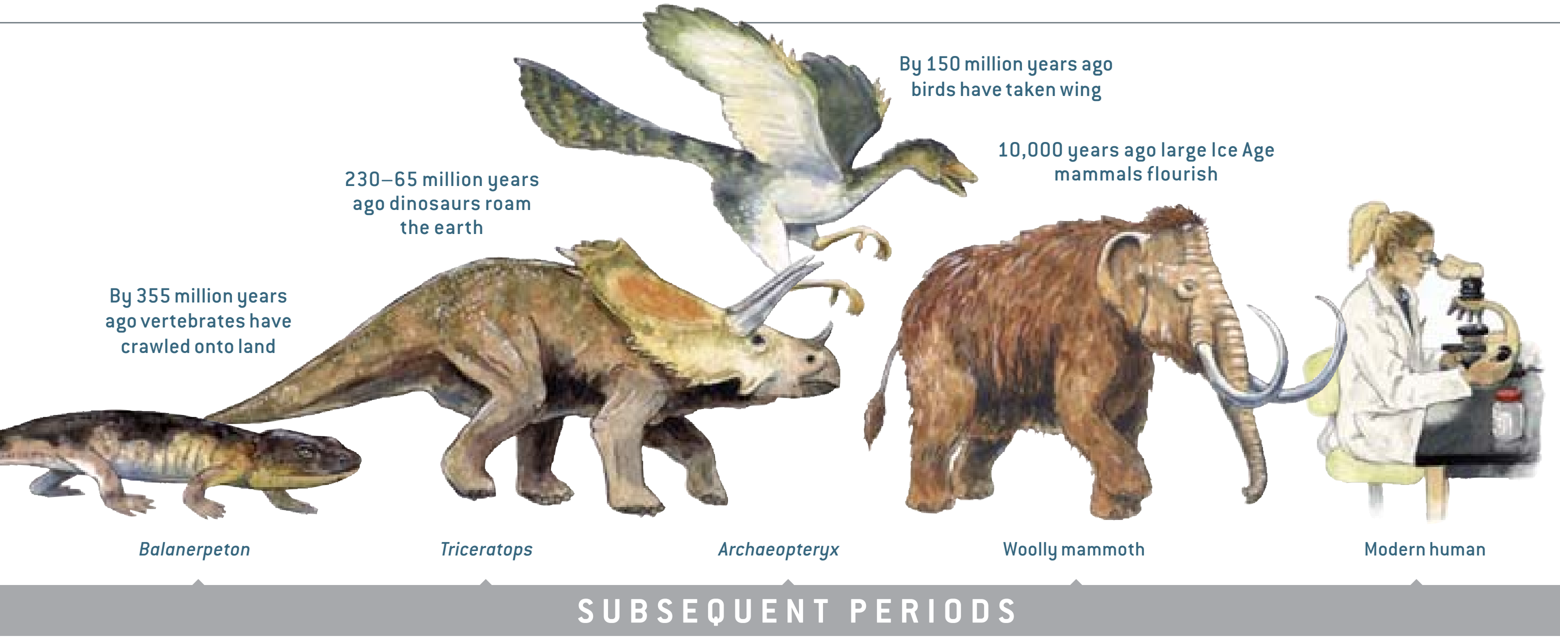
First, animals began to alter the environment, and the new conditions created both opportunities and barriers for other denizens of the ancient world. For example, Precambrian animals that lived on the seafloor were adapted to moving about on cushiony microbial mats, which covered most of the ocean floor and had been part of the ecosystem since life originated. At the beginning of the Cambrian (which lasted from 542 million to 488 million years ago), however, evolutionary innovations enabled bilaterian animals to burrow vertically through sediment. The burrowing destroyed the ubiquitous mats and replaced them with a surface that was soupy and unstable. Some organisms, such as the helicoplacoids, small top-shaped animals that lived embedded in the seafloor, most likely became extinct as the sea bottom grew increasingly unstable. In contrast, other organisms reacted to this increase in bioturbation by evolving adaptations for living in the new environments.

Second, the Early Cambrian marks the time when paleobiologists detect the first presence of bilaterian predators that had evolved to eat other animals. For example, Jun-Yuan Chen and Di-Ying Huang of the Chinese Academy of Sciences in Nanjing and others report several new types of predators from the Chengjiang lagerstätte in China. These include arthropods with strange frontal appendages for capturing prey (below), as well as ubiquitous burrowing worms that moved just below the seafloor and fed on other small animals.

These biological interactions played a strong role in the early evolution of animals. Yet as Charles Marshall of Harvard University has argued and as our findings support, the genetic tool kit and pattern-forming mechanisms characteristic of bilaterians had likely evolved by the time of the Cambrian explosion. Thus, the "explosion" of animal types was more accurately the exploitation of newly present conditions by animals that had already evolved the genetic tools to take advantage of these novel habitats rather than a fundamental change in the genetic makeup of the animals. —D.J.B.

EARLY PREDATOR, *Haikoucaris* (about four centimeters long)

AMADEO BACHAR



the creature probably scooted along the seafloor to feed. At one end of the oval, the mouth sucked up microbes like a vacuum cleaner. Pits on either side of the mouth may have been sense organs.

We named our find *Vernanimalcula,* which means "small spring animal." The name refers to the long winter of "snowball Earth," when glaciers covered the planet [see "Snowball Earth," by Paul F. Hoffman and Daniel P. Schrag; Scientific American, January 2000]; the rocks holding *Vernanimalcula* are slightly above those marking the final glacial episode.

Legacy of a Small Spring Animal

BIOLOGICAL COMPLEXITY of the kind seen in *Vernanimalcula* implies a period of evolution that transpired long before the 580-million- to 600-million-year-old world in which the tiny animal lived. After all, it could not have gained that degree of symmetry and complexity all at once. We now need to find older lagerstätten that might hold clues to its ancestors.

We also need to move forward in time to try to puzzle out what happened to its descendants. What we know about life during the gap between *Vernanimalcula* and the creatures of the Cambrian explosion 40 million to 55 million years later comes primarily from studies of lagerstätten that contain the Ediacara biota—impressions and casts of soft-bodied organisms that were considerably larger than *Vernanimalcula,* ranging in size from centimeters to as much as a meter. New discoveries by Guy Narbonne of Queen's University in Ontario and his colleagues have confirmed the existence of these animals 575 million years ago; however, only in examples 555 million years old and younger do we find fossils that appear to represent bilaterians. Unlike the minuscule *Vernanimalcula,* these Ediacara bilaterians were macroscopic organisms, such as *Kimberella,* a soft-bodied sea dweller some 10 centimeters long that may have been an ancestor to the mollusks, animals that in today's seas include clams, snails and squid. Unfortunately, no Ediacaran deposits that we have located so far evince the unusual mineral setting essential for preserving microscopic creatures. To learn whether microscopic bilaterians existed alongside the larger Ediacara creatures we must find a fossil deposit of Ediacaran age that has preservation similar to that in the older Doushantuo Formation.

Although we cannot yet track the ancestors and descendants of *Vernanimalcula,* these tiny fossils have revealed a critical step in evolution: they show that bilaterians had the ability to make complex bodies before they could make large ones. Scientists are now speculating on what might have led to the eventual scaling-up of bodies. The most likely explanation is that a drastic rise in the amount of dissolved oxygen in seawater provided the impetus: more oxygen for respiration reduces constraints on size.

Vernanimalcula certainly gives paleontologists new inducements to go out and hunt for fossils of soft-bodied animals. We have a good deal left to learn, but the work so far has given substance to our earlier suspicion that complex animals have a much deeper root in time, suggesting that the Cambrian was less of an explosion and more of a flowering of animal life. SA

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GETTING A LEG UP ON LAND

Recent fossil discoveries cast light on the evolution of four-limbed animals from fish

BY JENNIFER A. CLACK

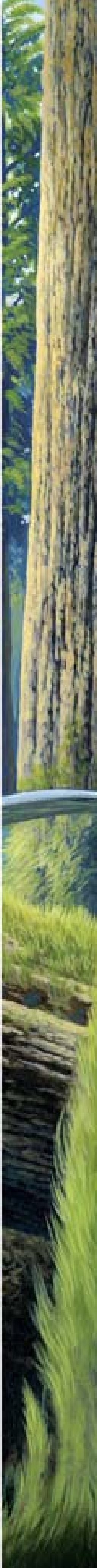
IN THE ALMOST four billion years since life on earth oozed into existence, evolution has generated some marvelous metamorphoses. One of the most spectacular is surely that which produced terrestrial creatures bearing limbs, fingers and toes from water-bound fish with fins. Today this group, the tetrapods, encompasses everything from birds and their dinosaur ancestors to lizards, snakes, turtles, frogs and mammals, including us. Some of these animals have modified or lost their limbs, but their common ancestor had them—two in front and two in back, where fins once flicked instead.

The replacement of fins with limbs was a crucial step in this transformation, but it was by no means the only one. As tetrapods ventured onto shore, they encountered challenges that no vertebrate had ever faced before—it was not just a matter of developing legs and walking away. Land is a radically different medium from water, and to conquer it, tetrapods had to evolve novel ways to breathe, hear, and contend with gravity—the list goes on. Once this extreme makeover reached completion, however, the land was theirs to exploit.

Until about 15 years ago, paleontologists understood very little about the sequence of events that made up the transition from fish to tetrapod. We knew that tetrapods had evolved from fish with fleshy fins akin to today's lungfish and coelacanth, a relation first proposed by American paleontologist Edward D. Cope in the late 19th century. But the details of this seminal shift remained hidden from view. Furthermore, estimates of when this event transpired varied wildly, ranging from 400 million to 350 million years ago, during the Devonian period. The problem was that the pertinent fossil record was sparse, consisting of essentially a single fish of this type, *Eusthenopteron,* and a single Devonian tetrapod, *Ichthyostega,* which was too advanced to elucidate tetrapod roots.

With such scant clues to work from, scientists could only speculate about the nature of the transition. Perhaps the best known of the scenarios produced by this guesswork was that championed by famed vertebrate paleontologist Alfred Sherwood Romer of Harvard University, who proposed in the 1950s that fish like *Eusthenopteron,* stranded under arid conditions, used their muscular appendages to drag themselves to a new body of water. Over time, so the idea went, those fish able to cover more ground—and thus reach ever more distant water sources—were selected for, eventually leading to the origin of true limbs. In other words, fish came out of the water before they evolved legs.

Since then, however, many more fossils documenting this transformation have come to light. These discoveries have expanded almost exponentially our understanding of this critical chapter in the history of life on earth—and turned old notions about early tetrapod evolution, diversity, biogeography and paleoecology on their heads.



UP FOR AIR: *Acanthostega,* an early tetrapod, surfaces in a swamp in what is now eastern Greenland, some 360 million years ago. Although this animal had four legs, they would not have been able to support its body on land. Thus, rather than limbs evolving as an adaptation to life on land, it seems that they may have initially functioned to help the animal lift its head out of oxygen-poor water to breathe. Only later did they find use ashore.

Finding a Foothold

AMONG THE FIRST fossil finds to pave the way for our modern conception of tetrapod origins were those of a creature called *Acanthostega,* which lived about 360 million years ago in what is now eastern Greenland. It was first identified in 1952 by Erik Jarvik of the Swedish Museum of Natural History in Stockholm on the basis of two partial skull roofs. But not until 1987 did my colleagues and I finally find specimens revealing the postcranial skeleton of *Acanthostega.*

Although in many ways this animal proved to be exactly the kind of anatomical intermediary between fish and full-blown tetrapods that experts might have imagined, it told a different story from the one predicted. Here was a creature that had legs and feet but that was otherwise ill equipped for a terrestrial existence. *Acanthostega*'s limbs lacked proper ankles to support the animal's weight on land, looking more like paddles for swimming. And although it had lungs, its ribs were too short to prevent the collapse of the chest cavity once out of water. In fact, many of *Acanthostega*'s features were undeniably fishlike. The bones of the forearm displayed proportions reminiscent of the pectoral fin of *Eusthenopteron.* And the rear of the skeleton showed a deep, oar-shaped tail sporting long, bony rays that would have provided the scaffolding for a fin. Moreover, the beast still had gills in addition to lungs.

The piscine resemblance suggested that the limbs of *Acanthostega* were not only adapted for use in water but that this was the ancestral tetrapod condition. In other words, this animal, though clearly a tetrapod, was primarily an aquatic creature whose immediate forerunners were essentially fish that had never left the water. The discovery forced scholars to rethink the sequence in which key changes to the skeleton took place. Rather than portraying a creature like *Eusthenopteron* crawling onto land and then gaining legs and feet, as Romer postulated, the new fossils indicated that tetrapods evolved these features while they were still aquatic and only later coopted them for walking. This, in turn, meant that researchers needed to reconsider the ecological circumstances under which limbs developed, because *Acanthostega* indicated that terrestrial demands may not have been the driving force in early tetrapod evolution.

Acanthostega took pride of place as the missing link between terrestrial vertebrates and their aquatic forebears. There was, however, one characteristic of *Acanthostega* that called to mind neither tetrapod nor fish. Each of its limbs terminated in a foot bearing eight well-formed digits, rather than the familiar five. This was quite curious, because before this discovery anatomists believed that in the transition from fish to tetrapod, the five-digit foot derived directly from the bones constituting the fin of *Eusthenopteron* or a similar creature. Ordinarily, scientists might have dismissed this as an aberrant specimen. But a mysterious partial skeleton of *Tulerpeton,* a previously known early tetrapod from Russia, had a six-digit foot. And specimens of *Ichthyostega* also found on our expedition to eastern Greenland revealed that it, too, had a foot with more than five digits.

Many of the critical innovations arose while these beasts were still largely aquatic. And the first changes appear to have been related not to locomotion but to an increased reliance on breathing air.

Findings from developmental biology have helped unravel some of this mystery. We now know that several genes, including the *Hox* series and *Sonic Hedgehog,* control elements of fin and limb development. The same sets of these genes occur in both fish and tetrapods, but they do different jobs in each. *Hoxd 11* and *Hoxd 13,* for instance, appear to play a more pronounced role in tetrapods, where their domains in the limb bud are enlarged and skewed relative to those in the fish fin bud. It is in these regions that the digits form. How the five-digit foot evolved from the eight-digit one of *Acanthostega* remains to be determined, but we do have a plausible explanation for why the five-digit foot became the default tetrapod pattern: it may have helped make ankle joints that are both stable enough to bear weight and flexible enough to allow the walking gait that tetrapods eventually invented.

Acanthostega also drew attention to a formerly underappreciated part of early tetrapod anatomy: the inside of the lower jaw. Fish generally have two rows of teeth along their lower jaw, with a large number of small teeth on the outer row complementing a pair of large fangs and some small teeth on the inner row. *Acanthostega* showed that early tetrapods possessed a different dental plan: a small number of larger teeth on the outer row and a reduction in the size of the teeth populating the inner row—changes that probably accompanied a shift from feed-

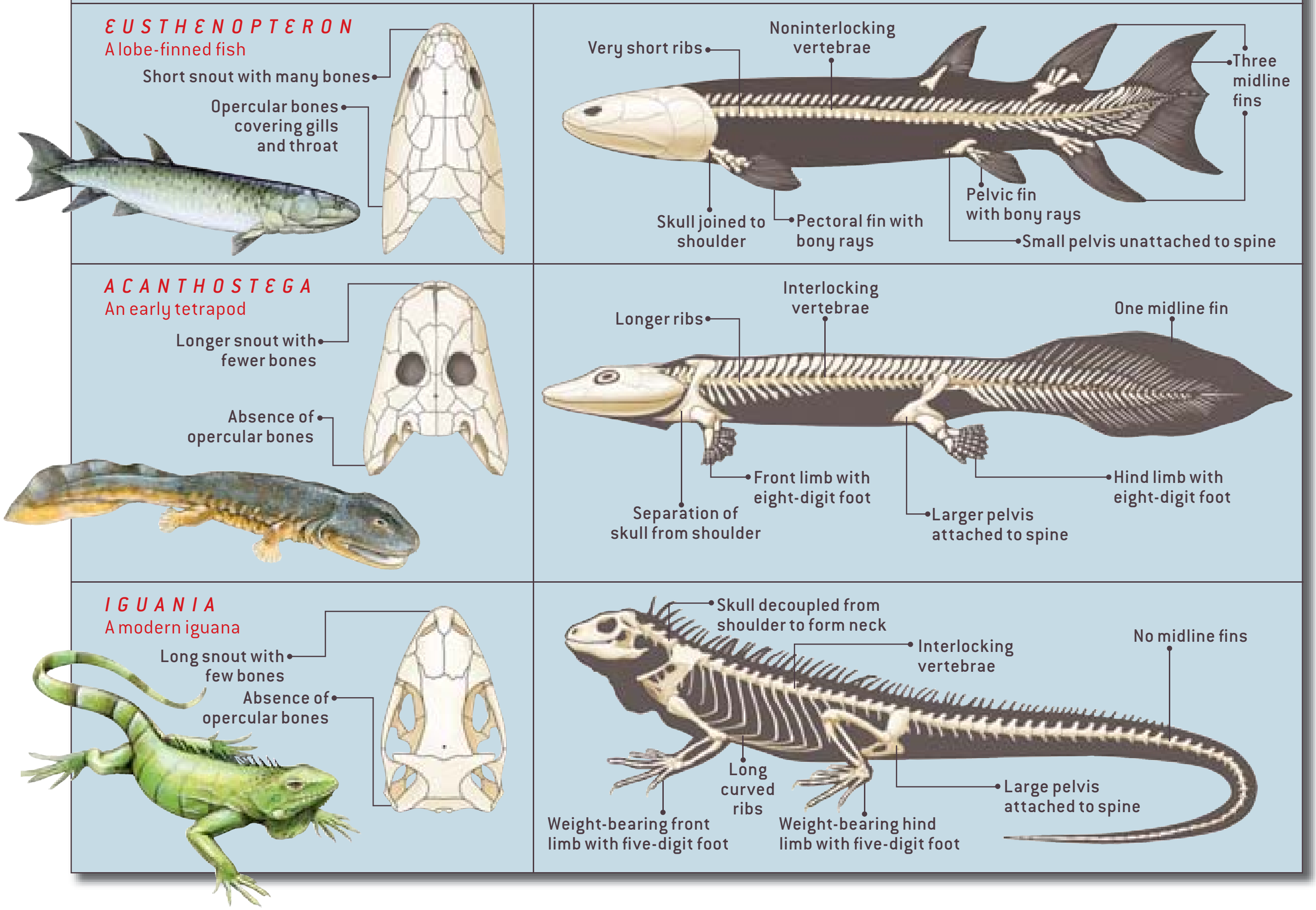
Overview/*The Origin of Tetrapods*

- The emergence of land-going vertebrates was a cornerstone event in the evolution of life on earth.
- For decades, a paltry fossil record obfuscated efforts to trace the steps that eventually produced these terrestrial tetrapods from their fish ancestors.
- Fossils recovered over the past 15 years have filled many of the gaps in the story and revolutionized what is known about tetrapod evolution, diversity, biogeography and paleoecology.
- These recent finds indicate that tetrapods evolved many of their characteristic features while they were still aquatic. They also reveal that early members of the group were more specialized and more geographically and ecologically widespread than previously thought.

RAÚL MARTÍN *(preceding pages)*

TURNING TETRAPOD

The evolution of terrestrial tetrapods from aquatic lobe-finned fish involved a radical transformation of the skeleton. Among other changes, the pectoral and pelvic fins became limbs with feet and toes, the vertebrae became interlocking, and the tail fin disappeared, as did a series of bones that joined the head to the shoulder girdle (*skeletons*). Meanwhile the snout elongated and the bones that covered the gills and throat were lost (*skulls*).



ing exclusively in the water to feeding on land or with the head above the water.

This insight enabled experts to recognize additional tetrapods among remains that had long sat unidentified in museum drawers. One of the most spectacular of these finds was that of a Late Devonian genus from Latvia called *Ventastega*. In the 1990s, following the discovery of *Acanthostega*, researchers realized that a lower jaw collected in 1933 was that of a tetrapod. Further excavation at the original *Ventastega* site soon yielded more material of exceptional quality, including an almost complete skull.

Meanwhile a number of near-tetrapod fish have also been unveiled, bridging the morphological gap between *Eusthenopteron* and *Acanthostega*. Two of these genera paleontologists have known about for several decades but have only recently scrutinized: 380-million- to 375-million-year-old *Panderichthys* from Europe's Baltic region, a large fish with a pointy snout and eyes that sat atop its head, and 375-million- to 370-million-year-old *Elpistostege* from Canada, which was very similar in size and shape to *Panderichthys*. Both are much closer to tetrapods than is *Eusthenopteron*. And just last year an expedition to Ellesmere Island in the Canadian Arctic led by paleontologist Neil Shubin of the University of Chicago produced some outstandingly well preserved remains of a fish that is even more tetrapodlike than either *Panderichthys* or *Elpistostege*. Shubin and his team have yet to describe and name this species formally, but it is shaping up to be a fascinating animal.

A Breath of Fresh Air

THANKS TO THESE recent finds and analyses, we now have the remains of nine genera documenting around 20 million years of early tetrapod evolution and an even clearer idea of how the rest of the vertebrate body became adapted for life on land. One of the most interesting revelations to emerge from this work is that, as in the case of limb development, many of the critical innovations arose while these beasts were still largely aquatic. And the first changes appear to have been related not to locomotion but to an increased reliance on breathing air.

Oddly enough, this ventilation shift

ANDREW RECHER

PRIMEVAL PROMENADE: *Ichthyostega* is the earliest known tetrapod to show adaptations for nonswimming locomotion, although it seems likely to have moved more like a seal than a typical land vertebrate. This animal also had some aquatic features, including a large tail and flipperlike hind limbs, as well as an ear that appears to have been specialized for underwater use. How *Ichthyostega* divided its time between the terrestrial and aquatic realms is uncertain. But it may have dug nests for its eggs on land and hunted and fed in the water.

RAÚL MARTÍN

may have kicked off the gradual morphing of the shoulder girdle and pectoral fins. Indeed, evolutionary biologists have struggled to explain what transitional forms like *Acanthostega* did with their proto-limbs, if not locomote. The hypothesis favored on current evidence is that as the backwardly directed fins gradually turned into sideways-facing limbs with large areas for muscle attachments, they gained in strength. And although it would be millions of years before the forelimbs developed to the point of being able to support the body on land, they may well have functioned in the interim to allow the animal to raise its head out of the water to breathe. The toes could have facilitated this activity by helping to spread the load on the limbs.

Last year Shubin's team announced the discovery of a 365-million-year-old tetrapod upper arm bone, or humerus, that has bolstered this idea. The bone, dug from a fossil-rich site in north central Pennsylvania known as Red Hill, appears to have joined the rest of the body via a hingelike joint, as opposed to the ball-and-socket variety that we and other terrestrial vertebrates have. This arrangement would not have permitted a walking gait, but it would have enabled just the kind of push-up that a tetrapod needing a gulp of air might employ. It also might have helped the animal hold its position in the water while waiting to ambush prey.

Breathing above water also required a number of changes to the skull and jaw. In the skull, the snout elongated and the bones that form it grew fewer in number and more intimately sutured together, strengthening the snout in a way that enabled the animal to lift it clear of water and into an unsupportive medium. The bones at the back of the head, for their part, became the most firmly integrated of any in the skull, providing sturdy anchors for muscles from the vertebral column that raise the head relative to the body. And the fusing of bones making up the lower jaw fortified this region, facilitating the presumed "buccal pump" mode of tetrapod ventilation. In this type of breathing, employed by modern amphibians and air-breathing fish, the mouth cavity expands and contracts like bellows to gulp air and force it into the lungs. Buccal pumping may have demanded more jaw power under the influence of gravity than in the water, where organisms are more or less weightless.

Might the strengthening of the jaws have instead come about as an adaptation for feeding on land? Possibly. The earliest tetrapods were all carnivorous, so it is unlikely that, as adults, they fed much on land during the first phases of their evolution, because the only prey they would have found there were insects and other small arthropods. The babies, on the other hand, needed just this type of prey, and they may have been the ones that initially ventured farthest out of the water to get them.

Meanwhile, farther back in the skeleton, a series of bones that joins the head to the shoulder girdle in fish disappeared. As a result, tetrapods, unlike fish, have a muscular neck that links the head to the rest of the skeleton and allows for movement of the head separate from the body. The gill system also underwent substantial renovation, losing some bones but increasing the size of the spiracle—an opening on the top of the head that led to an air-filled sac in the throat region, making the entire respiratory apparatus better suited to breathing air.

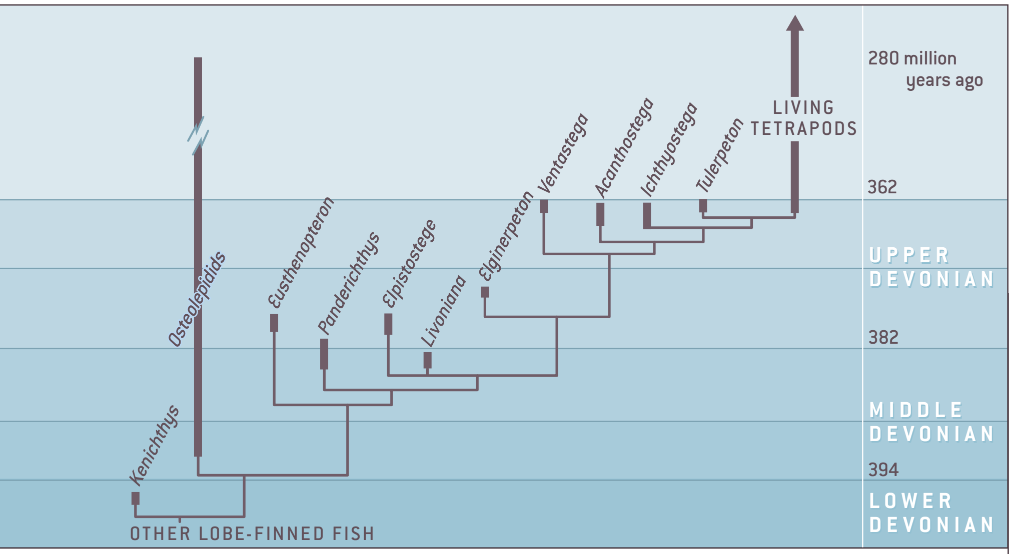
But why, after millions of years of successfully breathing underwater, did some fish begin turning to the air for their oxygen? Clues have come from the overall shape of the skull, which in all early tetrapods and near-tetrapods discovered so far is quite flat when viewed head-on. This observation, combined with paleoenvironmental data gleaned from the deposits in which the fossils have been found, suggests that these creatures were shallow-water specialists, going to low-water places to hunt for smaller fish and possibly to mate and lay their eggs. Perhaps not coincidentally, vascular plants were flourishing during the Devonian, transforming both the terrestrial and aquatic realms. For the first time, deciduous plants shed their leaves into the water with the changing seasons, creating environments that were attractive to small prey but difficult for big fish to swim in. Moreover, because warm water holds less oxygen than colder water does, these areas would have been oxygen-poor. If so, the changes to the skeleton described here may have given early tetrapods access to waters that sharks and other large fish could not reach by putting them literally head and shoulders above the competition. It was just happenstance that these same features would later come in handy ashore.

These breathing-related innovations sent tetrapods well on their way to becoming land-worthy. Getting a grip on terra firma required further modifications to the skeleton, however. An overhaul of the ear region was one such development. Many of the details of this transformation are still largely unknown. But it is clear that even in the tetrapodlike fish that still had fins, *Panderichthys* among them, the part of the skull behind the eyes had already become shorter, following a shrinking of the capsules that house the inner ears. If, as paleoenvironmental evidence suggests, *Panderichthys* dwelled in shallow tidal flats or estuaries, the reduction in the inner ear may reflect the growing influence of gravity on the vestibular system, which coordinates balance and orientation. At the same time an increase in the size of the air chamber in its throat may have aided hearing. In some modern fish this air sac "catches" sound waves, preventing them from simply passing straight through the animal's body. From there they are transmitted by the surrounding bones to the inner ear. The enlarged air chamber evident in *Panderichthys* would have been able to intercept more sound waves, thereby enhancing the animal's hearing ability.

Modifications to the ear region were also closely tied to those in the gill system. To wit: a bone known as the hyomandibula—which in fish orchestrates feeding and breathing movements—shrank in size and got lodged in a hole in the braincase, where it became the stapes. In modern tetrapods the stapes magnifies sound waves and transmits them from the eardrum across the air space in the throat to the inner ear. (In mammals, which have a unique hearing system, the stapes is one of the three ossicles making up the middle ear.) The first stage of conversion must have occurred rapidly, given that it was in place by the time of *Acanthostega*. Quite possibly it proceeded in tandem with the shift from fins to limbs with digits. But the stapes would not take on its familiar role as a component of the terrestrially adapted tympanic ear for millions of years. In the meantime, it apparently functioned in these still aquatic tetrapods as a structural component of the skull.

Taken together, these skeletal changes have necessitated a sea change in the way we regard early tetrapods. Gone are the clumsy chimeras of popular imagination, fit for neither water nor land. What were once considered evolutionary works in progress—an incompletely developed limb or ear, for example—we now know were adaptations in their own right. They were not always successful, but they were adaptations nonetheless. At each stage of this transition were innovators pushing into new niches. Some, in fact, were highly specialized to do this.

LUCY READING-IKKANDA



TETRAPOD RELATIONS: Tetrapods arose from lobe-finned fish like *Eusthenopteron* some 380 million to 375 million years ago, in the late Middle Devonian period.

THE AUTHOR

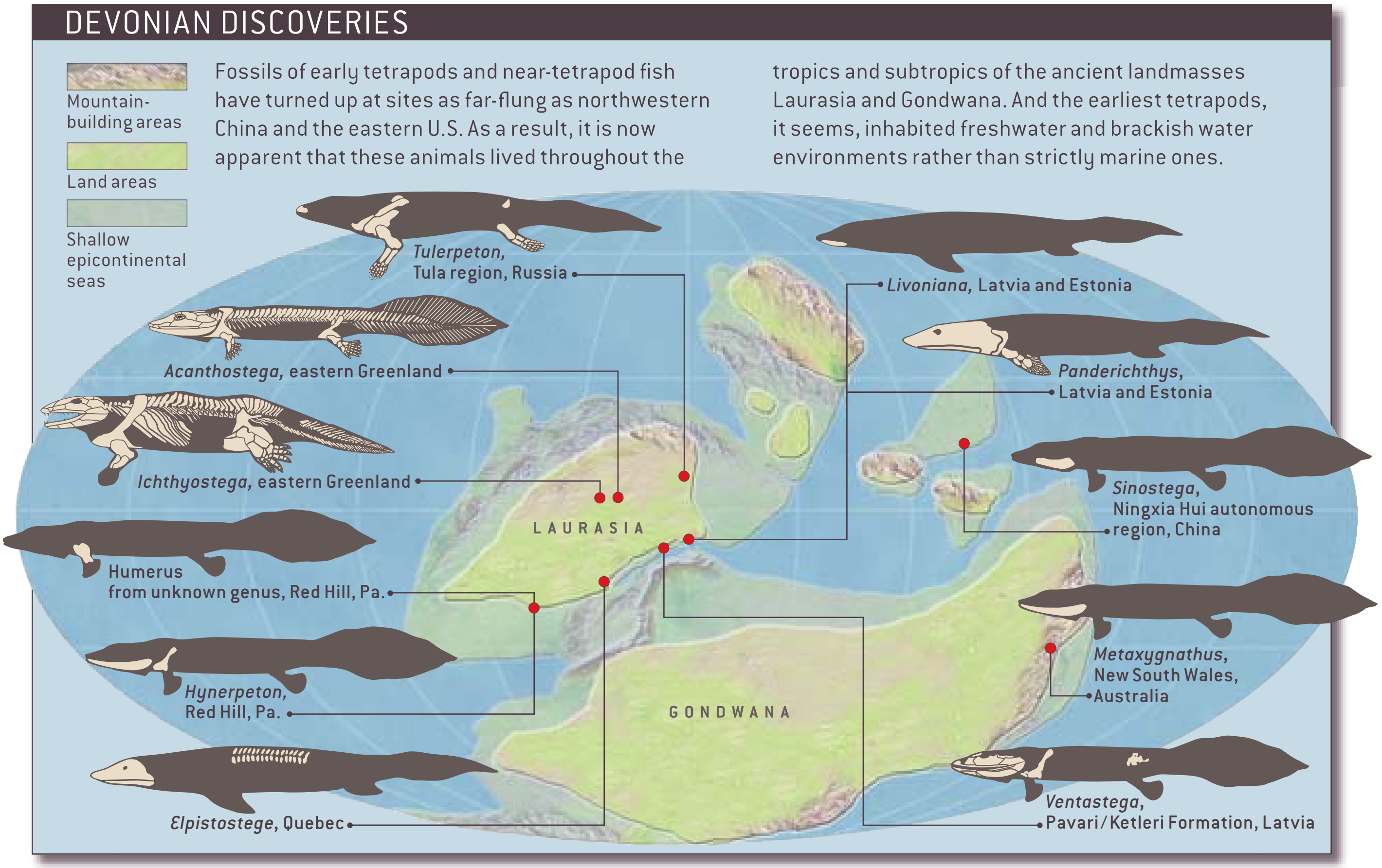
JENNIFER A. CLACK, a Reader in vertebrate paleontology and doctor of science at the University of Cambridge, has been studying tetrapod origins for 25 years. A fellow of the Linnean Society, Clack's outside interests include choral singing (particularly of early sacred music) and gardening. She is also a motorcyclist and rides a Yamaha Diversion 900.

Breaking the Mold

BY AND LARGE, the limbed tetrapods and near-tetrapods unearthed thus far have been sizeable beasts, around a meter long. They preyed on a wide variety of invertebrates and fish and were probably not fussy about which ones. We are beginning to find exceptions to this generalist rule, however. One is *Livoniana*, discovered in a museum in Latvia by Per Erik Ahlberg of Sweden's Uppsala University in 2000. This animal is represented by some lower jaw fragments that exhibit a bizarre morphology: instead of the usual two rows of teeth lining each side of the jaw, it had seven rows. Exactly what *Livoniana* might have been consuming with this corn-on-the-cob dentition we do not know. But it most likely had a diet apart from that of its brethren.

Renewed work on the first known Devonian tetrapod, *Ichthyostega*, is showing that it, too, diverged from the norm—contrary to earlier preconceptions. The ear region and associated parts of the braincase of *Ichthyostega* have long baffled researchers because they display a construction unlike that of any other tetrapod or fish from any period.

DEVONIAN DISCOVERIES



Fossils of early tetrapods and near-tetrapod fish have turned up at sites as far-flung as northwestern China and the eastern U.S. As a result, it is now apparent that these animals lived throughout the tropics and subtropics of the ancient landmasses Laurasia and Gondwana. And the earliest tetrapods, it seems, inhabited freshwater and brackish water environments rather than strictly marine ones.

But with the aid of new fossils, fresh preparation of previously collected material and, crucially, CT scanning of key specimens, my colleagues and I have begun to make sense of this mysterious construction. The best interpretation seems to be that *Ichthyostega* possessed a highly specialized ear, but one that was geared for use underwater. Instead of having an eardrum, as many modern terrestrial animals do, at each side of the back of the head lay a chamber with strengthened top and side walls that was probably filled with air. Into the membranous floor of this chamber stretched a spoon-shaped and very delicate stapes, which presumably vibrated in response to sound impinging directly on the air in the chamber, transmitting these vibrations to the inner ear through a hole in the wall of the braincase. This arrangement would imply that *Ichthyostega* spent a good deal of time in water. Likewise, the animal's tail fin and flipperlike hind limbs suggest an aquatic lifestyle.

Yet other parts of the *Ichthyostega* skeleton bespeak an ability to get around on land. It had incredibly powerful shoulders and forearms. And the ribs of the chest region were very broad and overlapping, forming a corset that would have prevented the chest cavity and lungs from collapsing when on the ground. Even so, *Ichthyostega* probably did not locomote like a standard-issue land vertebrate. For one thing, its ribcage would have restricted the lateral undulation of the trunk that typically occurs in tetrapod movement. And in contrast to fish, *Acanthostega* or other early tetrapods, *Ichthyostega* had spines on its vertebrae that changed direction along the spinal column, hinting that the muscles they supported were specialized for different jobs and that it moved in a unique fashion. This multidirectional arrangement of the vertebral spines parallels that in mammals today, but it was unheard of in Devonian tetrapods until we studied *Ichthyostega*. All told, this latest evidence suggests that, rather than bending in the horizontal plane, as the body of a fish does, the body of *Ichthyostega* bent mainly in a vertical plane. The paddlelike hind limbs do not seem to have contributed much forward thrust during locomotion—the robust forelimbs and large shoulders provided that. Thus, on land *Ichthyostega* may have moved rather like a seal, first raising its back, then advancing both forelimbs simultaneously, and finally hauling the rest of its body forward.

In September, Ahlberg, Henning Blom of Uppsala University and I published a paper detailing these findings in the journal *Nature*. If we are correct, *Ichthyostega* is the earliest vertebrate on record that shows some adaptations for nonswimming locomotion. It is impossible to say with certainty what *Ichthyostega* was doing ashore. It may have been eating stranded fish there but reproducing in water, in which case it could have used its specialized ear to listen for potential mates. (This scenario implies that *Ichthyostega* was making noises as well as listening to them.) Alternatively, *Ichthyostega* may have been eating in the water and listening for prey there, whereas it was using its forelimbs to dig nests for its eggs on land. Ultimately, however,

ANDREW RECHER (*tetrapods*); LUCY READING-IKKANDA (*map*)

its particular body plan was doomed, because no fossil dating later than 360 million years ago can be reliably attributed to the *Ichthyostega* lineage. No doubt there were many such superseded designs over the course of early tetrapod evolution. Further work will be needed to confirm these ideas, but the latest data demonstrate that Devonian tetrapods were more diverse than previously suspected. We are learning to expect more such surprises as these animals and their relatives become better known.

Have Legs, Will Travel

THE FOSSILS UNCOVERED over the past two decades have done more than allowed scientists to trace many of the changes to the tetrapod skeleton. They have also provided fresh insights into when and where these creatures evolved. We are now reasonably certain that tetrapods had emerged by 380 million to 375 million years ago, in the late Middle Devonian, a far tighter date range than the one researchers had previously postulated. We have also determined that the early representatives of this group were nothing if not cosmopolitan.

Devonian tetrapods were scattered across the globe, ranging from locations that are now China and Australia, where creatures known as *Sinostega* and *Metaxygnathus,* respectively, have turned up, to the eastern U.S., where the Red Hill humerus and a beast called *Hynerpeton* were found. Placing the fossil localities onto a paleogeographic map of the time, we see that these animals dwelled throughout the tropics and subtropics of a supercontinent comprising Laurasia to the north and Gondwana to the south. Their near-ubiquitous distribution in the warmer climes is a testament to how successful these creatures were.

Within these locales, Devonian tetrapods inhabited a startlingly wide range of environments. Deposits in eastern Greenland that were the first to yield such creatures indicate that the area was once a broad river basin dominated by periodic floods alternating with drier conditions. The river was unequivocally freshwater in origin and thus formed the basis for received wisdom about the environments in which tetrapods evolved. But the discoveries of such creatures as *Ventastega* and *Tulerpeton* in deposits representing settings of varying salinity have called that notion into question. The Red Hill site in Pennsylvania has proved particularly rich in providing a context for the tetrapods, yielding many fish species as well as invertebrates and plants. Like the eastern Greenland deposits, it represents a river basin. Yet paleoenvironmental studies suggest that the region had a temperate climate, rather than the monsoonal conditions associated with the Greenland finds. That is to say, early tetrapods may have been even more widespread than we thought.

Unfinished Business

WE STILL HAVE MUCH to learn about changes in anatomy that accompanied the rise of tetrapods. Although we now have a reasonable hypothesis for why the shoulder girdle and front limbs evolved the way they did, we lack an adequate explanation for the origin of the robust hind-limb complex—the hallmark of a tetrapod—because none of the fossils recovered so far contains any clues about it. Only specimens of *Ichthyostega* and *Acanthostega* preserve this part of the anatomy, and in both these animals the hind limbs are too well formed to reveal how they took shape. Almost certainly no single scenario can account for all the stages of the transition. We also want to acquire a higher-resolution picture of the order in which the changes to the skeleton occurred, say, when the hind limb evolved relative to the forelimb and the ear.

The discovery and description of additional fossils will resolve some of these mysteries, as will insights from evolutionary developmental biology. To that end, studies of the genetic-control mechanisms governing the formation of the gill region in fish and the neck area in mammals and birds are just beginning to provide hints about which processes characterize both tetrapods and fish and which are unique to tetrapods. For example, we know that tetrapods have lost all the bones that protect the gills in fish but that the genes that govern their formation are still present in mice, where they function differently. We have also ascertained that in the neck region, the biochemical pathways that preside over the development of limbs have broken down. Although biologists can easily induce extra limbs to grow on the flank of a tetrapod, this cannot be done in the neck. Something special happened when tetrapods first evolved a neck that prevented limbs from sprouting there.

> Although we now have a good explanation for why the front limbs evolved the way they did, we lack one for the origin of the hind limbs because none of the fossils recovered so far contains any clues about them.

Other questions may be more difficult to answer. It would be wonderful to know which one of the many environmental contexts in which tetrapod fossils have turned up nurtured the very first members of this group (the available evidence indicates only that these animals did not debut in strictly marine settings). We would also like to comprehend fully the evolutionary pressures at work during each phase of the transition. Lacking a perfect fossil record or recourse to a time machine, we may never piece together the entire puzzle of tetrapod evolution. But with continued work, we can expect to close many of the remaining gaps in the story of how fish gained ground.

MORE TO EXPLORE

Gaining Ground: The Origin and Evolution of Tetrapods. Jennifer A. Clack. Indiana University Press, 2002.

The Emergence of Early Tetrapods. Jennifer A. Clack in *Paleogeography, Paleoclimatology, Paleoecology* (in press).

originally published in February 1998

The Origin of Birds and Their Flight

Anatomical and aerodynamic analyses of fossils and living birds show that birds evolved from small, predatory dinosaurs that lived on the ground

by Kevin Padian and Luis M. Chiappe

ILLUSTRATIONS BY ED HECK

Until recently, the origin of birds was one of the great mysteries of biology. Birds are dramatically different from all other living creatures. Feathers, toothless beaks, hollow bones, perching feet, wishbones, deep breastbones and stumplike tailbones are only part of the combination of skeletal features that no other living animal has in common with them. How birds evolved feathers and flight was even more imponderable.

In the past 20 years, however, new fossil discoveries and new research methods have enabled paleontologists to determine that birds descend from ground-dwelling, meat-eating dinosaurs of the group known as theropods. The work has also offered a picture of how the earliest birds took to the air.

Scientists have speculated on the evolutionary history of birds since shortly after Charles Darwin set out his theory of evolution in *On the Origin of Species.* In 1860, the year after the publication of Darwin's treatise, a solitary feather of a bird was found in Bavarian limestone deposits dating to about 150 million years ago (just before the Jurassic period gave way to the Cretaceous). The next year a skeleton of an animal that had birdlike wings and feathers—but a very unbirdlike long, bony tail and toothed jaw—turned up in the same region. These finds became the first two specimens of the blue jay–size *Archaeopteryx lithographica,* the most archaic, or basal, known member of the birds [see "*Archaeopteryx,*" by Peter Wellnhofer; SCIENTIFIC AMERICAN, May 1990].

Archaeopteryx's skeletal anatomy provides clear evidence that birds descend from a dinosaurian ancestor, but in 1861 scientists were not yet in a position to make that connection. A few years later, though, Thomas Henry Huxley, Darwin's staunch defender, became the first person to connect birds to dinosaurs. Comparing the hind limbs of *Megalosaurus,* a giant theropod, with those of the ostrich, he noted 35 features that the two groups shared but that did not occur as a suite in any other animal. He concluded that birds and theropods could be closely related, although whether he thought birds were cousins of theropods or were descended from them is not known.

Huxley presented his results to the Geological Society of London in 1870, but paleontologist Harry Govier Seeley contested Huxley's assertion of kinship between theropods and birds. Seeley suggested that the hind limbs of the ostrich and *Megalosaurus* might look similar just because both animals were large and bipedal and used their hind limbs in similar ways. Besides, dinosaurs were even larger than ostriches, and none of them could fly; how, then, could flying birds have evolved from a dinosaur?

The mystery of the origin of birds gained renewed attention about half a century later. In 1916 Gerhard Heilmann, a medical doctor with a penchant for paleontology, published (in Danish) a brilliant book that in 1926 was translated into English as *The Origin of Birds.* Heilmann showed that birds were anatomically more similar to theropod dinosaurs than to any other fossil group but for one inescapable discrepancy: theropods apparently lacked clavicles, the two collarbones that are fused into a wishbone in birds. Because other reptiles had clavicles, Heilmann inferred that theropods had lost them. To him, this loss meant birds could not have evolved from theropods, because he was convinced (mistakenly, as it turns out) that a feature lost during evolution could not be regained. Birds, he asserted, must have evolved from a more archaic reptilian group that had clavicles. Like Seeley before him, Heilmann concluded that the similarities between birds and dinosaurs must simply reflect the fact that both groups were bipedal.

Heilmann's conclusions influenced thinking for a long time, even though new information told a different story. Two separate findings indicated that theropods did, in fact, have clavicles. In 1924 a published anatomical drawing of the bizarre, parrot-headed theropod *Oviraptor* clearly showed a wishbone, but the structure was misidentified. Then, in 1936, Charles Camp of the University of California at Berkeley found the remains of a small Early Jurassic theropod, complete with clavicles. Heilmann's fatal objection had been overcome, although few scientists recognized it. Recent studies have found clavicles in a broad spectrum of the theropods related to birds.

Finally, a century after Huxley's disputed presentation to

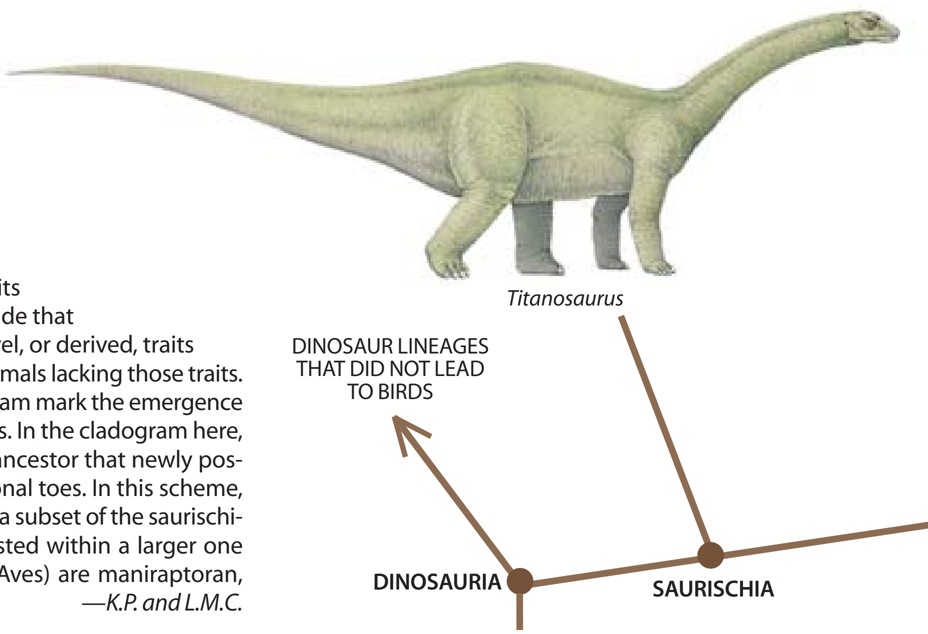
EARLY BIRDS living more than 100 million years ago looked quite different from birds of today. For instance, as these artist's reconstructions demonstrate, some retained the clawed fingers and toothed jaw characteristic of nonavian dinosaurs. Fossils of *Sinornis* (*left*) were uncovered in China; those of *Iberomesornis* and *Eoalulavis* (*right*) in Spain. All three birds were about the size of a sparrow. *Eoalulavis* sported the first known alula, or "thumb wing," an adaptation that helps today's birds navigate through the air at slow speeds.

Tracking the Dinosaur Lineage Leading to Birds

The family tree at the right traces the ancestry of birds back to their early dinosaurian ancestors. This tree, otherwise known as a cladogram, is the product of today's gold standard for analyzing the evolutionary relations among animals—a method called cladistics.

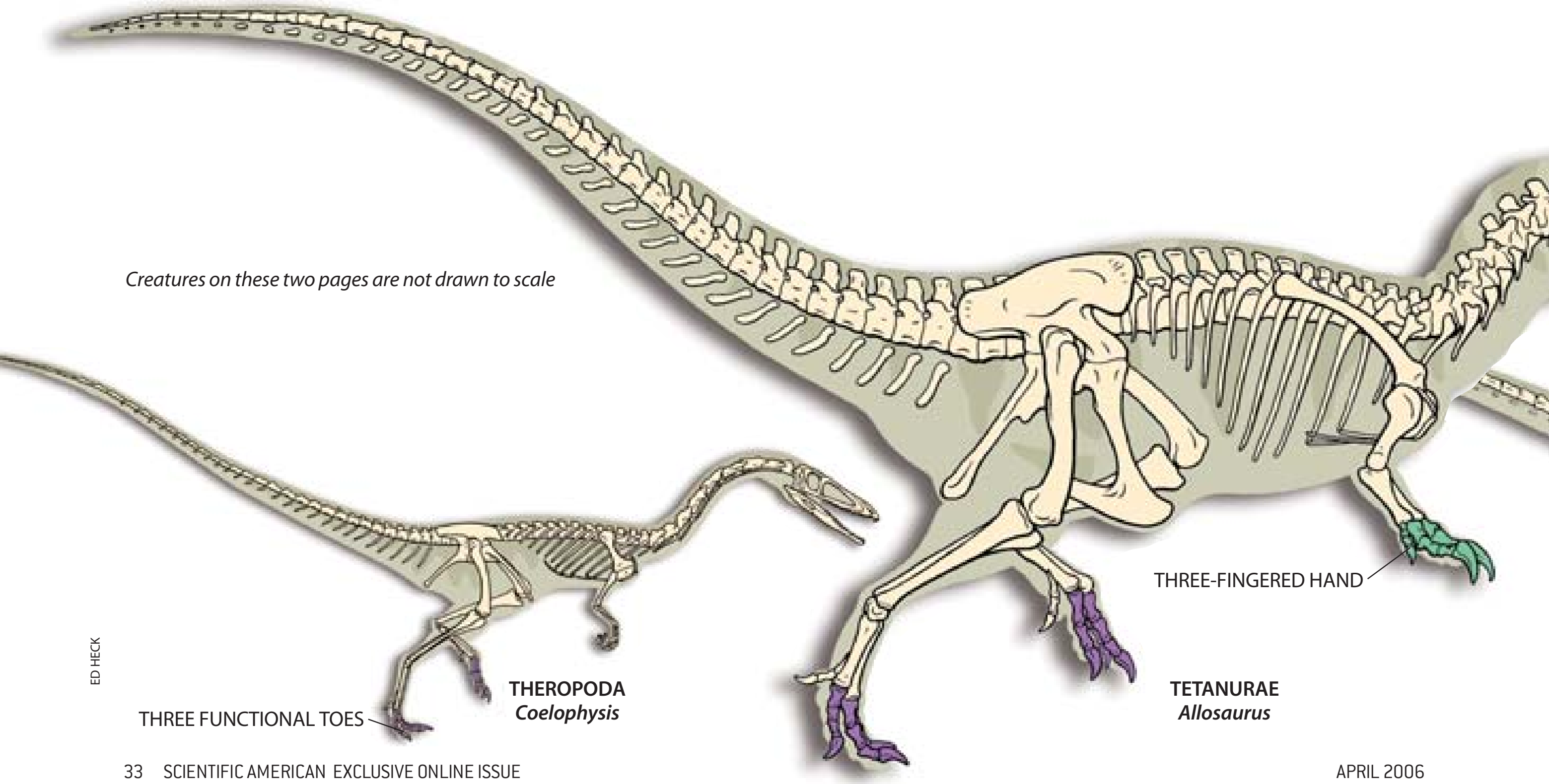
Practitioners of cladistics determine the evolutionary history of a group of animals by examining certain kinds of traits. During evolution, some animal will display a new, genetically determined trait that will be passed to its descendants. Hence, paleontologists can conclude that two groups uniquely sharing a suite of such novel, or derived, traits are more closely related to each other than to animals lacking those traits.

Nodes, or branching points (*dots*), on a cladogram mark the emergence of a lineage possessing a new set of derived traits. In the cladogram here, the Theropoda all descend from a dinosaurian ancestor that newly possessed hollow bones and had only three functional toes. In this scheme, the theropods are still dinosaurs; they are simply a subset of the saurischian dinosaurs. Each lineage, or clade, is thus nested within a larger one (*colored rectangles*). By the same token, birds (Aves) are maniraptoran, tetanuran and theropod dinosaurs. *—K.P. and L.M.C.*

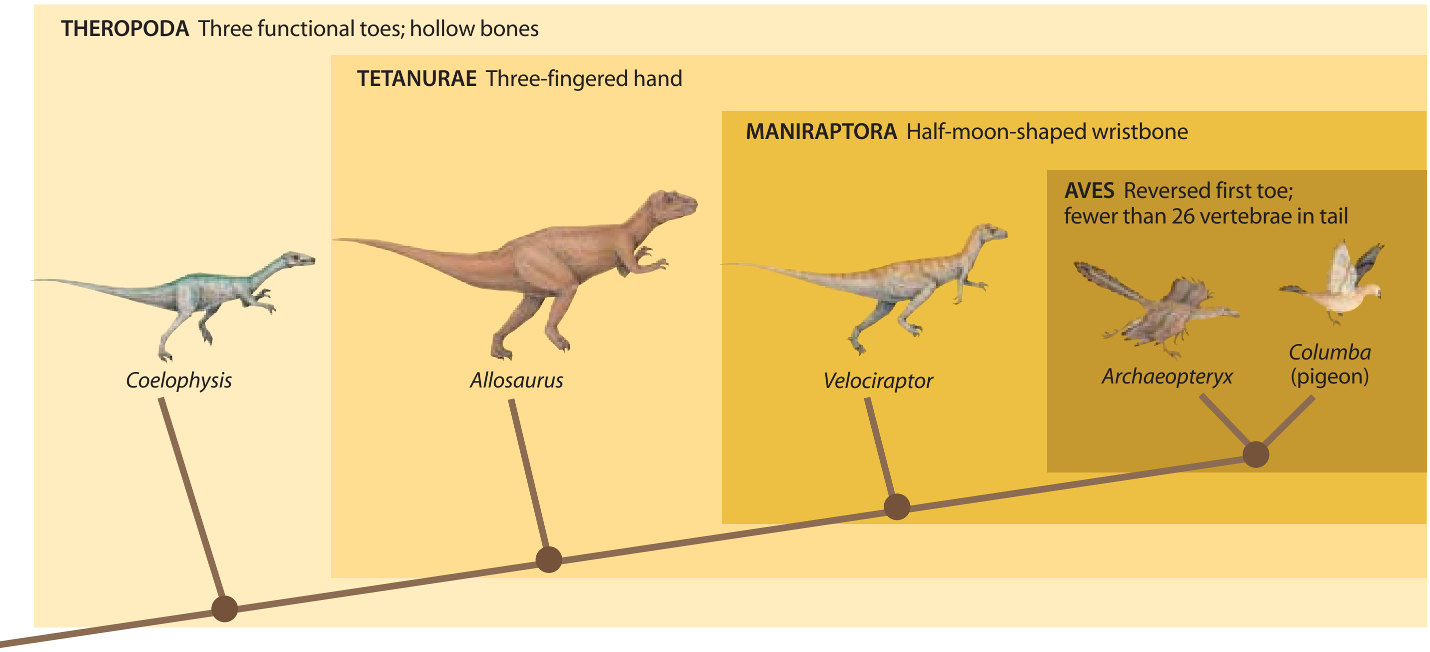


the Geological Society of London, John H. Ostrom of Yale University revived the idea that birds were related to theropod dinosaurs, and he proposed explicitly that birds were their direct descendants. In the late 1960s Ostrom had described the skeletal anatomy of the theropod *Deinonychus,* a vicious, sickle-clawed predator about the size of an adolescent human, which roamed in Montana some 115 million years ago (in the Early Cretaceous). In a series of papers published during the next decade, Ostrom went on to identify a collection of features that birds, including *Archaeopteryx,* shared with *Deinonychus* and other theropods but not with other reptiles. On the basis of these findings, he concluded that birds are descended directly from small theropod dinosaurs.

As Ostrom was assembling his evidence for the theropod origin of birds, a new method of deciphering the relations among organisms was taking hold in natural history museums in New York City, Paris and elsewhere. This method—called phylogenetic systematics or, more commonly, cladis-


Creatures on these two pages are not drawn to scale

ED HECK

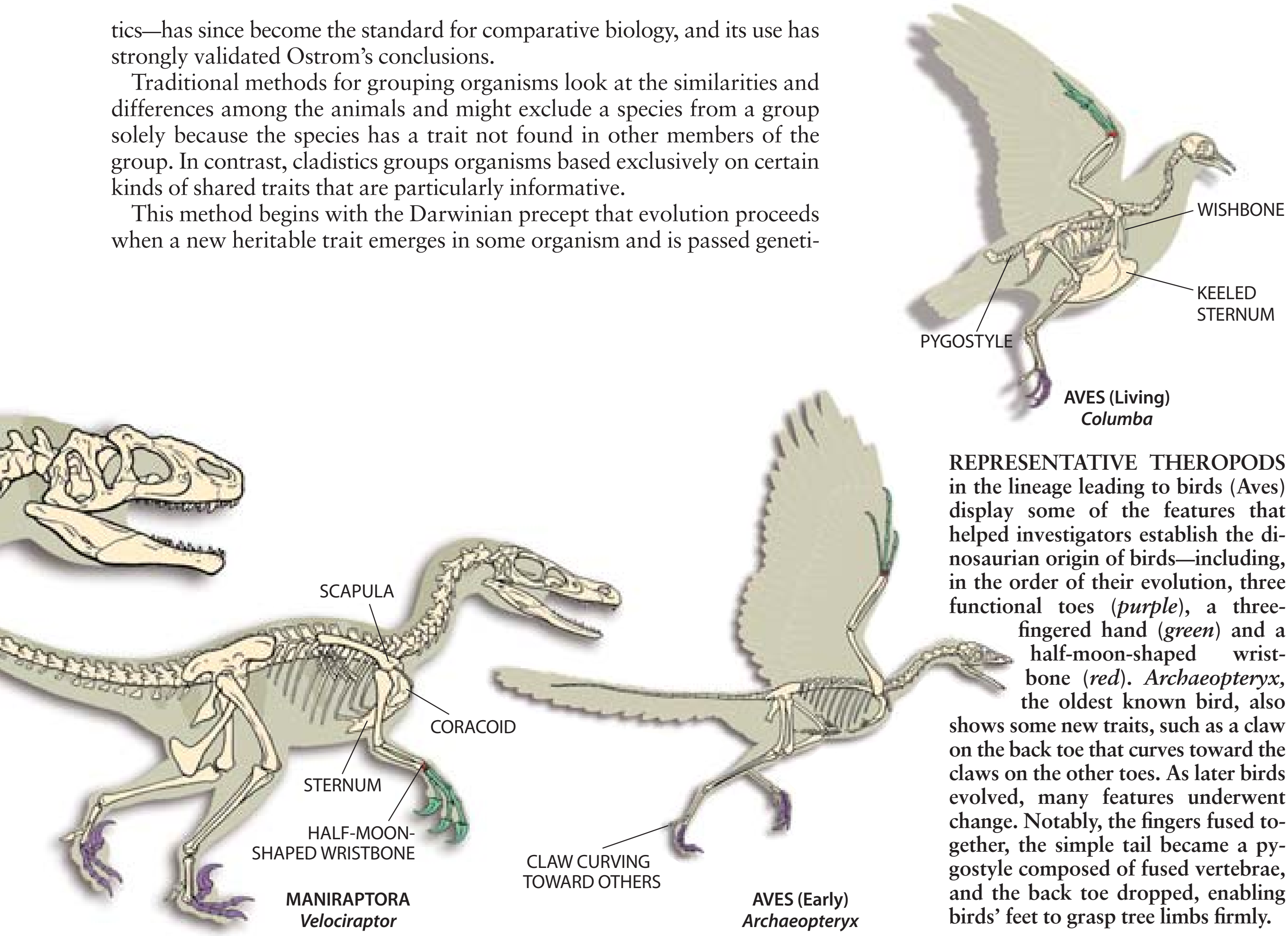


TOMO NARASHIMA

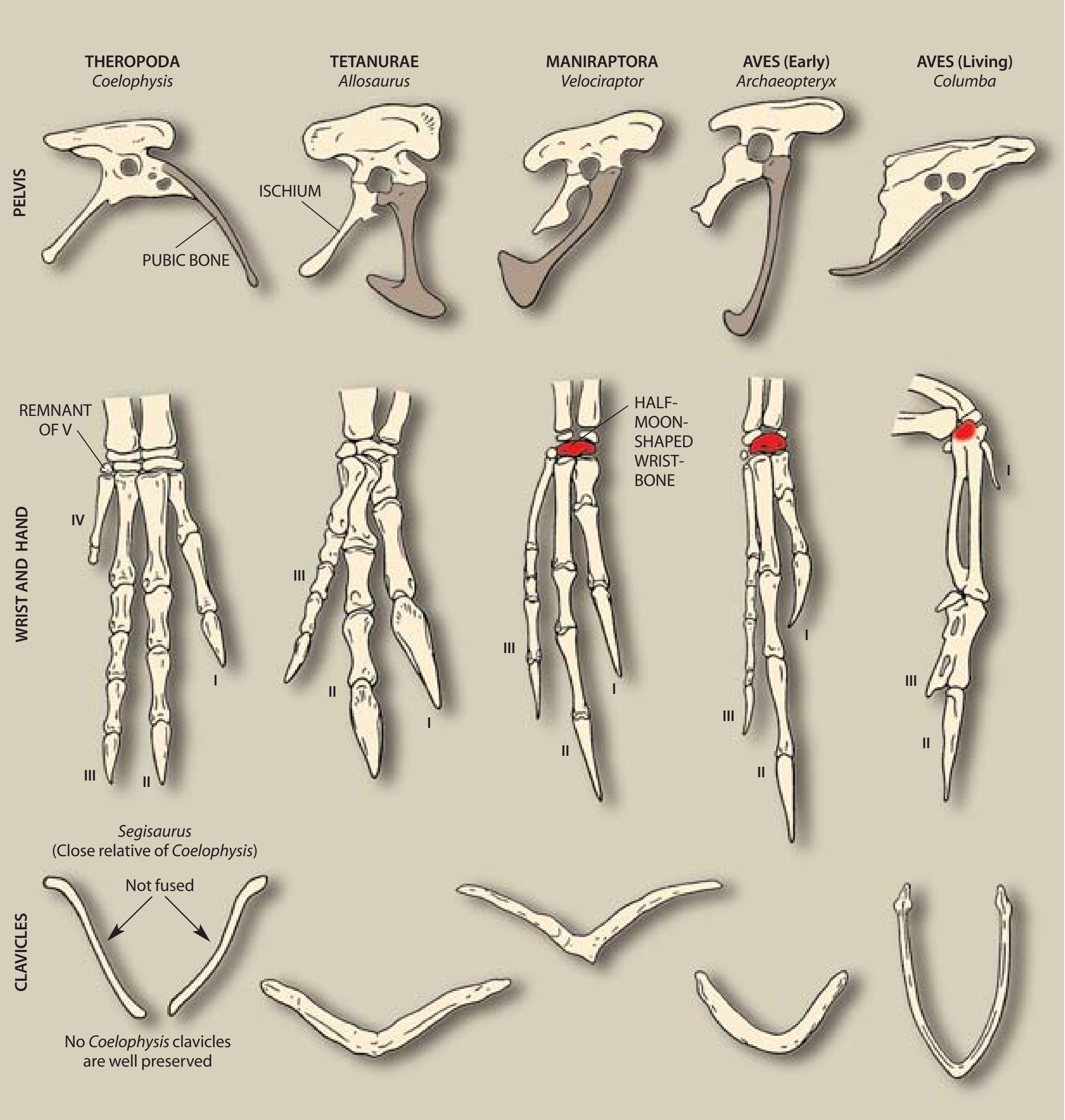
tics—has since become the standard for comparative biology, and its use has strongly validated Ostrom's conclusions.

Traditional methods for grouping organisms look at the similarities and differences among the animals and might exclude a species from a group solely because the species has a trait not found in other members of the group. In contrast, cladistics groups organisms based exclusively on certain kinds of shared traits that are particularly informative.

This method begins with the Darwinian precept that evolution proceeds when a new heritable trait emerges in some organism and is passed geneti-



REPRESENTATIVE THEROPODS in the lineage leading to birds (Aves) display some of the features that helped investigators establish the dinosaurian origin of birds—including, in the order of their evolution, three functional toes (*purple*), a three-fingered hand (*green*) and a half-moon-shaped wristbone (*red*). *Archaeopteryx*, the oldest known bird, also shows some new traits, such as a claw on the back toe that curves toward the claws on the other toes. As later birds evolved, many features underwent change. Notably, the fingers fused together, the simple tail became a pygostyle composed of fused vertebrae, and the back toe dropped, enabling birds' feet to grasp tree limbs firmly.



ED HECK

COMPARISONS OF ANATOMICAL STRUCTURES not only helped to link birds to theropods, they also revealed some of the ways those features changed as dinosaurs became more birdlike and birds became more modern. In the pelvis (*side view*), the pubic bone (*brown*) initially pointed forward (toward the right), but it later shifted to be vertical or pointed backward. In the hand (*top view*), the relative proportions of the bones remained quite constant through the early birds, but the wrist changed. In the maniraptoran wrist, a disklike bone took on the half-moon shape (*red*) that ultimately promoted flapping flight in birds. The wide, boomerang-shaped wishbone (fused clavicles) in tetanurans and later groups compares well with that of archaic birds, but it became thinner and formed a deeper U shape as it became more critical in flight.

cally to its descendants. The precept indicates that two groups of animals sharing a set of such new, or "derived," traits are more closely related to each other than they are to groups that display only the original traits but not the derived ones. By identifying shared derived traits, practitioners of cladistics can determine the relations among the organisms they study.

The results of such analyses, which generally examine many traits, can be represented in the form of a cladogram: a treelike diagram depicting the order in which new characteristics, and new creatures, evolved [*see box on preceding two pages*]. Each branching point, or node, reflects the emergence of an ancestor that founded a group having derived characteristics not present in groups that evolved earlier. This ancestor and all its descendants constitute a "clade," or closely related group.

Ostrom did not apply cladistic methods to determine that birds evolved from small theropod dinosaurs; in the 1970s the approach was just coming into use. But about a decade later Jacques A. Gauthier, then at the University of California at Berkeley, did an extensive cladistic analysis of birds, dinosaurs and their reptilian relatives. Gauthier put Ostrom's comparisons and many other features into a cladistic framework and confirmed that birds evolved from small theropod dinosaurs. Indeed, some of the closest relatives of birds include the sickle-clawed maniraptoran *Deinonychus* that Ostrom had so vividly described.

Today a cladogram for the lineage leading from theropods to birds shows that the clade labeled Aves (birds) consists of the ancestor of *Archaeopteryx* and all other descendants of that ancestor. This clade is a subgroup of a broader clade consisting of so-called maniraptoran theropods—itself a subgroup of the tetanuran theropods that descended from the most basal theropods. Those archaic theropods in turn evolved from nontheropod dinosaurs. The cladogram shows that birds are not only *descended* from dinosaurs, they *are* dinosaurs (and reptiles)—just as humans are mammals, even though people are as different from other mammals as birds are from other reptiles.

Early Evolutionary Steps to Birds

Gauthier's studies and ones conducted more recently demonstrate that many features traditionally considered "birdlike" actually appeared before the advent of birds, in their preavian theropod ancestors. Many of those properties undoubtedly helped their original possessors to survive as terrestrial dinosaurs; these same traits and others were eventually used directly or were transformed to support flight and an arboreal way of life. The short length of this article does not allow us to catalogue the many dozens of details that combine to support the hypothesis that birds evolved from small theropod dinosaurs, so we will concentrate mainly on those related to the origin of flight.

The birdlike characteristics of the theropods that evolved prior to birds did not appear all at once, and some were present before the theropods themselves emerged—in the earliest dinosaurs. For instance, the immediate reptilian ancestor of dinosaurs was already bipedal and upright in its stance (that is, it basically walked like a bird), and it was small and carnivorous. Its hands, in common with those of early birds, were free for grasping (although the hand still had five digits, not the three found in all but the most basal theropods and in birds). Also, the second finger was longest—not the third, as in other reptiles.

Further, in the ancestors of dinosaurs, the ankle joint had already become hingelike, and the metatarsals, or foot bones, had became elongated. The metatarsals were held off the ground, so the immediate relatives of dinosaurs, and dinosaurs themselves, walked on their toes and put one foot in front of the other, instead of sprawling. Many of the changes in the feet are thought to have increased stride length and running speed, a property that would one day help avian theropods to fly.

The earliest theropods had hollow bones and cavities in the skull; these adjustments lightened the skeleton. They also had a long neck and held their back horizontally, as birds do today. In the hand, digits four and five (the equivalent of the pinky and its neighbor) were already reduced in the first dinosaurs; the fifth finger was virtually gone. Soon it was completely lost, and the fourth was reduced to a nubbin. Those reduced fingers disappeared altogether in tetanuran theropods, and the remaining three (I, II, III) became fused together sometime after *Archaeopteryx* evolved.

In the first theropods, the hind limbs became more birdlike as well. They were long; the thigh was shorter than the shin, and the fibula, the bone to the side of the shinbone, was reduced. (In birds today the toothpicklike bone in the drumstick is all that is left of the fibula.) These dinosaurs walked on the three middle toes—the same ones modern birds use. The fifth toe was shortened and tapered, with no joints, and the first toe included a shortened metatarsal (with a small joint and a claw) that projected from the side of the second toe. The first toe was held higher than the others and had no apparent function, but it was later put to good use in birds. By the time *Archaeopteryx* appeared, that toe had rotated to lie behind the others. In later birds, it descended to become opposable to the others and eventually formed an important part of the perching foot.

More Changes

Through the course of theropod evolution, more features once thought of as strictly avian emerged. For instance,

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Bones of Contention

Although many lines of evidence establish that birds evolved from small, terrestrial theropod dinosaurs, a few scientists remain vocally unconvinced. They have not, however, tested any alternative theory by cladistics or by any other method that objectively analyzes relationships among animals. Here is a sampling of their arguments, with some of the evidence against those assertions.

Bird and theropod hands differ: theropods retain fingers I, II and III (having lost the "pinky" and "ring finger"), but birds have fingers II, III and IV. This view of the bird hand is based on embryological research suggesting that when digits are lost from the five-fingered hand, the outer fingers (I and V) are the first to go. No one doubts that theropods retain fingers I, II and III, however, so this "law" clearly has exceptions and does not rule out retention of the first three fingers in birds. More important, the skeletal evidence belies the alleged difference in the hands of birds and nonavian theropods. The three fingers that nonavian theropods kept after losing the fourth and fifth have the same forms, proportions and connections to the wristbones as the fingers in *Archaeopteryx* and later birds [*see middle row of illustration on opposite page*].

Theropods appear too late to give rise to birds. Proponents of this view have noted that *Archaeopteryx* appears in the fossil record about 150 million years ago, whereas the fossil remains of various nonavian maniraptors—the closest known relatives of birds—date only to about 115 million years ago. But investigators have now uncovered bones that evidently belong to small, nonavian maniraptors and that date to the time of *Archaeopteryx*. In any case, failure to find fossils of a predicted kind does not rule out their existence in an undiscovered deposit.

The wishbone (composed of fused clavicles) of birds is not like the clavicles in theropods. This objection was reasonable when only the clavicles of early theropods had been discovered, but boomerang-shaped wishbones that look just like that of *Archaeopteryx* have now been uncovered in many theropods.

The complex lungs of birds could not have evolved from theropod lungs. This assertion cannot be supported or falsified at the moment, because no fossil lungs are preserved in the paleontological record. Also, the proponents of this argument offer no animal whose lungs could have given rise to those in birds, which are extremely complex and are unlike the lungs of any living animal.

—K.P. and L.M.C.

major changes occurred in the forelimb and shoulder girdle; these adjustments at first helped theropods to capture prey and later promoted flight. Notably, during theropod evolution, the arms became progressively longer, except in such giant carnivores as *Carnotaurus, Allosaurus* and *Tyrannosaurus,* in which the forelimbs were relatively small. The forelimb was about half the length of the hind limb in very early theropods. By the time *Archaeopteryx* appeared, the forelimb was longer than the hind limb, and it grew still more in later birds. This lengthening in the birds allowed a stronger flight stroke.

The hand became longer, too, accounting for a progressively greater proportion of the forelimb, and the wrist underwent dramatic revision in shape. Basal theropods possessed a flat wristbone (distal carpal) that overlapped the bases of the first and second palm bones (metacarpals) and fingers. In maniraptorans, though, this bone assumed a half-moon shape along the surface that contacted the arm bones. The half-moon, or semilunate, shape was very important because it allowed these animals to flex the wrist sideways in addition to up and down. They could thus fold the long hand, almost as living birds do. The longer hand could then be rotated and whipped forward suddenly to snatch prey.

In the shoulder girdle of early theropods, the scapula (shoulder blade) was long and straplike; the coracoid (which along with the scapula forms the shoulder joint) was rounded, and two separate, S-shaped clavicles connected the shoulder to the sternum, or breastbone. The scapula soon became longer and narrower; the coracoid also thinned and elongated, stretching toward the breastbone. The clavicles fused at the midline and broadened to form a boomerang-shaped wishbone. The sternum, which consisted originally of cartilage, calcified into two fused bony plates in tetanurans. Together these changes strengthened the skeleton; later this strengthening was used to reinforce the flight apparatus and support the flight muscles. The new wishbone, for instance, probably became an anchor for the muscles that moved the forelimbs, at first during foraging and then during flight.

In the pelvis, more vertebrae were added to the hip girdle, and the pubic bone (the pelvic bone that is attached in front of and below the hip socket) changed its orientation. In the first theropods, as in most other reptiles, the pubis pointed down and forward, but then it began to point straight down or backward. Ultimately, in birds more advanced than *Archaeopteryx,* it became parallel to the ischium, the pelvic bone that extends backward from below the hip socket. The benefits derived from these changes, if any, remain unknown, but the fact that these features are unique to birds and other maniraptorans shows their common origin.

Finally, the tail gradually became shorter and stiffer throughout theropod history, serving more and more as a balancing organ during running, somewhat as it does in today's roadrunners. Steven M. Gatesy of Brown University has demonstrated that this transition in tail structure paralleled another change in function: the tail became less and less an anchor for the leg muscles. The pelvis took over that function, and in maniraptorans the muscle that once drew back the leg now mainly controlled the tail. In birds that followed *Archaeopteryx,* these muscles would be used to adjust the feathered tail as needed in flight.

In summary, a great many skeletal features that were once thought of as uniquely avian innovations—such as light, hollow bones, long arms, three-fingered hands with a long second finger, a wishbone, a backward-pointing pelvis, and long hind limbs with a three-toed foot—were already present in theropods before the evolution of birds. Those features generally served different uses than they did in birds and were only later co-opted for flight and other characteristically avian functions, eventually including life in the trees.

Evidence for the dinosaurian origin of birds is not confined to the skeleton. Recent discoveries of nesting sites in Mongolia and Montana reveal that some reproductive behaviors of birds originated in nonavian dinosaurs. These theropods did not deposit a large clutch of eggs all at once, as most other reptiles do. Instead they filled a nest more gradually, laying one or two eggs at a time, perhaps over several days, as birds do. Recently skeletons of the Cretaceous theropod *Oviraptor* have been found atop nests of eggs; the dinosaurs were apparently buried while protecting the eggs in very birdlike fashion. This find is ironic because *Oviraptor,* whose name means "egg stealer," was first thought to have been raiding the eggs of other dinosaurs, rather than protecting them. Even the structure of the eggshell in theropods shows features otherwise seen only in bird eggs. The shells consist of two layers of calcite, one prismatic (crystalline) and one spongy (more irregular and porous).

As one supposedly uniquely avian trait after another has been identified in nonavian dinosaurs, feathers have continued to stand out as a prominent feature belonging to birds alone. Some intriguing evidence, however, hints that even feathers might have predated the emergence of birds.

In 1996 and 1997 Ji Qiang and Ji Shu'an of the National Geological Museum of China published reports on two fossil animals found in Liaoning Province that date to late in the Jurassic or early in the Cretaceous. One, a turkey-size dinosaur named *Sinosauropteryx,* has fringed, filamentous structures along its backbone and on its body surface. These structures of the skin, or integument, may have been precursors to feathers. But the animal is far from a bird. It has short arms and other skeletal properties indicating that it may be related to the theropod *Compsognathus,* which is not especially close to birds or other maniraptorans.

The second creature, *Protarchaeopteryx,* apparently has short, true feathers on its body and has longer feathers attached to its tail. Preliminary observations suggest that the animal is a maniraptoran theropod. Whether it is also a bird will depend on a fuller description of its anatomy. Nevertheless, the Chinese finds imply that, at the least, the structures that gave rise to feathers probably appeared before birds did and almost certainly before birds began to fly. Whether their original function was for insulation, display or something else cannot yet be determined.

The Beginning of Bird Flight

The origin of birds and the origin of flight are two distinct, albeit related, problems. Feathers were present for other functions before flight evolved, and *Archaeopteryx* was probably not the very first flying theropod, although at present we have no fossils of earlier flying precursors. What can we say about how flight began in bird ancestors?

Traditionally, two opposing scenarios have been put forward. The "arboreal" hypothesis holds that bird ancestors began to fly by climbing trees and gliding down from branches with the help of incipient feathers. The height of trees provides a good starting place for launching flight, especially through gliding. As feathers became larger over time, flapping flight evolved, and birds finally became fully airborne.

This hypothesis makes intuitive sense, but certain aspects are troubling. *Archaeopteryx* and its maniraptoran cousins have no obviously arboreal adaptations, such as feet fully adapted for perching. Perhaps some of them could climb trees, but no convincing analysis has demonstrated how *Archaeopteryx* would have climbed and flown with its forelimbs, and there were no plants taller than a few meters in the environments where *Archaeopteryx* fossils have been found. Even if the animals could climb trees, this ability is not synonymous with arboreal habits or gliding ability. Most small animals, and even some goats and kangaroos, can climb trees, but that does not make them tree dwellers. Besides, *Archaeopteryx* shows no obvious features of gliders, such as a broad membrane connecting forelimbs and hind limbs.

The "cursorial" (running) hypothesis holds that small dinosaurs ran along the ground and stretched out their arms for balance as they leaped into the air after insect prey or, perhaps, to avoid predators. Even rudimentary feathers on forelimbs could have expanded the arm's surface area to enhance lift slightly. Larger feathers could have increased lift incrementally, until sustained flight was gradually achieved. Of course, a leap into the air does not provide the acceleration produced by dropping out of a tree; an animal would have to run quite fast to take off. Still, some small terrestrial animals can achieve high speeds.

The cursorial hypothesis is strengthened by the fact that the immediate theropod ancestors of birds were terrestrial. And they had the traits needed for high liftoff speeds: they were small, active, agile, lightly built, long-legged and good runners. And because they were bipedal, their arms were free to evolve flapping flight, which cannot be said for other reptiles of their time.

Although our limited evidence is tantalizing, probably neither the arboreal nor the cursorial model is correct in its extreme form. More likely, the ancestors of birds used a combination of taking off from the ground and taking advantage of accessible heights (such as hills, large boulders or fallen trees). They may not have climbed trees, but they could have used every available object in their landscape to assist flight.

More central than the question of ground versus trees, however, is the evolution of a flight stroke. This stroke generates not only the lift that gliding animals obtain from moving their wings through the air (as an airfoil) but also the thrust that enables a flapping animal to move forward. (In contrast, the "organs" of lift and thrust in airplanes—the wings and jets—are separate.) In birds and bats, the hand part of the wing generates the thrust, and the rest of the wing provides the lift.

Jeremy M. V. Rayner of the University of Bristol showed in the late 1970s that the down-and-forward flight stroke of birds and bats produces a series of doughnut-shaped vortices that propel the flying animal forward. One of us (Padian) and Gauthier then demonstrated in the mid-1980s that the movement generating these vortices in birds is the same action—sideways flexion of the hand—that was already present in the maniraptorans *Deinonychus* and *Velociraptor* and in *Archaeopteryx*.

As we noted earlier, the first maniraptorans must have used this movement to grab prey. By the time *Archaeopteryx* and other birds appeared, the shoulder joint had changed its angle to point more to the side than down and backward. This alteration in the angle transformed the forelimb motion from a prey-catching one to a flight stroke. New evidence from Argentina suggests that the shoulder girdle in the closest maniraptorans to birds (the new dinosaur *Unenlagia*) was already angled outward so as to permit this kind of stroke.

Recent work by Farish A. Jenkins, Jr., of Harvard University, George E. Goslow of Brown University and their colleagues has revealed much about the role of the wishbone in flight and about how the flight stroke is achieved. The wishbone in some living birds acts as a spacer between the shoulder girdles, one that stores energy expended during the flight stroke. In the first birds, in contrast, it probably was less elastic, and its main function may have been simply to anchor the forelimb muscles. Apparently, too, the muscle most responsible for rotating and raising the wing during the recovery stroke of flight was not yet in the modern position in *Archaeopteryx* or other very early birds. Hence, those birds were probably not particularly skilled fliers; they would have been unable to flap as quickly or as precisely as today's birds can. But it was not long—perhaps just several million years—before birds acquired the apparatus they needed for more controlled flight.

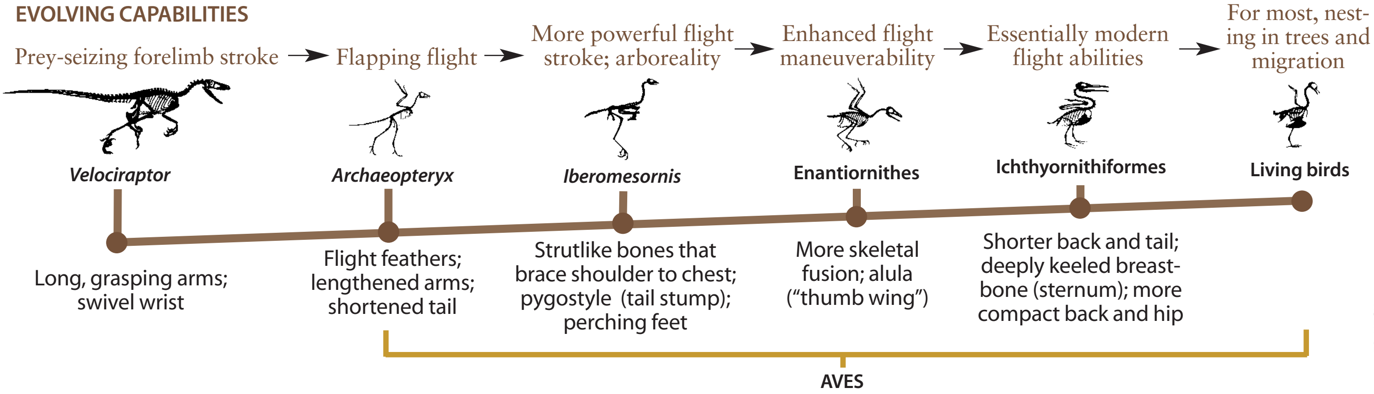
Beyond *Archaeopteryx*

More than three times as many bird fossils from the Cretaceous period have been found since 1990 than in all the rest of recorded history. These new specimens—uncovered in such places as Spain, China, Mongolia, Madagascar and Argentina—are helping paleontologists to flesh out the early evolution of the birds that followed *Archaeopteryx,* including their acquisition of an improved flying system. Analyses of these finds by one of us (Chiappe) and others have shown that birds quickly took on many different sizes, shapes and behaviors (ranging from diving to flightlessness) and diversified all through the Cretaceous period, which ended about 65 million years ago.

A bird-watching trek through an Early Cretaceous forest would bear little resemblance to such an outing now. These early birds might have spent much of their time in the trees and were able to perch, but there is no evidence that the first birds nested in trees, had complex songs or migrated great distances. Nor did they fledge at nearly adult size, as birds do now, or grow as rapidly as today's birds do. Scientists can only imagine what these animals looked like. Undoubtedly, however, they would have seemed very strange, with their clawed fingers and, in many cases, toothed beaks.

Underneath the skin, though, some skeletal features certainly became more birdlike during the Early Cretaceous and enabled birds to fly quite well. Many bones in the hand and in the hip girdle fused, providing strength to the skeleton for flight. The breastbone became broader and developed a keel down the midline of the chest for flight muscle attachment. The forearm became much longer, and the skull bones and vertebrae became lighter and more hollowed out. The tailbones became a short series of free segments ending in a fused stump (the familiar "parson's nose" or "Pope's nose" of roasted birds) that controlled the tail feathers. And the alula, or "thumb wing," a part of the bird wing essential for flight control at low speed, made its debut, as did a long first toe useful in perching.

Inasmuch as early birds could fly, they certainly had higher metabolic rates than cold-blooded reptiles; at least they were



ED HECK

CLADOGRAM OF BIRD EVOLUTION indicates that birds (Aves) perfected their flight stroke gradually after they first appeared approximately 150 million years ago. They became arboreal (able to live in trees) relatively early in their history, however. Some of the skeletal innovations that supported their emerging capabilities are listed at the bottom.

able to generate the heat and energy needed for flying without having to depend on being heated by the environment. But they might not have been as fully warm-blooded as today's birds. Their feathers, in addition to aiding flight, provided a measure of insulation—just as the precursors of feathers could have helped preserve heat and conserve energy in nonavian precursors of birds. These birds probably did not fly as far or as strongly as birds do now.

Bird-watchers traipsing through a forest roughly 50 million years later would still have found representatives of very primitive lineages of birds. Yet other birds would have been recognizable as early members of living groups. Recent research shows that at least four major lineages of living birds—including ancient relatives of shorebirds, seabirds, loons, ducks and geese—were already thriving several million years before the end of the Cretaceous period, and new paleontological and molecular evidence suggests that forerunners of other modern birds were around as well.

Most lineages of birds that evolved during the Cretaceous died out during that period, although there is no evidence that they perished suddenly. Researchers may never know whether the birds that disappeared were outcompeted by newer forms, were killed by an environmental catastrophe or were just unable to adapt to changes in their world. There is no reasonable doubt, however, that all groups of birds, living and extinct, are descended from small, meat-eating theropod dinosaurs, as Huxley's work intimated more than a century ago. In fact, living birds are nothing less than small, feathered, short-tailed theropod dinosaurs.

OVIRAPTOR, a maniraptoran theropod that evolved before birds, sat in its nest to protect its eggs (*bottom*), just as the ostrich (*top*) and other birds do today. In other words, such brooding originated before birds did. In the fossil that served as the basis for the *Oviraptor* drawing, the position of the claws indicates that the limbs were drawn in around the eggs, to protect them.

ILLUSTRATIONS BY ED HECK

The Authors

KEVIN PADIAN and LUIS M. CHIAPPE are frequent collaborators. Padian is professor of integrative biology and curator in the Museum of Paleontology at the University of California, Berkeley. He is also president of the National Center for Science Education. Chiappe, who has extensively studied the radiation of birds during the Cretaceous period, is Chapman Fellow and research associate at the American Museum of Natural History in New York City and adjunct professor at the City University of New York.

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The Mammals That Conquered

New fossils and DNA analyses elucidate the remarkable evolutionary history of whales

originally published in May 2002

“They say the sea is cold,
but the sea contains
the hottest blood of all,
and the wildest, the most urgent.”

—D. H. Lawrence,
“Whales Weep Not!”

the Seas

By Kate Wong

Dawn breaks over the Tethys Sea, 48 million years ago, and the blue-green water sparkles with the day’s first light. But for one small mammal, this new day will end almost as soon as it has started.

ANCIENT WHALE *Rodhocetus* (*right* and *left front*) feasts on the bounty of the sea, while *Ambulocetus* (*rear*) attacks a small land mammal some 48 million years ago in what is now Pakistan.

Tapir-like *Eotitanops* has wandered perilously close to the water's edge, ignoring its mother's warning call. For the brute lurking motionless among the mangroves, the opportunity is simply too good to pass up. It lunges landward, propelled by powerful hind limbs, and sinks its formidable teeth into the calf, dragging it back into the surf. The victim's frantic struggling subsides as it drowns, trapped in the unyielding jaws of its captor. Victorious, the beast shambles out of the water to devour its kill on terra firma. At first glance, this fearsome predator resembles a crocodile, with its squat legs, stout tail, long snout and eyes that sit high on its skull. But on closer inspection, it has not armor but fur, not claws but hooves. And the cusps on its teeth clearly identify it not as a reptile but as a mammal. In fact, this improbable creature is *Ambulocetus,* an early whale, and one of a series of intermediates linking the land-dwelling ancestors of cetaceans to the 80 or so species of whales, dolphins and porpoises that rule the oceans today.

Until recently, the emergence of whales was one of the most intractable mysteries facing evolutionary biologists. Lacking fur and hind limbs and unable to go ashore for so much as a sip of freshwater, living cetaceans represent a dramatic departure from the mammalian norm. Indeed, their piscine form led Herman Melville in 1851 to describe Moby Dick and his fellow whales as fishes. But to 19th-century naturalists such as Charles Darwin, these air-breathing, warm-blooded animals that nurse their young with milk distinctly grouped with mammals. And because ancestral mammals lived on land, it stood to reason that whales ultimately descended from a terrestrial ancestor. Exactly how that might have happened, however, eluded scholars. For his part, Darwin noted in *On the Origin of Species* that a bear swimming with its mouth agape to catch insects was a plausible evolutionary starting point for whales. But the proposition attracted so much ridicule that in later editions of the book he said just that such a bear was "almost like a whale."

Guide to *Terminology*

CETACEA is the order of mammals that comprises living whales, dolphins and porpoises and their extinct ancestors, the archaeocetes. Living members fall into two suborders: the odontocetes, or toothed whales, including sperm whales, pilot whales, belugas, and all dolphins and porpoises; and the mysticetes, or baleen whales, including blue whales and fin whales. The term "whale" is often used to refer to all cetaceans.

ARTIODACTYLA is the order of even-toed, hoofed mammals that includes camels; ruminants such as cows; hippos; and, most researchers now agree, whales.

MESONYCHIDS are a group of primitive hoofed, wolflike mammals once widely thought to have given rise to whales.

EOCENE is the epoch between 55 million and 34 million years ago, during which early whales made their transition from land to sea.

OLIGOCENE is the epoch between 34 million and 24 million years ago, during which odontocetes and mysticetes evolved from their archaeocete ancestors.

The fossil record of cetaceans did little to advance the study of whale origins. Of the few remains known, none were sufficiently complete or primitive to throw much light on the matter. And further analyses of the bizarre anatomy of living whales led only to more scientific head scratching. Thus, even a century after Darwin, these aquatic mammals remained an evolutionary enigma. In fact, in his 1945 classification of mammals, famed paleontologist George Gaylord Simpson noted that whales had evolved in the oceans for so long that nothing informative about their ancestry was left. Calling them "on the whole, the most peculiar and aberrant of mammals," he inserted cetaceans arbitrarily among the other orders. Where whales belonged in the mammalian family tree and how they took to the seas defied explanation, it seemed.

Over the past two decades, however, many of the pieces of this once imponderable puzzle have fallen into place. Paleontologists have uncovered a wealth of whale fossils spanning the Eocene epoch, the time between 55 million and 34 million years ago when archaic whales, or archaeocetes, made their transition from land to sea. They have also unearthed some clues from the ensuing Oligocene, when the modern suborders of cetaceans—the mysticetes (baleen whales) and the odontocetes (toothed whales)—arose. That fossil material, along with analyses of DNA from living animals, has enabled scientists to paint a detailed picture of when, where and how whales evolved from their terrestrial forebears. Today their transformation—from landlubbers to leviathans—stands as one of the most profound evolutionary metamorphoses on record.

Evolving Ideas

AT AROUND THE SAME TIME that Simpson declared the relationship of whales to other mammals undecipherable on the basis of anatomy, a new comparative approach emerged, one that looked at antibody-antigen reactions in living animals. In response to Simpson's assertion, Alan Boyden of Rutgers University and a colleague applied the technique to the whale question. Their results showed convincingly that among living animals, whales are most closely related to the even-toed hoofed mammals, or artiodactyls, a group whose members include camels, hippopotamuses, pigs and ruminants such as cows. Still, the exact nature of that relationship remained unclear. Were whales themselves artiodactyls? Or did they occupy their own branch of the mammalian family tree, linked to the artiodactyl branch via an ancient common ancestor?

Support for the latter interpretation came in the 1960s, from studies of primitive hoofed mammals known as condylarths that had not yet evolved the specialized characteristics of artiodactyls or the other mammalian orders. Paleontologist Leigh Van Valen, then at the American Museum of Natural History in New York City, discovered striking resemblances between the three-cusped teeth of the few known fossil whales and those of a group of meat-eating condylarths called mesonychids. Likewise, he found shared dental characteristics between artiodactyls and another group of condylarths, the arctocyonids,

KAREN CARR *(preceding pages)*

THE WHALE'S CHANGING WORLD

It might seem odd that 300 million years after vertebrates first established a toehold on land, some returned to the sea. But the setting in which early whales evolved offers hints as to what lured them back to the water. For much of the Eocene epoch (roughly between 55 million and 34 million years ago), a sea called Tethys, after a goddess of Greek mythology, stretched from Spain to Indonesia. Although the continents and ocean plates we know now had taken shape, India was still adrift, Australia hadn't yet fully separated from Antarctica, and great swaths of Africa and Eurasia lay submerged under Tethys. Those shallow, warm waters incubated abundant nutrients and teemed with fish. Furthermore, the space vacated by the plesiosaurs, mosasaurs and other large marine reptiles that perished along with the dinosaurs created room for new top predators (although sharks and crocodiles still provided a healthy dose of competition). It is difficult to imagine a more enticing invitation to aquatic life for a mammal.

During the Oligocene epoch that followed, sea levels sank and India docked with the rest of Asia, forming the crumpled interface we know as the Himalayas. More important, University of Michigan paleontologist Philip Gingerich notes, Australia and Antarctica divorced, opening up the Southern Ocean and creating a south circumpolar current that eventually transformed the balmy Eocene Earth into the ice-capped planet we inhabit today. The modern current and climate systems brought about radical changes in the quantity and distribution of nutrients in the sea, generating a whole new set of ecological opportunities for the cetaceans.

As posited by paleontologist Ewan Fordyce of the University of Otago in New Zealand, that set the stage for the replacement of the archaeocetes by the odontocetes and mysticetes (toothed and baleen whales, respectively). The earliest known link between archaeocetes and the modern cetacean orders, Fordyce says, is *Llanocetus,* a 34-million-year-old protobaleen whale from Antarctica that may well have trawled for krill in the chilly Antarctic waters, just as living baleen whales do. Odontocetes arose at around the same time, he adds, specializing to become echolocators that could hunt in the deep.

Unfortunately, fossils documenting the origins of mysticetes and odontocetes are vanishingly rare. Low sea levels during the Middle Oligocene exposed most potential whale-bearing sediments from the Early Oligocene to erosive winds and rains, making that period largely "a fossil wasteland," says paleontologist Mark Uhen of the Cranbrook Institute of Science in Bloomfield Hills, Mich. The later fossil record clearly shows, however, that shortly after, by about 30 million years ago, the baleen and toothed whales had diversified into many of the cetacean families that reign over the oceans today. *—K.W.*

SARA CHEN AND EDWARD BELL

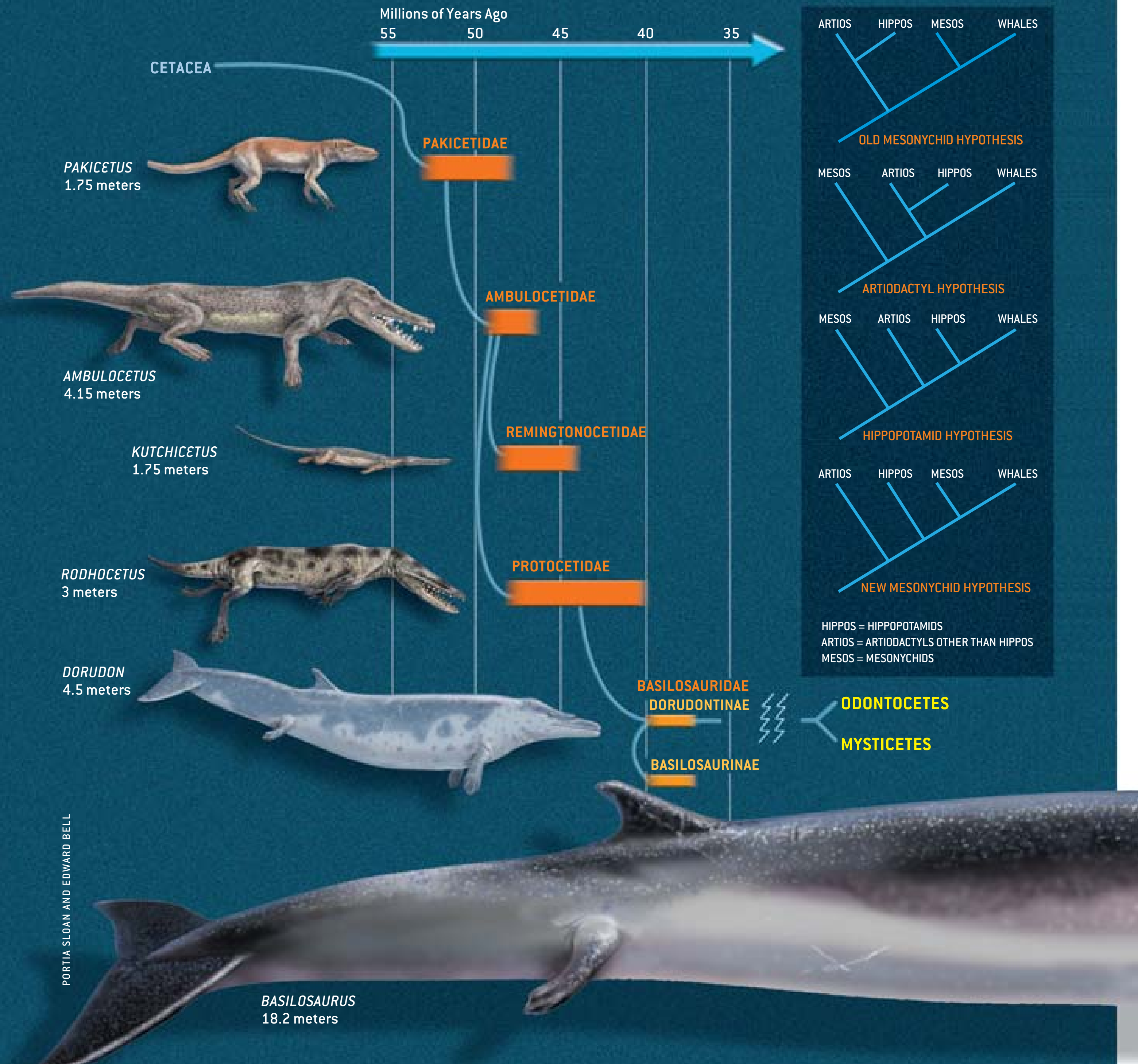
close relatives of the mesonychids. Van Valen concluded that whales descended from the carnivorous, wolflike mesonychids and thus appeared to be linked to artiodactyls through the condylarths.

Walking Whales

A DECADE OR SO PASSED before paleontologists finally began unearthing fossils close enough to the evolutionary branching point of whales to address Van Valen's mesonychid hypothesis. Even then the significance of these finds took a while to sink in. It started when University of Michigan paleontologist Philip D. Gingerich went to Pakistan in 1977 in search of Eocene land mammals. The expedition proved disappointing because just marine fossils turned up. Finding traces of ancient ocean life in Pakistan, far from the country's modern coast, is not surprising: during the Eocene, the vast Tethys Sea periodically covered great swaths of what is now the Indian subcontinent [*see box above*]. Intriguingly, though, the team discovered among those ancient fish and snail remnants two pelvis fragments that appeared to have come from relatively large, walking beasts. "We joked about walking whales," Gingerich recalls with a chuckle. "It was unthinkable." Curious as the pelvis

CETACEAN RELATIONS

FAMILY TREE OF CETACEANS shows the descent of the two modern suborders of whales, the odontocetes and mysticetes, from the extinct archaeocetes. Representative members of each archaeocete family or subfamily are depicted (*left*). Branching diagrams illustrate various hypotheses of the relationship of whales to other mammals (*right*). The old mesonychid hypothesis, which posits that extinct wolflike beasts known as mesonychids are the closest relatives of whales, now seems unlikely in light of recent fossil whale discoveries. The anklebones of those ancient whales bear the distinctive characteristics of artiodactyl ankles, suggesting that whales are themselves artiodactyls, as envisioned by the artiodactyl hypothesis. Molecular studies indicate that whales are more closely related to hippopotamuses than to any other artiodactyl group. Whether the fossil record can support the hippopotamid hypothesis, however, remains to be seen. A fourth scenario, denoted here as the new mesonychid hypothesis, proposes that mesonychids could still be the whale's closest kin if they, too, were included in the artiodactyl order, instead of the extinct order Condylarthra, in which they currently reside. If so, they would have to have lost the ankle traits that characterize all known artiodactyls. *—K.W.*



PORTIA SLOAN AND EDWARD BELL

pieces were, the only fossil collected during that field season that seemed important at the time was a primitive artiodactyl jaw that had turned up in another part of the country.

Two years later, in the Himalayan foothills of northern Pakistan, Gingerich's team located another weird whale clue: a partial braincase from a wolf-size creature—found in the company of 50-million-year-old land mammal remains—that bore distinctive cetacean characteristics. All modern whales have features in their ears that do not appear in any other vertebrates. Although the fossil skull lacked the anatomy necessary for hearing directionally in water (a critical skill for living whales), it clearly had the diagnostic cetacean ear traits. The team had discovered the oldest and most primitive whale then known—one that must have spent some, if not most, of its time on land. Gingerich christened the creature *Pakicetus* for its place of origin and, thus hooked, began hunting for ancient whales in earnest.

Meanwhile another group recovered additional remains of *Pakicetus*—a lower jaw fragment and isolated teeth—that bolstered the link to mesonychids through strong dental similarities. With *Pakicetus* showing up around 50 million years ago and mesonychids known from around the same time in the same part of the world, it seemed increasingly likely that cetaceans had indeed descended from the mesonychids or something closely related to them. Still, what the earliest whales looked like from the neck down was a mystery.

Further insights from Pakistan would have to wait, however. By 1983 Gingerich was no longer able to work there because of the Soviet Union's invasion of Afghanistan. He decided to cast his net in Egypt instead, journeying some 95 miles southwest of Cairo to the Western Desert's Zeuglodon Valley, so named for early 20th-century reports of fossils of archaic whales—or zeuglodons, as they were then known—in the area. Like Pakistan, much of Egypt once lay submerged under Tethys. Today the skeletons of creatures that swam in that ancient sea lie entombed in sandstone. After several field seasons, Gingerich and his crew hit pay dirt: tiny hind limbs belonging to a 60-foot-long sea snake of a whale known as *Basilosaurus* and the first evidence of cetacean feet.

Earlier finds of *Basilosaurus,* a fully aquatic monster that slithered through the seas between about 40 million and 37 million years ago, preserved only a partial femur, which its discoverers interpreted as vestigial. But the well-formed legs and feet revealed by this discovery hinted at functionality. At less than half a meter in length, the diminutive limbs probably would not have assisted *Basilosaurus* in swimming and certainly would not have enabled it to walk on land, but they may well have helped guide the beast's serpentine body during the difficult activity of aquatic mating. Whatever their purpose, if any, the little legs had big implications. "I immediately thought, we're *10 million* years after *Pakicetus,*" Gingerich recounts excitedly. "If these things still have feet and toes, we've got 10 million years of history to look at." Suddenly, the walking whales they had scoffed at in Pakistan seemed entirely plausible.

Just such a remarkable creature came to light in 1992. A team led by J.G.M. (Hans) Thewissen of the Northeastern Ohio Universities College of Medicine recovered from 48-million-year-old marine rocks in northern Pakistan a nearly complete skeleton of a perfect intermediate between modern whales and their terrestrial ancestors. Its large feet and powerful tail bespoke strong swimming skills, while its sturdy leg bones and mobile elbow and wrist joints suggested an ability to locomote on land. He dubbed the animal *Ambulocetus natans,* the walking and swimming whale.

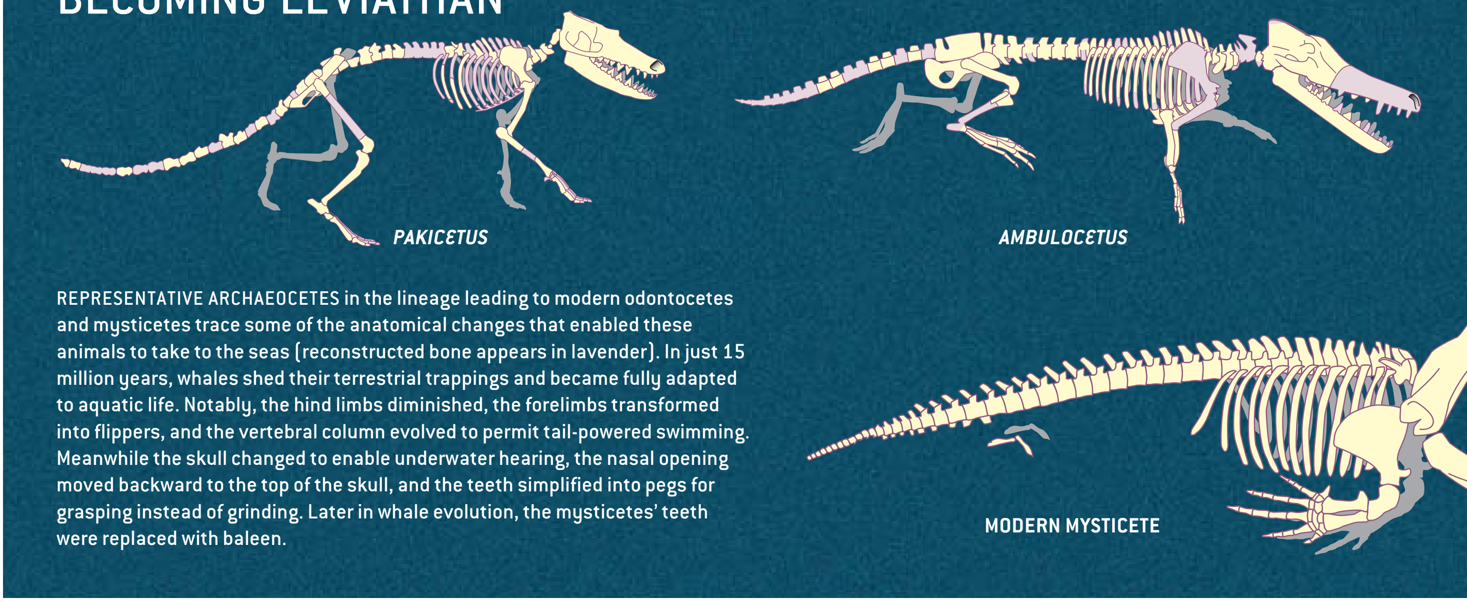
Shape Shifters

SINCE THEN, Thewissen, Gingerich and others have unearthed a plethora of fossils documenting subsequent stages of the whale's transition from land to sea. The picture emerging from those specimens is one in which *Ambulocetus* and its kin—themselves descended from the more terrestrial pakicetids—spawned needle-nosed beasts known as remingtonocetids as well as the intrepid protocetids, the first whales seaworthy enough to fan out from Indo-Pakistan across the globe. From the protocetids arose the dolphinlike dorudontines, the probable progenitors of the snakelike basilosaurines and modern whales [*see box on preceding page*].

In addition to furnishing supporting branches for the whale family tree, these discoveries have enabled researchers to chart many of the spectacular anatomical and physiological changes that allowed cetaceans to establish permanent residency in the ocean realm. Some of the earliest of these adaptations to emerge, as *Pakicetus* shows, are those related to hearing. Sound travels differently in water than it does in air. Whereas the ears of humans and other land-dwelling animals have delicate, flat eardrums, or tympanic membranes, for receiving airborne sound, modern whales have thick, elongate tympanic ligaments that cannot receive sound. Instead a bone called the bulla, which in whales has become quite dense and is therefore capable of transmitting sound coming from a denser medium to deeper parts of the ear, takes on that function. The *Pakicetus* bulla shows some modification in that direction, but the animal retained a land mammal–like eardrum that could not work in water.

What, then, might *Pakicetus* have used its thickened bullae for? Thewissen suspects that, much as turtles hear by picking up vibrations from the ground through their shields, *Pakicetus* may have employed its bullae to pick up ground-borne sounds. Taking new postcranial evidence into consideration

BECOMING LEVIATHAN



REPRESENTATIVE ARCHAEOCETES in the lineage leading to modern odontocetes and mysticetes trace some of the anatomical changes that enabled these animals to take to the seas (reconstructed bone appears in lavender). In just 15 million years, whales shed their terrestrial trappings and became fully adapted to aquatic life. Notably, the hind limbs diminished, the forelimbs transformed into flippers, and the vertebral column evolved to permit tail-powered swimming. Meanwhile the skull changed to enable underwater hearing, the nasal opening moved backward to the top of the skull, and the teeth simplified into pegs for grasping instead of grinding. Later in whale evolution, the mysticetes' teeth were replaced with baleen.

PORTIA SLOAN

along with the ear morphology, he envisions *Pakicetus* as an ambush predator that may have lurked around shallow rivers, head to the ground, preying on animals that came to drink. *Ambulocetus* is even more likely to have used such inertial hearing, Thewissen says, because it had the beginnings of a channel linking jaw and ear. By resting its jaw on the ground—a strategy seen in modern crocodiles—*Ambulocetus* could have listened for approaching prey. The same features that allowed early whales to receive sounds from soil, he surmises, preadapted them to hearing in the water.

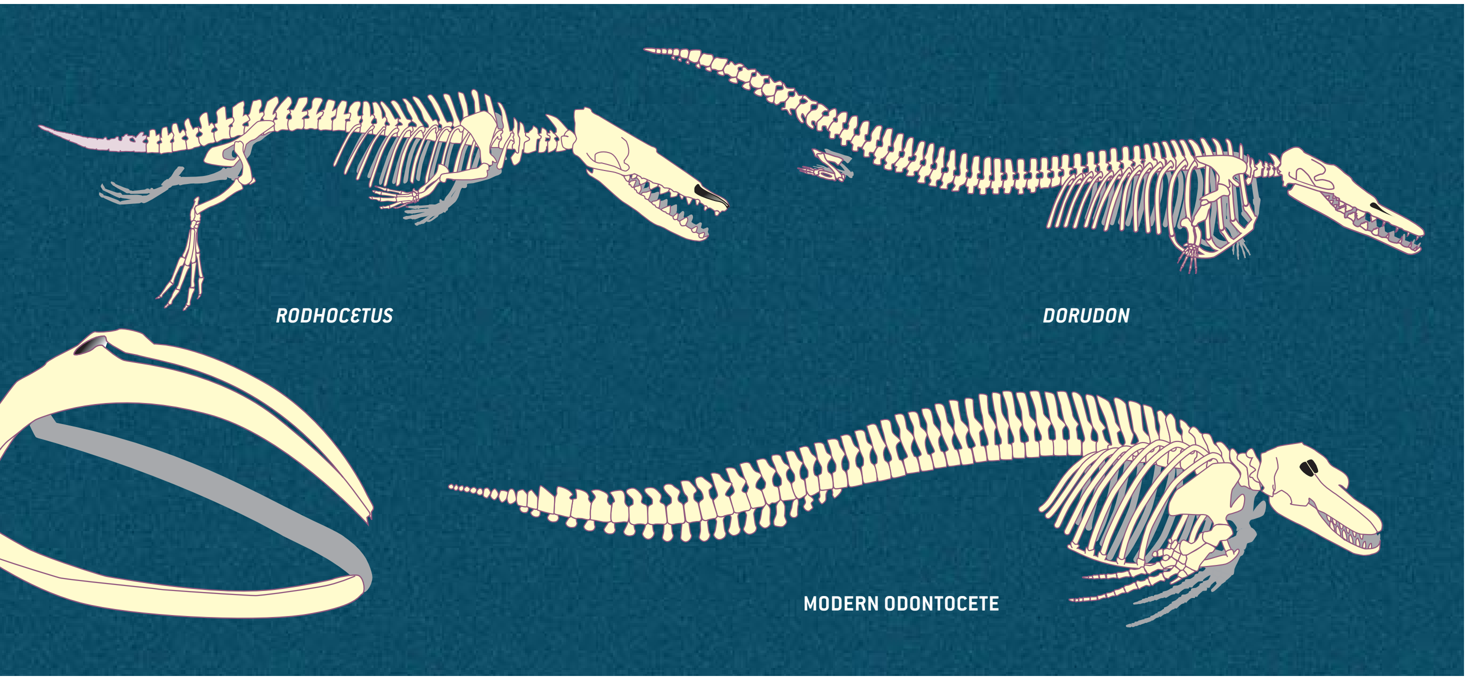
Zhe-Xi Luo of the Carnegie Museum of Natural History in Pittsburgh has shown that by the time of the basilosaurines and dorudontines, the first fully aquatic whales, the ropelike tympanic ligament had probably already evolved. Additionally, air sinuses, presumably filled with spongy tissues, had formed around the middle ear, offering better sound resolution and directional cues for underwater hearing. Meanwhile, with the external ear canal closed off (a prerequisite for deep-sea diving), Luo adds, the lower jaw was taking on an increasingly important auditory role, developing a fat-filled canal capable of conducting sound back to the middle ear.

Later in the evolution of whale hearing, the toothed and baleen whales parted ways. Whereas the toothed whales evolved the features necessary to produce and receive high-frequency sounds, enabling echolocation for hunting, the baleen whales developed the ability to produce and receive very low frequency sounds, allowing them to communicate with one another over vast distances. Fossil whale ear bones, Luo says, show that by around 28 million years ago early odontocetes already had some of the bony structures necessary for hearing high-pitched sound and were thus capable of at least modest echolocation. The origin of the mysticete's low-frequency hearing is far murkier, even though the fossil evidence of that group now dates back to as early as 34 million years ago.

Other notable skull changes include movement of the eye sockets from a crocodilelike placement atop the head in *Pakicetus* and *Ambulocetus* to a lateral position in the more aquatic protocetids and later whales. And the nasal opening migrated back from the tip of the snout in *Pakicetus* to the top of the head in modern cetaceans, forming the blowhole. Whale dentition morphed, too, turning the complexly cusped, grinding molars of primitive mammalian ancestors into the simple, prong-shaped teeth of modern odontocetes, which grasp and swallow their food without chewing. Mysticetes lost their teeth altogether and developed plates of baleen that hang from their upper jaws and strain plankton from the seawater.

The most obvious adaptations making up the whale's protean shift are those that produced its streamlined shape and unmatched swimming abilities. Not surprisingly, some bizarre amphibious forms resulted along the way. *Ambulocetus,* for one, retained the flexible shoulder, elbow, wrist and finger joints of its terrestrial ancestors and had a pelvis capable of supporting its weight on land. Yet the creature's disproportionately large hind limbs and paddlelike feet would have made walking rather awkward. These same features were perfect for paddling around in the fish-filled shallows of Tethys, however.

Moving farther out to sea required additional modifications, many of which appear in the protocetid whales. Studies of one member of this group, *Rodhocetus,* indicate that the lower arm bones were compressed and already on their way to becoming hydrodynamically efficient, says University of Michigan paleontologist William J. Sanders. The animal's long, delicate feet were probably webbed, similar to the fins used by scuba divers. *Rodhocetus* also exhibits aquatic adaptations in its pelvis, where the fusion between the vertebrae that form the sacrum is reduced, loosening up the lower spine to power tail movement. These features, says Gingerich, whose team discovered the creature, suggest that *Rodhocetus* performed a leisurely dog paddle at the sea surface and a swift combination of otterlike hind-limb paddling and tail propulsion underwater. When it



went ashore to breed or perhaps to bask in the sun, he proposes, *Rodhocetus* probably hitched itself around in the manner of a modern eared seal or sea lion.

By the time of the basilosaurines and dorudontines, whales were fully aquatic. As in modern cetaceans, the shoulder remained mobile while the elbow and wrist stiffened, forming flippers for steering and balance. Farther back on the skeleton, only tiny legs remained, and the pelvis had dwindled accordingly. Analyses of the vertebrae of *Dorudon,* conducted by Mark D. Uhen of the Cranbrook Institute of Science in Bloomfield Hills, Mich., have revealed one tail vertebra with a rounded profile. Modern whales have a similarly shaped bone, the ball vertebra, at the base of their fluke—the flat, horizontal structure capping the tail. Uhen thus suspects that basilosaurines and dorudontines had tail flukes and swam much as modern whales do, using so-called caudal oscillation. In this energetically efficient mode of locomotion, motion generated at a single point in the vertebral column powers the tail's vertical movement through the water, and the fluke generates lift.

Exactly when whales lost their legs altogether remains unknown. In fact, a recent discovery made by Lawrence G. Barnes of the Natural History Museum of Los Angeles County hints at surprisingly well developed hind limbs in a 27-million-year-old baleen whale from Washington State, suggesting that whale legs persisted far longer than originally thought. Today, however, some 50 million years after their quadrupedal ancestors first waded into the warm waters of Tethys, whales are singularly sleek. Their hind limbs have shrunk to externally invisible vestiges, and the pelvis has diminished to the point of serving merely as an anchor for a few tiny muscles unrelated to locomotion.

Making Waves

THE FOSSILS UNCOVERED during the 1980s and 1990s advanced researchers' understanding of whale evolution by leaps and bounds, but all morphological signs still pointed to a mesonychid origin. An alternative view of cetacean roots was gaining currency in genetics laboratories in the U.S., Belgium and Japan, however. Molecular biologists, having developed sophisticated techniques for analyzing the DNA of living creatures, took Boyden's 1960s immunology-based conclusions a step further. Not only were whales more closely related to artiodactyls than to any other living mammals, they asserted, but whales were themselves artiodactyls, one of many twigs on that branch of the mammalian family tree. Moreover, a number of these studies pointed to an especially close relationship between whales and hippopotamuses. Particularly strong evidence for this idea came in 1999 from analyses of snippets of noncoding DNA called SINES (short interspersed elements), conducted by Norihiro Okada and his colleagues at the Tokyo Institute of Technology.

The whale-hippo connection did not sit well with paleontologists. "I thought they were nuts," Gingerich recollects. "Everything we'd found was consistent with a mesonychid origin. I was happy with that and happy with a connection through mesonychids to artiodactyls." Whereas mesonychids appeared at the right time, in the right place and in the right form to be considered whale progenitors, the fossil record did not seem to contain a temporally, geographically and morphologically plausible artiodactyl ancestor for whales, never mind one linking whales and hippos specifically. Thewissen, too, had largely dismissed the DNA findings. But "I stopped rejecting it when Okada's SINE work came out," he says.

It seemed the only way to resolve the controversy was to find, of all things, an ancient whale anklebone. Morphologists have traditionally defined artiodactyls on the basis of certain features in one of their anklebones, the astragalus, that enhance mobility. Specifically, the unique artiodactyl astragalus has two grooved, pulleylike joint surfaces. One connects to the tibia, or shinbone; the other articulates with more distal anklebones. If whales descended from artiodactyls, researchers reasoned, those that had not yet fully adapted to life in the sea should exhibit this double-pulleyed astragalus.

That piece of the puzzle appeared in 2001, when Gingerich and Thewissen both announced discoveries of new primitive whale fossils in Pakistan. In the eastern part of Baluchistan Province, Gingerich's team had found partially articulated skeletons of *Rodhocetus balochistanensis* and a new protocetid genus, *Artiocetus*. Thewissen and his colleagues recovered from a bone bed in Punjab much of the long-sought postcranial skeleton of *Pakicetus*, as well as that of a smaller member of the pakicetid family, *Ichthyolestes*. Each came with an astragalus bearing the distinctive artiodactyl characteristics.

The anklebones convinced both longtime proponents of the mesonychid hypothesis that whales instead evolved from artiodactyls. Gingerich has even embraced the hippo idea. Although hippos themselves arose long after whales, their purported ancestors—dog- to horse-size, swamp-dwelling beasts called anthracotheres—date back to at least the Middle Eocene and may thus have a forebear in common with the cetaceans. In fact, Gingerich notes that *Rodhocetus* and anthracotheres share features in their hands and wrists not seen in any other later artiodactyls. Thewissen agrees that the hippo hypothesis holds much more appeal than it once did. But he cautions that the morphological data still do not point to a particular artiodactyl, such as the hippo, being the whale's closest relative, or sister group. "We don't have the resolution yet to get them there," he remarks, "but I think that will come."

What of the evidence that seemed to tie early whales to mesonychids? In light of the recent ankle data, most workers now suspect that those similarities probably reflect convergent evolution rather than shared ancestry and that mesonychids represent an evolutionary dead end. But not everyone is convinced. Maureen O'Leary of Stony Brook University argues that until all the available evidence—both morphological and molecular—is incorporated into a single phylogenetic analysis, the possibility remains that mesonychids belong at the base of the whale pedigree. It is conceivable, she says, that mesonychids are actually ancient artiodactyls but ones that reversed the ankle trend. If so, mesonychids could still be whales' closest relative and hippos could be their closest living relative [*see box on page 44*]. Critics of that idea, however, point out that although folding the mesonychids into the artiodactyl order offers an escape hatch of sorts to supporters of the mesonychid hypothesis, it would upset the long-standing notion that the ankle makes the artiodactyl.

Investigators agree that determining the exact relationship between whales and artiodactyls will most likely require finding additional fossils—particularly those that can illuminate the beginnings of artiodactyls in general and hippos in particular. Yet even with those details still unresolved, "we're really getting a handle on whales from their origin to the end of archaeocetes," Uhen reflects. The next step, he says, will be to figure out how the mysticetes and odontocetes arose from the archaeocetes and when their modern features emerged. Researchers may never solve all the mysteries of whale origins. But if the extraordinary advances made over the past two decades are any indication, with continued probing, answers to many of these lingering questions will surface from the sands of time.

Kate Wong is editorial director of ScientificAmerican.com

WATER, WATER EVERYWHERE

MOST MAMMALS—big ones in particular—cannot live without freshwater. For marine mammals, however, freshwater is difficult to come by. Seals and sea lions obtain most of their water from the fish they eat (some will eat snow to get freshwater), and manatees routinely seek out freshwater from rivers. For their part, cetaceans obtain water both from their food and from sips of the briny deep.

When did whales, which evolved from a fairly large (and therefore freshwater-dependent) terrestrial mammal, develop a system capable of handling the excess salt load associated with ingesting seawater? Evidence from so-called stable oxygen isotopes has provided clues. In nature, oxygen mainly occurs in two forms, or isotopes: ^{16}O and ^{18}O. The ratios of these isotopes in freshwater and seawater differ, with seawater containing more ^{18}O. Because mammals incorporate oxygen from drinking water into their developing teeth and bones, the remains of those that imbibe seawater can be distinguished from those that take in freshwater.

J.G.M. (Hans) Thewissen of the Northeastern Ohio Universities College of Medicine and his colleagues thus analyzed the oxygen isotope ratios in ancient whale teeth to gain insight into when these animals might have moved from a freshwater-based osmoregulatory system to a seawater-based one. Oxygen isotope values for pakicetids, the most primitive whales, indicate that they drank freshwater, as would be predicted from other indications that these animals spent much of their time on land. Isotope measurements from amphibious *Ambulocetus,* on the other hand, vary widely, and some specimens show no evidence of seawater intake. In explanation, the researchers note that although *Ambulocetus* is known to have spent time in the sea (based on the marine nature of the rocks in which its fossils occur), it may still have had to go ashore to drink. Alternatively, it may have spent the early part of its life (when its teeth mineralized) in freshwater and only later entered the sea.

The protocetids, however, which show more skeletal adaptations to aquatic life, exhibit exclusively marine isotope values, indicating that they drank only seawater. Thus, just a few million years after the first whales evolved, their descendants had adapted to increased salt loads. This physiological innovation no doubt played an important role in facilitating the protocetids' dispersal across the globe. *—K.W.*

MORE TO EXPLORE

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AN ANCESTOR TO CALL OUR OWN

BY KATE WONG

Controversial new fossils could bring scientists closer than ever to the origin of humanity

POITIERS, FRANCE—Michel Brunet removes the cracked, brown skull from its padlocked, foam-lined metal carrying case and carefully places it on the desk in front of me. It is about the size of a coconut, with a slight snout and a thick brow visoring its stony sockets. To my inexpert eye, the face is at once foreign and inscrutably familiar. To Brunet, a paleontologist at the University of Poitiers, it is the visage of the lost relative he has sought for 26 years. "He is the oldest one," the veteran fossil hunter murmurs, "the oldest hominid."

Brunet and his team set the field of paleoanthropology abuzz when they unveiled their find last July. Unearthed from sandstorm-scoured deposits in northern Chad's Djurab Desert, the astonishingly complete cranium—dubbed *Sahelanthropus tchadensis* (and nicknamed Toumaï, which means "hope of life" in the local Goran language)—dates to nearly seven million years ago. It may thus represent the earliest human forebear on record, one who Brunet says "could touch with his finger" the point at which our lineage and the one leading to our closest living relative, the chimpanzee, diverged.

KAZUHIKO SANO

APE OR ANCESTOR? *Sahelanthropus tchadensis,* potentially the oldest hominid on record, forages in a woodland bordering Lake Chad some seven million years ago. Thus far the creature is known only from cranial and dental remains, so its body in this artist's depiction is entirely conjectural.

Less than a century ago simian human precursors from Africa existed only in the minds of an enlightened few. Charles Darwin predicted in 1871 that the earliest ancestors of humans would be found in Africa, where our chimpanzee and gorilla cousins live today. But evidence to support that idea didn't come until more than 50 years later, when anatomist Raymond Dart of the University of the Witwatersrand described a fossil skull from Taung, South Africa, as belonging to an extinct human he called *Australopithecus africanus,* the "southern ape from Africa." His claim met variously with frosty skepticism and outright rejection—the remains were those of a juvenile gorilla, critics countered. The discovery of another South African specimen, now recognized as *A. robustus,* eventually vindicated Dart, but it wasn't until the 1950s that the notion of ancient, apelike human ancestors from Africa gained widespread acceptance.

In the decades that followed, pioneering efforts in East Africa headed by members of the Leakey family, among others, turned up additional fossils. By the late 1970s the australopithecine cast of characters had grown to include *A. boisei, A. aethiopicus* and *A. afarensis* (Lucy and her kind, who lived between 2.9 million and 3.6 million years ago during the Pliocene epoch and gave rise to our own genus, *Homo*). Each was adapted to its own environmental niche, but all were bipedal creatures with thick jaws, large molars and small canines—radically different from the generalized, quadrupedal Miocene apes known from farther back on the family tree. To probe human origins beyond *A. afarensis,* however, was to fall into a gaping hole in the fossil record between 3.6 million and 12 million years ago. Who, researchers wondered, were Lucy's forebears?

Despite widespread searching, diagnostic fossils of the right age to answer that question eluded workers for nearly two decades. Their luck finally began to change around the mid-1990s, when a team led by Meave Leakey of the National Museums of Kenya announced its discovery of *A. anamensis,* a four-million-year-old species that, with its slightly more archaic characteristics, made a reasonable ancestor for Lucy [see "Early Hominid Fossils from Africa," by Meave Leakey and Alan Walker; Scientific American, June 1997]. At around

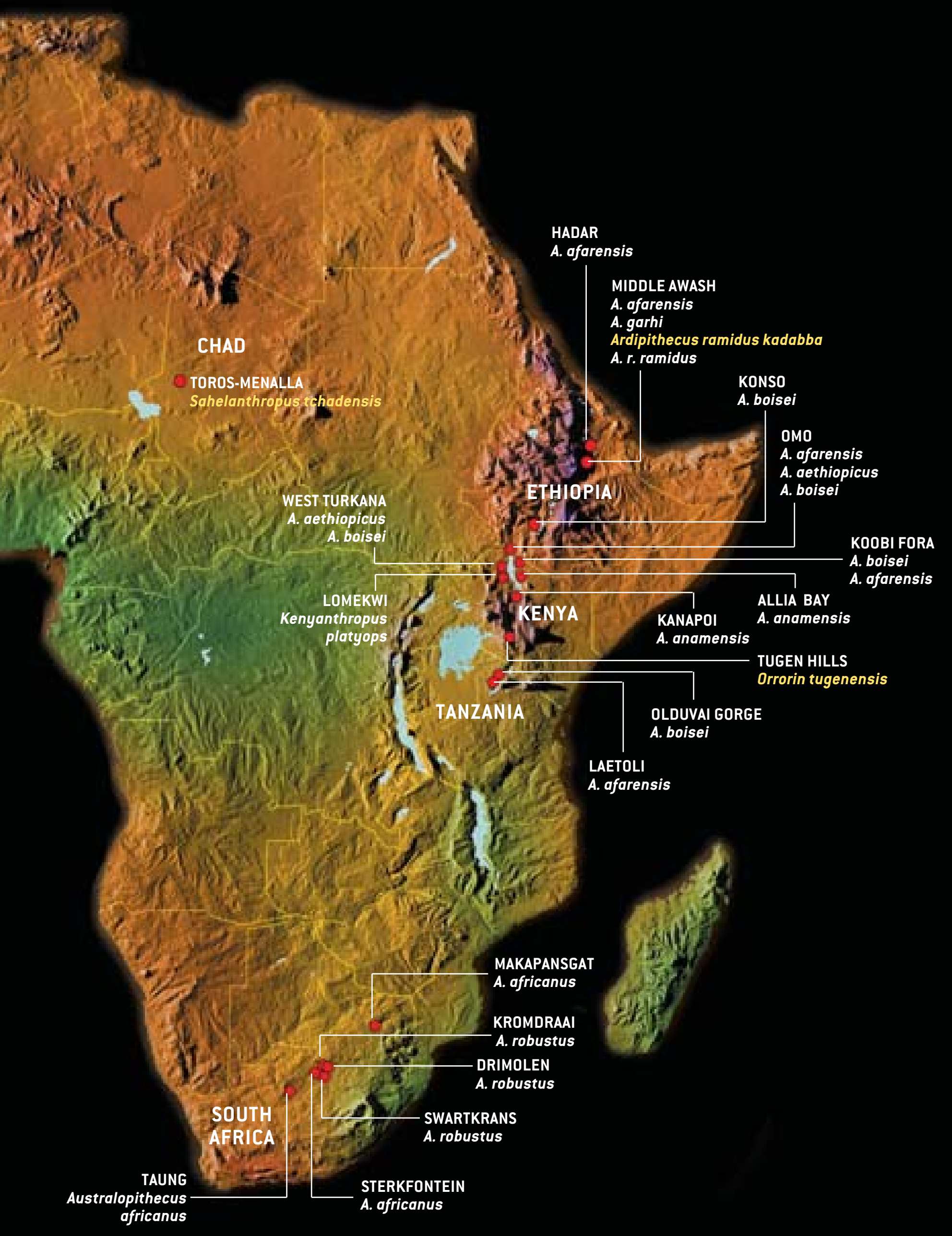
Overview/*The Oldest Hominids*

- The typical textbook account of human evolution holds that humans arose from a chimpanzeelike ancestor between roughly five million and six million years ago in East Africa and became bipedal on the savanna. But until recently, hominid fossils more than 4.4 million years old were virtually unknown.
- Newly discovered fossils from Chad, Kenya and Ethiopia may extend the human record back to seven million years ago, revealing the earliest hominids yet.
- These finds cast doubt on conventional paleoanthropological wisdom. But experts disagree over how these creatures are related to humans—if they are related at all.

African Roots

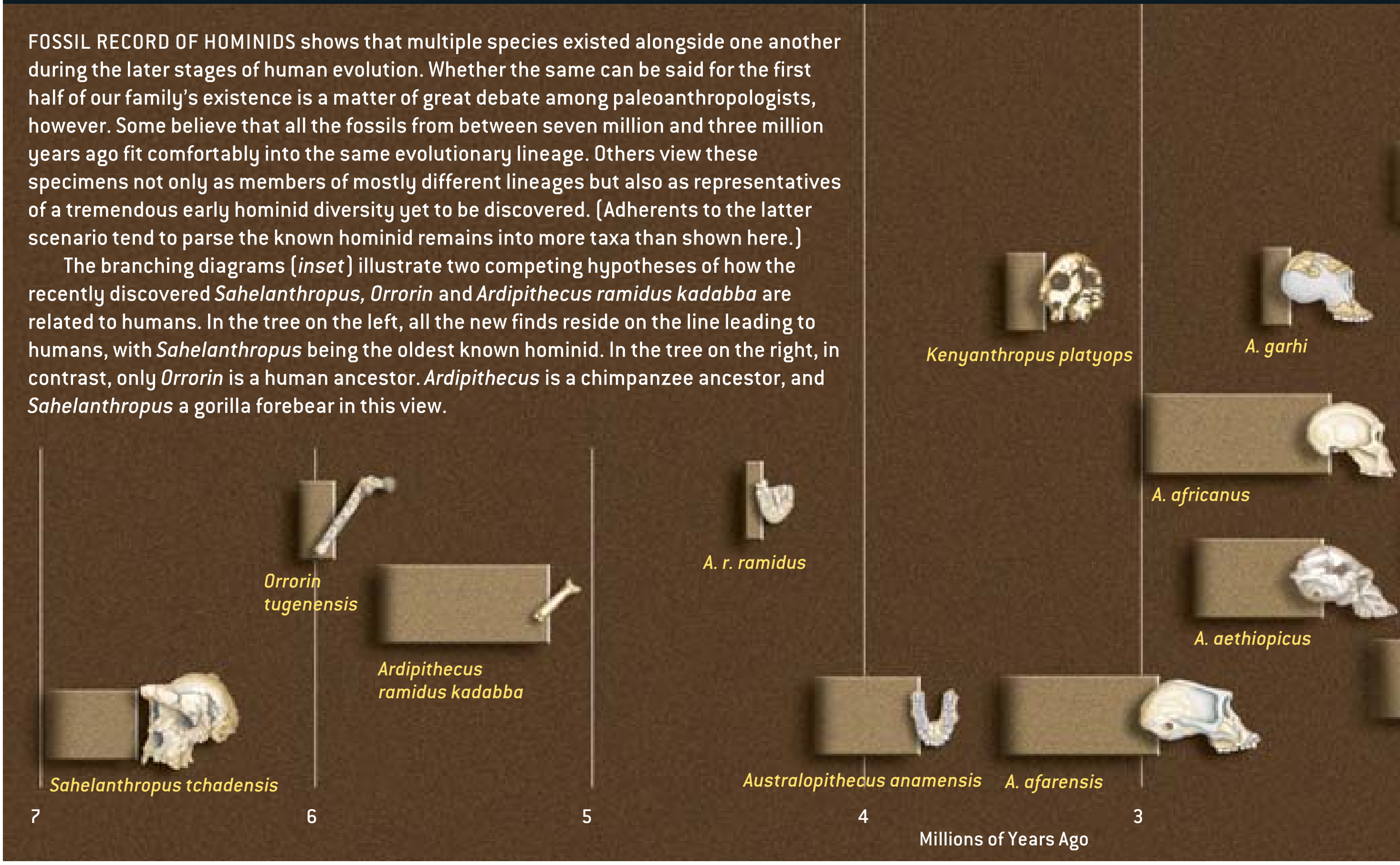
RECENT FINDS from Africa could extend in time and space the fossil record of early human ancestors. Just a few years ago, remains more than 4.4 million years old were essentially unknown, and the oldest specimens all came from East Africa. In 2001 paleontologists working in Kenya's Tugen Hills and Ethiopia's Middle Awash region announced that they had discovered hominids dating back to nearly six million years ago (*Orrorin tugenensis* and *Ardipithecus ramidus kadabba,* respectively). Then, last July, University of Poitiers

paleontologist Michel Brunet and his Franco-Chadian Paleoanthropological Mission reported having unearthed a nearly seven-million-year-old hominid, called *Sahelanthropus tchadensis,* at a site known as Toros-Menalla in northern Chad. The site lies some 2,500 kilometers west of the East African fossil localities. “I think the most important thing we have done in terms of trying to understand our story is to open this new window,” Brunet remarks. “We are proud to be the pioneers of the West.”



EDWARD BELL

Hominids in Time



FOSSIL RECORD OF HOMINIDS shows that multiple species existed alongside one another during the later stages of human evolution. Whether the same can be said for the first half of our family's existence is a matter of great debate among paleoanthropologists, however. Some believe that all the fossils from between seven million and three million years ago fit comfortably into the same evolutionary lineage. Others view these specimens not only as members of mostly different lineages but also as representatives of a tremendous early hominid diversity yet to be discovered. (Adherents to the latter scenario tend to parse the known hominid remains into more taxa than shown here.)

The branching diagrams (*inset*) illustrate two competing hypotheses of how the recently discovered *Sahelanthropus, Orrorin* and *Ardipithecus ramidus kadabba* are related to humans. In the tree on the left, all the new finds reside on the line leading to humans, with *Sahelanthropus* being the oldest known hominid. In the tree on the right, in contrast, only *Orrorin* is a human ancestor. *Ardipithecus* is a chimpanzee ancestor, and *Sahelanthropus* a gorilla forebear in this view.

the same time, Tim D. White of the University of California at Berkeley and his colleagues described a collection of 4.4-million-year-old fossils from Ethiopia representing an even more primitive hominid, now known as *Ardipithecus ramidus ramidus*. Those findings gave scholars a tantalizing glimpse into Lucy's past. But estimates from some molecular biologists of when the chimp-human split occurred suggested that even older hominids lay waiting to be discovered.

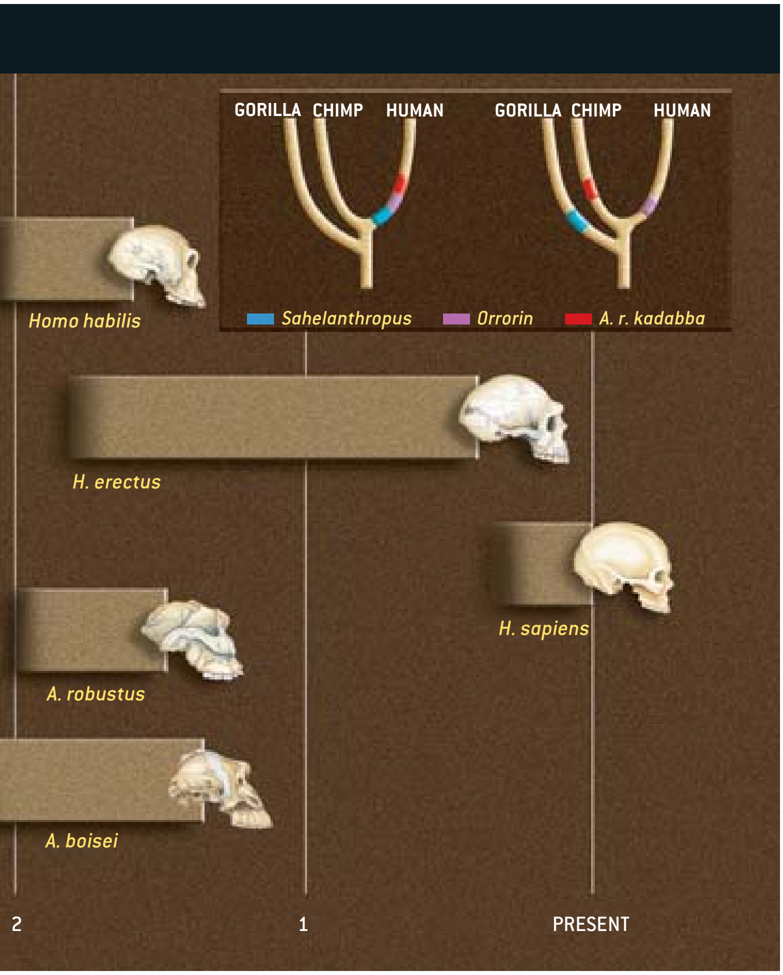
Those predictions have recently been borne out. Over the past few years, researchers have made a string of stunning discoveries—Brunet's among them—that may go a long way toward bridging the remaining gap between humans and their African ape ancestors. These fossils, which range from roughly five million to seven million years old, are upending long-held ideas about when and where our lineage arose and what the last common ancestor of humans and chimpanzees looked like. Not surprisingly, they have also sparked vigorous debate. Indeed, experts are deeply divided over where on the family tree the new species belong and even what constitutes a hominid in the first place.

Standing Tall

THE FIRST HOMINID CLUE to come from beyond the 4.4-million-year mark was announced in the spring of 2001. Paleontologists Martin Pickford and Brigitte Senut of the National Museum of Natural History in Paris found in Kenya's Tugen Hills the six-million-year-old remains of a creature they called *Orrorin tugenensis*. To date the researchers have amassed 19 specimens, including bits of jaw, isolated teeth, finger and arm bones, and some partial upper leg bones, or femurs. According to Pickford and Senut, *Orrorin* exhibits several characteristics that clearly align it with the hominid family—notably those suggesting that, like all later members of our group, it walked on two legs. "The femur is remarkably humanlike," Pickford observes. It has a long femoral neck, which would have placed the shaft at an angle relative to the lower leg (thereby stabilizing the hip), and a groove on the back of that femoral neck, where a muscle known as the obturator externus pressed against the bone during upright walking. In other respects, *Orrorin* was a primitive animal: its canine teeth are large and pointed relative to human canines, and its arm and finger bones retain adaptations for climbing. But the femur characteristics signify to Pickford and Senut that when it was on the ground, *Orrorin* walked like a man.

In fact, they argue, *Orrorin* appears to have had a more hu-

ILLUSTRATIONS BY PATRICIA J. WYNNE AND CORNELIA BLIK



manlike gait than the much younger Lucy did. Breaking with paleoanthropological dogma, the team posits that *Orrorin* gave rise to *Homo* via the proposed genus *Praeanthropus* (which comprises a subset of the fossils currently assigned to *A. afarensis* and *A. anamensis*), leaving Lucy and her kin on an evolutionary sideline. *Ardipithecus,* they believe, was a chimpanzee ancestor.

Not everyone is persuaded by the femur argument. C. Owen Lovejoy of Kent State University counters that published computed tomography scans through *Orrorin*'s femoral neck—which Pickford and Senut say reveal humanlike bone structure—actually show a chimplike distribution of cortical bone, an important indicator of the strain placed on that part of the femur during locomotion. Cross sections of *A. afarensis*'s femoral neck, in contrast, look entirely human, he states. Lovejoy suspects that *Orrorin* was frequently—but not habitually—bipedal and spent a significant amount of time in the trees. That wouldn't exclude it from hominid status, because full-blown bipedalism almost certainly didn't emerge in one fell swoop. Rather *Orrorin* may have simply not yet evolved the full complement of traits required for habitual bipedalism. Viewed that way, *Orrorin* could still be on the ancestral line, albeit further removed from *Homo* than Pickford and Senut would have it.

Better evidence of early routine bipedalism, in Lovejoy's view, surfaced a few months after the *Orrorin* report, when Berkeley graduate student Yohannes Haile-Selassie announced the discovery of slightly younger fossils from Ethiopia's Middle Awash region. Those 5.2-million- to 5.8-million-year-old remains, which have been classified as a subspecies of *Ardipithecus ramidus, A. r. kadabba,* include a complete foot phalanx, or toe bone, bearing a telltale trait. The bone's joint is angled in precisely the way one would expect if *A. r. kadabba* "toed off" as humans do when walking, reports Lovejoy, who has studied the fossil.

Other workers are less impressed by the toe morphology. "To me, it looks for all the world like a chimpanzee foot phalanx," comments David Begun of the University of Toronto, noting from photographs that it is longer, slimmer and more curved than a biped's toe bone should be. Clarification may come when White and his collaborators publish findings on an as yet undescribed partial skeleton of *Ardipithecus,* which White says they hope to do within the next year or two.

Differing anatomical interpretations notwithstanding, if either *Orrorin* or *A. r. kadabba* were a biped, that would not only push the origin of our strange mode of locomotion back by nearly 1.5 million years, it would also lay to rest a popular idea about the conditions under which our striding gait evolved. Received wisdom holds that our ancestors became bipedal on the African savanna, where upright walking may have kept the blistering sun off their backs, given them access to previously out-of-reach foods, or afforded them a better view above the tall grass. But paleoecological analyses indicate that *Orrorin* and *Ardipithecus* dwelled in forested habitats, alongside monkeys and other typically woodland creatures. In fact, Giday WoldeGabriel of Los Alamos National Laboratory and his colleagues, who studied the soil chemistry and animal remains at the *A. r. kadabba* site, have noted that early hominids may not have ventured beyond these relatively wet and wooded settings until after 4.4 million years ago.

If so, climate change may not have played as important a role in driving our ancestors from four legs to two as has been thought. For his part, Lovejoy observes that a number of the savanna-based hypotheses focusing on posture were not especially well conceived to begin with. "If your eyes were in your toes, you could stand on your hands all day and look over tall grass, but you'd never evolve into a hand-walker," he jokes. In other words, selection for upright posture alone would not, in his view, have led to bipedal locomotion. The most plausible explanation for the emergence of bipedalism, Lovejoy says, is that it freed the hands and allowed males to collect extra food with which to woo mates. In this model, which he developed in the 1980s, females who chose good providers could devote more energy to child rearing, thereby maximizing their reproductive success.

The Oldest Ancestor?

THE PALEOANTHROPOLOGICAL community was still digesting the implications of the *Orrorin* and *A. r. kadabba* discoveries when Brunet's fossil find from Chad came to light. With *Sahelanthropus* have come new answers—and new ques-

Humanity may have arisen more than a million years earlier than a number of molecular studies had estimated. More important, it may have originated in a different locale.

tions. Unlike *Orrorin* and *A. r. kadabba,* the *Sahelanthropus* material does not include any postcranial bones, making it impossible at this point to know whether the animal was bipedal, the traditional hallmark of humanness. But Brunet argues that a suite of features in the teeth and skull, which he believes belongs to a male, judging from the massive brow ridge, clearly links this creature to all later hominids. Characteristics of *Sahelanthropus*'s canines are especially important in his assessment. In all modern and fossil apes, and therefore presumably in the last common ancestor of chimps and humans, the large upper canines are honed against the first lower premolars, producing a sharp edge along the back of the canines. This so-called honing canine-premolar complex is pronounced in males, who use their canines to compete with one another for females. Humans lost these fighting teeth, evolving smaller, more incisorlike canines that occlude tip to tip, an arrangement that creates a distinctive wear pattern over time. In their size, shape and wear, the *Sahelanthropus* canines are modified in the human direction, Brunet asserts.

At the same time, *Sahelanthropus* exhibits a number of apelike traits, such as its small braincase and widely spaced eye sockets. This mosaic of primitive and advanced features, Brunet says, suggests a close relationship to the last common ancestor. Thus, he proposes that *Sahelanthropus* is the earliest member of the human lineage and the ancestor of all later hominids, including *Orrorin* and *Ardipithecus*. If Brunet is correct, humanity may have arisen more than a million years earlier than a number of molecular studies had estimated. More important, it may have originated in a different locale than has been posited. According to one model of human origins, put forth in the 1980s by Yves Coppens of the College of France, East Africa was the birthplace of humankind. Coppens, noting that the oldest human fossils came from East Africa, proposed that the continent's Rift Valley—a gash that runs from north to south—split a single ancestral ape species into two populations. The one in the east gave rise to humans; the one in the west spawned today's apes [see "East Side Story: The Origin of Humankind," by Yves Coppens; Scientific American, May 1994]. Scholars have recognized for some time that the apparent geographic separation might instead be an artifact of the scant fossil record. The discovery of a seven-million-year-old hominid in Chad, some 2,500 kilometers west of the Rift Valley, would deal the theory a fatal blow.

Most surprising of all may be what *Sahelanthropus* reveals about the last common ancestor of humans and chimpanzees. Paleoanthropologists have typically imagined that that creature resembled a chimp in having, among other things, a strongly projecting lower face, thinly enameled molars and large canines. Yet *Sahelanthropus,* for all its generally apelike traits, has only a moderately prognathic face, relatively thick enamel, small canines and a brow ridge larger than that of any living ape. "If *Sahelanthropus* shows us anything, it shows us that the last common ancestor was not a chimpanzee," Berkeley's White remarks. "But why should we have expected otherwise?" Chimpanzees have had just as much time to evolve as humans have had, he points out, and they have become highly specialized, fruit-eating apes.

Brunet's characterization of the Chadian remains as those of a human ancestor has not gone unchallenged, however. "Why *Sahelanthropus* is necessarily a hominid is not particularly clear," comments Carol V. Ward of the University of Missouri. She and others are skeptical that the canines are as humanlike as Brunet claims. Along similar lines, in a letter published last October in the journal *Nature,* in which Brunet's team initially reported its findings, University of Michigan paleoanthropologist Milford H. Wolpoff, along with *Orrorin* discoverers Pickford and Senut, countered that *Sahelanthropus* was an ape rather than a hominid. The massive brow and certain features on the base and rear of *Sahelanthropus*'s skull, they observed, call to mind the anatomy of a quadrupedal ape with a difficult-to-chew diet, whereas the small canine suggests that it was a female of such a species, not a male human ancestor. Lacking proof that *Sahelanthropus* was bipedal, so their reasoning goes, Brunet doesn't have a leg to stand on. (Pickford and Senut further argue that the animal was specifically a gorilla ancestor.) In a barbed response, Brunet likened his detractors to those Dart encountered in 1925, retorting that *Sahelanthropus*'s apelike traits are simply primitive holdovers from its own ape predecessor and therefore uninformative with regard to its relationship to humans.

The conflicting views partly reflect the fact that researchers disagree over what makes the human lineage unique. "We have trouble defining hominids," acknowledges Roberto Macchiarelli, also at the University of Poitiers. Traditionally paleoanthropologists have regarded bipedalism as the characteristic that first set human ancestors apart from other apes. But subtler changes—the metamorphosis of the canine, for instance—may have preceded that shift.

To understand how animals are related to one another, evolutionary biologists employ a method called cladistics, in which organisms are grouped according to shared, newly evolved traits. In short, creatures that have these derived characteristics in common are deemed more closely related to one another than they are to those that exhibit only primitive traits inherited from a more distant common ancestor. The first occurrence in the fossil record of a shared, newly acquired trait serves as a baseline indicator of the biological division of an ancestral species into two daughter species—in this case, the point at which chimps and humans diverged from their common ancestor—and that trait is considered the defining characteristic of the group.

Thus, cladistically "what a hominid is from the point of view of skeletal morphology is summarized by those characters preserved in the skeleton that are present in populations that directly succeeded the genetic splitting event between chimps and humans," explains William H. Kimbel of Arizona State University. With only an impoverished fossil record to work from, paleontologists can't know for certain what those traits were. But the two leading candidates for the title of seminal hominid characteristic, Kimbel says, are bipedalism and the transformation of the canine. The problem researchers now face in trying to suss out what the initial changes were and which, if any, of the new putative hominids sits at the base of the human clade is that so far *Orrorin, A. r. kadabba* and *Sahelanthropus* are represented by mostly different bony elements, making comparisons among them difficult.

How Many Hominids?

MEANWHILE THE ARRIVAL of three new taxa to the table has intensified debate over just how diverse early hominids were. Experts concur that between three million and 1.5 million years ago, multiple hominid species existed alongside one another at least occasionally. Now some scholars argue that this rash of discoveries demonstrates that human evolution was a complex affair from the outset. Toronto's Begun—who believes that the Miocene ape ancestors of modern African apes and humans spent their evolutionarily formative years in Europe and western Asia before reentering Africa—observes that *Sahelanthropus* bears exactly the kind of motley features that one would expect to see in an animal that was part of an adaptive radiation of apes moving into a new milieu. "It would not surprise me if there were 10 or 15 genera of things that are more closely related to *Homo* than to chimps," he says. Likewise, in a commentary that accompanied the report by Brunet and his team in *Nature,* Bernard Wood of George Washington University wondered whether *Sahelanthropus* might hail from the African ape equivalent of Canada's famed Burgess Shale, which has yielded myriad invertebrate fossils from the Cambrian period, when the major modern animal groups exploded into existence. Viewed that way, the human evolutionary tree would look more like an unkempt bush, with some, if not all, of the new discoveries occupying terminal twigs instead of coveted spots on the meandering line that led to humans.

Other workers caution against inferring the existence of multiple, coeval hominids on the basis of what has yet been found. "That's *X-Files* paleontology," White quips. He and Brunet both note that between seven million and four million years ago, only one hominid species is known to have existed at any given time. "Where's the bush?" Brunet demands. Even at humanity's peak diversity, two million years ago, White says, there were only three taxa sharing the landscape. "That ain't the Cambrian explosion," he remarks dryly. Rather, White suggests, there is no evidence that the base of the family tree is anything other than a trunk. He thinks that the new finds might all represent snapshots of the *Ardipithecus* lineage through time, with *Sahelanthropus* being the earliest hominid and with *Orrorin* and *A. r. kadabba* representing its lineal descendants. (In this configuration, *Sahelanthropus* and *Orrorin* would become species of *Ardipithecus.*)

Investigators agree that more fossils are needed to elucidate how *Orrorin, A. r. kadabba* and *Sahelanthropus* are related to one another and to ourselves, but obtaining a higher-resolution picture of the roots of humankind won't be easy. "We're going to have a lot of trouble diagnosing the very earliest members of our clade the closer we get to that last common ancestor," Missouri's Ward predicts. Nevertheless, "it's really important to sort out what the starting point was," she observes. "Why the human lineage began is the question we're trying to answer, and these new finds in some ways may hold the key to answering that question—or getting closer than we've ever gotten before."

It may be that future paleoanthropologists will reach a point at which identifying an even earlier hominid will be well nigh impossible. But it's unlikely that this will keep them from trying. Indeed, it would seem that the search for the first hominids is just heating up. "The *Sahelanthropus* cranium is a messenger [indicating] that in central Africa there is a desert full of fossils of the right age to answer key questions about the genesis of our clade," White reflects. For his part, Brunet, who for more than a quarter of a century has doggedly pursued his vision through political unrest, sweltering heat and the blinding sting of an unrelenting desert wind, says that ongoing work in Chad will keep his team busy for years to come. "This is the beginning of the story," he promises, "just the beginning." As I sit in Brunet's office contemplating the seven-million-year-old skull of *Sahelanthropus,* the fossil hunter's quest doesn't seem quite so unimaginable. Many of us spend the better part of a lifetime searching for ourselves. SA

Kate Wong is editorial director of ScientificAmerican.com

MORE TO EXPLORE

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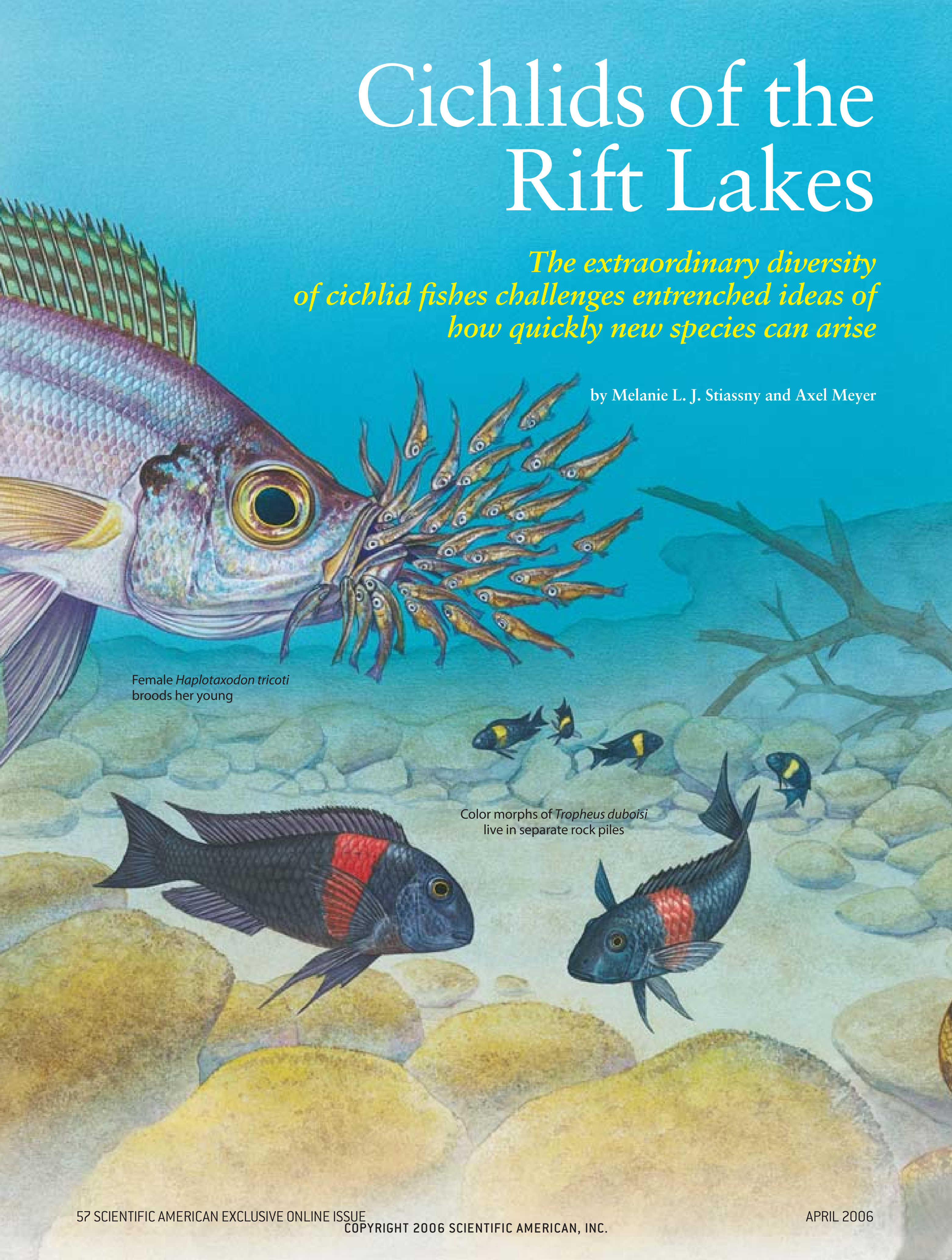
Cichlids of the Rift Lakes

The extraordinary diversity of cichlid fishes challenges entrenched ideas of how quickly new species can arise

by Melanie L. J. Stiassny and Axel Meyer

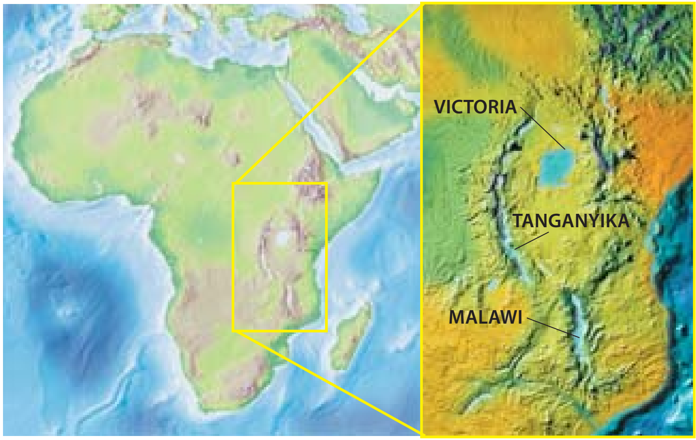


Female *Haplotaxodon tricoti* broods her young

Color morphs of *Tropheus duboisi* live in separate rock piles

LAKE TANGANYIKA'S rocky edges are home to hundreds of species of cichlids, each adapted to an exceedingly narrow ecological niche.

ROBERTO OSTI



EAST AFRICAN LAKES Tanganyika, Malawi and Victoria contain the greatest diversity of cichlid species. The family is spread, however, over the warm waters of much of the globe.

The waters of Lake Tanganyika are clear, dark and deep, but the shallow, sunlit edges are where most of the cichlids live. Brown or green *Eretmodus* algae scrapers, covered with blue spots, thrive among the breaking waves; the turbulent water pushes their rounded backs onto the rock surfaces instead of pulling them off. These fish nip algae off the rocks with their chisel-like teeth. Their neighbors the *Tanganicodus* insect pickers also have round backs. But the pointed heads, sharp snouts and long, fine teeth of these cichlids are adapted to plucking insect larvae from within the crevices.

In calmer waters, old snail shells are strewn on sandy shelves between the boulders. Inside these live tiny female *Lamprologus* cichlids, along with their eggs and young. The yellow, green or brown males are too large to enter the abode. Instead they steal shells—sometimes with females inside—from one another, and posture and preen around their harems.

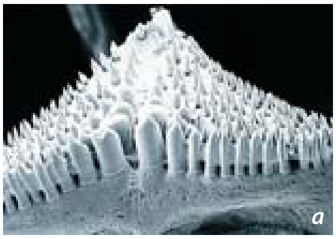
Other algae scrapers, of the genus *Tropheus,* also hover among sheltering rocks. Sometimes a cluster of boulders is separated from another by a sandbank a few hundred feet wide, far too exposed for a small fish to cross safely. As a result, *Tropheus* cichlids in scattered rock piles have evolved much like Charles Darwin's finches on islands of the Galápagos: diverging wildly in their isolation. In a certain rock outcrop one might find a black *Tropheus* with vertical yellow bars; in another, an identical fish but for white and blue bars. In all, researchers have identified almost 100 of these "color morphs."

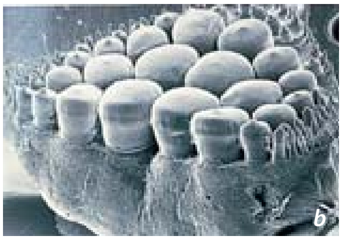
All in the Family

The exceptional diversity of the family Cichlidae has elevated it to the status of an icon in textbooks of evolutionary biology. Cichlids are spiny-rayed freshwater fishes that come in a vast assortment of colors, forms and habits. They are indigenous to warm rivers and lakes in Africa, Madagascar, southern India, Sri Lanka and South and Central America—with one species, the Texas cichlid, making it into North America. Most of these regions were part of the ancient southern continent of Gondwana, which fragmented 180 million years ago; the observation suggests an ancient lineage for the family. (Curiously, the fossil record is silent on this issue until the past 30 million years.)

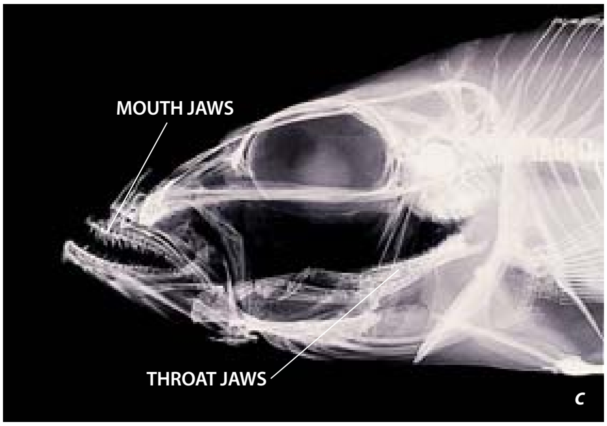
Research by one of us (Stiassny) has identified 15 species of cichlids in Madagascar, and three species are known in southern India. These fishes appear to be survivors from the very earliest lineages. (Many such ancient species survive in Madagascar, which their competitors, evolving in Africa, could not reach; India, too, was isolated for millions of years.) The Americas contain approximately 300 species. But by far the most abundant diversity of cichlids occurs in Africa, in particular the great East African lakes of Victoria, Malawi and Tanganyika.

Geologic data indicate that Lake Victoria, shaped like a saucer the size of Ireland, formed between 250,000 and 750,000 years ago; it contains more than 400 species of cichlids. Lakes Malawi and Tanganyika are narrow and extremely deep, for they fill the rift between the





AXEL MEYER



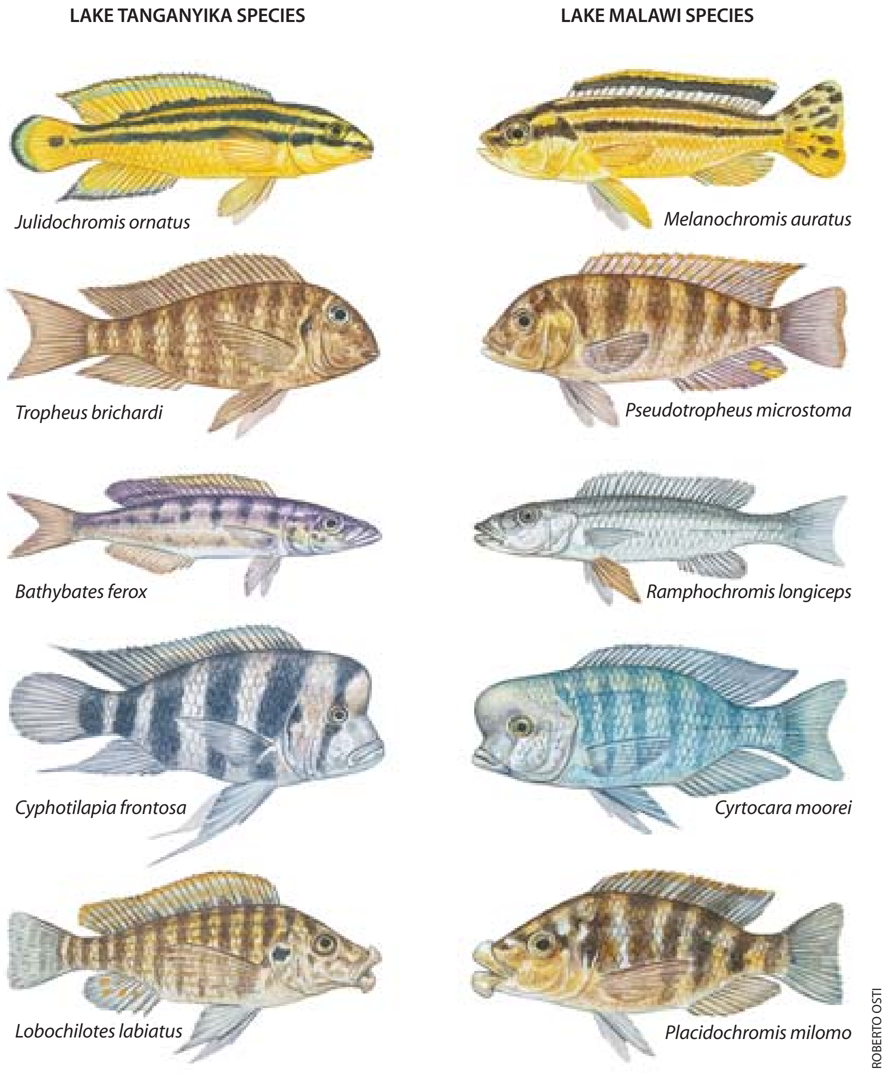
MELANIE L. J. STIASSNY

CICHLID ANATOMY is astonishingly adaptable. Teeth of *Cichlasoma citrinellum* can take the form of sharp piercers (*a*) or flat crushers (*b*). The radiograph (*c*) shows the two sets of jaws of a cichlid.

East African and Central African tectonic plates. Malawi is about four million years old and contains 300 to 500 cichlid species, whereas Tanganyika is nine to 12 million years old and has some 200 species. It turns out, however, that despite the advanced age of the cichlid family and of their native lakes, their amazing variety arose only in the past few million years.

Several factors are believed to lie behind the diversity of cichlids. One has to do with anatomy. Cichlids possess two sets of jaws: one in the mouth, to suck, scrape or bite off bits of food, and another in the throat, to crush, macerate, slice or pierce the morsel before it is ingested. They are the only freshwater fishes to possess such a modified second set of jaws, which are essentially remodeled gill arches (series of bones that hold the gills). Both sets of jaws are exceedingly manipulable and adaptable: one of us (Meyer) has shown that they can change form even within the lifetime of a single animal. (Even the teeth might transform, so that sharp, pointed piercers become flat, molarlike crushers.) Cichlids that are fed one kind of diet rather than another can turn out to look very different.

The two sets of jaws, fine-tuned according to food habits, allow each species to occupy its own very specific ecological niche. In this manner, hundreds of species can coexist without directly competing. If instead these cichlids had tried to exploit the same resources, most would have been driven to extinction.



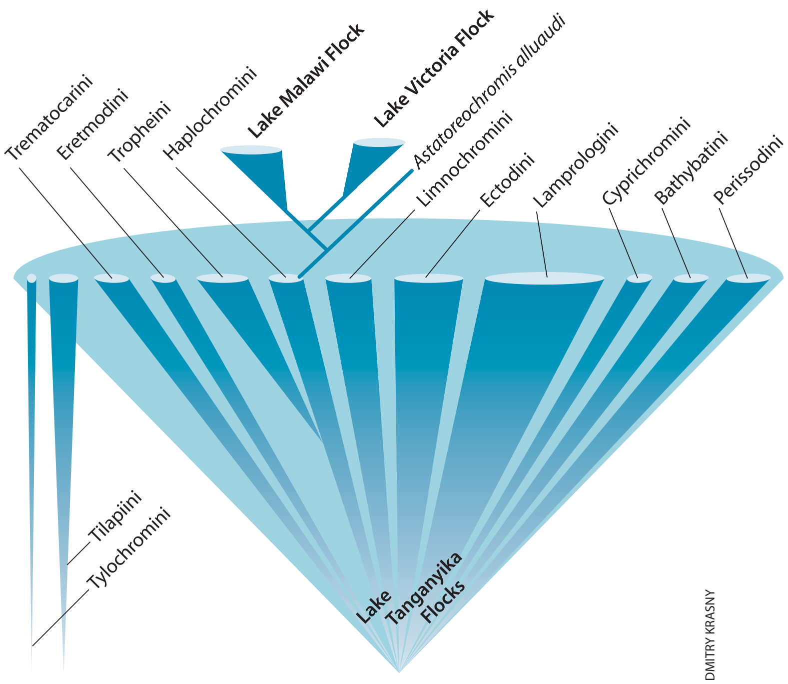
ROBERTO OSTI

DISTANTLY RELATED CICHLIDS from Lakes Tanganyika and Malawi have evolved to become uncannily alike by virtue of occupying similar ecological niches. They demonstrate how morphological resemblance may have little correlation with genetic closeness or evolutionary lineage (phylogenetic relationship). All the cichlids of Lake Malawi are more closely related to one another than to any cichlids in Lake Tanganyika.

One instance of such feeding specialization relates to the scale eaters. These cichlids, found in all three East African lakes, approach other cichlids from behind and rasp a mouthful of scales from their sides. Lake Tanganyika has seven such species, in the genus *Perissodus*. Michio Hori of Kyoto University discovered that *P. microlepis* scale eaters exist in two distinct forms, sporting heads and jaws curved either to the right or to the left. The fish not only feed on scales, and only on scales, but are specialized to scrape scales off only one side: the left-handed fish attack the right sides of their victims, and the right-handed ones the left sides. This astonishing asymmetry in morphology even within the same species very likely evolved because a twisted head allows the fish to grasp scales more efficiently. Inside the throat, the scales are stacked like leaves of a book by the second set of jaws before being ingested as packets of protein.

(The victims survive, though becoming wary of attackers from either side. If the population of left-handed scale eaters were to exceed that of right-handed scale eaters, however, the fish would become more wary of attacks from the right side. As a result, the right-handed scale eaters would have an advantage, and their population would increase. These forces ensure that the relative populations of left- and right-handed fish remain roughly equal.)

Another factor that has allowed cichlids to exploit a variety of habitats—and again, diversify—is their reproductive behavior. Nothing sets cichlids apart from other fishes more than the time and energy that they invest in their young. All cichlids care for their broods long



FAMILY TREE shows that cichlids of Lakes Malawi and Victoria probably descended from a single lineage of mouth brooders (Haplochromini) that escaped from Lake Tanganyika. The cichlids of the last, most ancient, lake display the largest degree of genetic diversity. The cross sections of the cones roughly indicate the number of species within a tribe.

after hatching, and the protracted association between parents and offspring involves elaborate communication. Whereas the fertilized eggs can be guarded by a single parent, once the brood becomes mobile both parents are often necessary. And then a fascinating assortment of social systems—monogamy, polyandry, even polygyny—come into play.

One strategy common to many cichlids is to hold fertilized eggs or young in their mouths. In this way, the fishes provide a safe haven into which their offspring can retreat when danger threatens. Moreover, the parent might graze algae or ingest other foods, nourishing the young inside its mouth. Many cichlid species will, like the cuckoo, sneak their fertilized eggs or young in with the broods of other cichlid parents and thereby relieve themselves of the effort required to raise offspring.

The mouth brooders lay far fewer eggs than other fishes—sometimes no more than 10—and so invest much time and energy per offspring. Moreover, the total population of a mouth-brooding species is often small, so that a few hundred fish living in one rock outcrop might constitute a species. Any mutation is likely to spread faster through a small population than a large one and to lead to differentiation of a species. Therefore, the limited population sizes favored by mouth brooding may have contributed to the diversification of cichlids.

In the East African lakes, males of mouth-brooding cichlids do not take care of offspring but vie with one another to fertilize the most eggs. Sometimes they form congregations, called leks, in which they dart and posture to attract females. A lek might consist of 20 to 50 males, but in some species more than 50,000 have been observed. Or the males—such as those of *Ophthalmotilapia,* with their flashy peacock colors—might construct elaborate bowers over which they display for females. Individuals typically weighing about 10 ounces might move upwards of 25 pounds of sand and gravel in constructing a bower. When a female is enticed to lay a few eggs over his bower (she usually picks the largest), the male quickly fertilizes them; she then takes the eggs into her mouth and swims on, looking for another male.

Female cichlids are often a drab gray or brown, but males tend to be brilliantly colored. The diverse hues (such as those of the color morphs described earlier) have probably arisen because of the preferences of the females. In this case, sexual selection, rather than pressure for physical survival, seems to have driven the diversification. The different colors of otherwise identical fish can serve as a barrier separating distinct species, because a female *Tropheus,* for instance, that prefers yellow males will not mate with a red one.

Secrets in the Genes

Until very recently, biologists did not know how these hundreds of cichlid species were related. Modern molecular techniques have now answered some of these questions and raised many others. Although the genetic research confirms several early hypotheses based on anatomy, it sometimes conflicts spectacularly with entrenched ideas.

As initially suggested by Mutsumi Nishida of Fukui Prefectural University, early lineages of cichlids from West Africa first colonized Lake Tanganyika. The cichlids of this ancient lake are genetically diverse, corresponding to 11 lineages (that is, deriving from 11 ancestral species). Much later some of these fishes left the lake's confines and invaded East African river systems, through which they reached Lakes Victoria and Malawi. Studies of the genetic material called mitochondrial DNA conducted by one of us (Meyer) and our colleagues show that the cichlids in Lake Victoria are genetically very close to one another—far closer than to morphologically similar cichlids in the other two lakes. They derive almost entirely from a single lineage of mouth brooders.

This scenario implies that almost identical evolutionary adaptations can and did evolve many times independently of one another. Cichlids with singular anatomical features—designed to feed on other fish or on eggs and larvae, to nip off fins, scrape algae, tear off scales, crush mollusks or any of myriad other functions—occur in all three lakes. To some of us biologists, such features had seemed so unique and so unlikely to evolve more than once that we had held that fishes with the same specializations should be closely related.

If that were so, the predilection to scrape algae (for instance) would have evolved only once, its practitioners having later dispersed. But algae scrapers in Lake Victoria and Lake Malawi have evolved independently of those in Lake Tanganyika, from an ancestor with more generalized capabilities. The genetic studies thus show that evolution repeatedly discovers the same solutions to the same ecological challenges.

It also appears that morphological characteristics can evolve at an incredibly uneven pace, sometimes completely out of step with genetic changes. Some of Lake Tanganyika's species have physically altered very little over time— a number of fossil cichlids, especially tilapias, look very similar to their modern descendants in the lake. And apart from their color, the *Tropheus* species remained (morphologically) almost unchanged. On the other hand, the cichlids of Lake Victoria—with their diversity in size, pattern and shape—evolved in an extremely short time span. Amazingly, the lake's more than 400 species contain less genetic variation than the single species *Homo sapiens*. Molecular clocks that are roughly calibrated on the rate of mutations in mitochondrial DNA suggest that the entire assemblage of Lake Victoria cichlids arose within the past 200,000 years.

Recent paleoclimatological data from Thomas C. Johnson of the University of Minnesota and his colleagues point to an even more restricted window for the origin of the Victoria cichlid flock: the lake seems to have dried out almost completely less than 14,000 years ago. No more than a small fraction of individual cichlids, let alone species, could have survived such an ordeal. In that case, the speciation rate exhibited by its cichlids is truly remarkable, being unmatched by other vertebrates. In addition, Lake Nabugabo, a small body of water separated from Lake Victoria by a sandbar that is no more than 4,000 years old, contains five endemic species of cichlids. These fishes are believed to have close relatives in Lake Victoria, which differ from the former mainly in the breeding coloration of the males. Even more remarkably, it turns out that the southern end of Lake Malawi was dry only two centuries ago. Yet it is now inhabited by numerous species and color morphs that are found nowhere else.

These examples, bolstered by recent DNA data from Lake Tanganyika, suggest a mechanism for the speciation of cichlids: repeated isolation. It appears that successive drops in the level of Lake Tanganyika, by as much as 2,000 feet, facilitated the formation of *Tropheus* color morphs and all the other rock-dwelling cichlids. Populations that used to exchange genes instead became isolated in small pockets of water. They developed independently, coming into contact once again as the water level rose—but could no longer interbreed.

A Sadder Record

If the speciation rate in Lake Victoria has been record-breaking, so also has been the extinction rate. Half a century ago cichlids made up more than 99 percent of the lake's fish biomass; today they are less than 1 percent. Many of the species are already extinct, and many others are so reduced in population that the chances of their recovery are minimal. The causes of this mass extinction can perhaps be best summarized by the HIPPO acronym: Habitat destruction, Introduced species, Pollution, Population growth and Overexploitation.

The "nail in Victoria's coffin" has been a voracious predatory fish, the giant Nile perch. It was introduced into the lake in the 1950s in a misguided attempt to increase fishery yields. By the mid-1980s the perch populations had exploded—and the abundance of cichlids had dropped by a factor of 10,000. Consequently, much of the lake has become anoxic. Many of the cichlids that the perch fed on were algae eaters: with them gone, the dead, decaying algae suck oxygen from the water. And when they are caught by local fishers, the six-foot perch cannot be laid out to dry like the small cichlids but must be smoked, using firewood from local forests. The resulting deforestation has led to rainwater carrying soil into the water, further increasing turbidity and anoxic conditions.

Whatever the causes behind the alteration, the end result is an all too familiar picture in which a once vibrant community is reduced to a shadow of its former diversity. The extraordinary evolutionary theater featuring Lake Victoria's cichlids is closing even more abruptly than it started.

The Authors

MELANIE L. J. STIASSNY and AXEL MEYER study different aspects of cichlids, a paradigm group in evolutionary biology. Stiassny received her Ph.D. in 1980 from the University of London and is currently chair of the department of ichthyology at the American Museum of Natural History. Her research centers on the systematics, evolutionary morphology and, most recently, the conservation biology of cichlids. Meyer obtained his Ph.D. in 1988 from the University of California, Berkeley, and is now a professor of biology at the University of Konstanz in Germany. His interests lie in the origins of biological diversity at both the molecular and organismal levels and especially as manifest in cichlid fishes. He was one of the first to use DNA sequences to study the processes of evolution.

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Evolution and the Origins of Disease

originally published in November 1998

The principles of evolution by natural selection are finally beginning to inform medicine

by Randolph M. Nesse and George C. Williams

Thoughtful contemplation of the human body elicits awe—in equal measure with perplexity. The eye, for instance, has long been an object of wonder, with the clear, living tissue of the cornea curving just the right amount, the iris adjusting to brightness and the lens to distance, so that the optimal quantity of light focuses exactly on the surface of the retina. Admiration of such apparent perfection soon gives way, however, to consternation. Contrary to any sensible design, blood vessels and nerves traverse the inside of the retina, creating a blind spot at their point of exit.

The body is a bundle of such jarring contradictions. For each exquisite heart valve, we have a wisdom tooth. Strands of DNA direct the development of the 10 trillion cells that make up a human adult but then permit his or her steady deterioration and eventual death. Our immune system can identify and destroy a million kinds of foreign matter, yet many bacteria can still kill us. These contradictions make it appear as if the body was designed by a team of superb engineers with occasional interventions by Rube Goldberg.

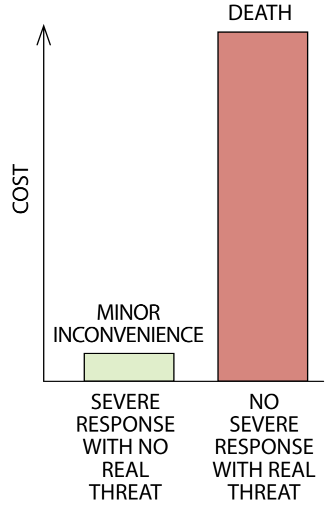
In fact, such seeming incongruities make sense but only when we investigate the origins of the body's vulnerabilities while keeping in mind the wise words of distinguished geneticist Theodosius Dobzhansky: "Nothing in biology makes sense except in the light of evolution." Evolutionary biology is, of course, the scientific foundation for all biology, and biology is the foundation for all medicine. To a surprising degree, however, evolutionary biology is just now being recognized as a basic medical science. The enterprise of studying medical problems in an evolutionary context has been termed Darwinian medicine. Most medical research tries to explain the causes of an individual's disease and seeks therapies to cure or relieve deleterious conditions. These efforts are traditionally based on consideration of proximate issues, the straightforward study of the body's anatomic and physiological mechanisms as they currently exist. In contrast, Darwinian medicine asks why the body is designed in a way that makes us all vulnerable to problems like cancer, atherosclerosis, depression and choking, thus offering a broader context in which to conduct research.

The evolutionary explanations for the body's flaws fall into surprisingly few categories. First, some discomforting conditions, such as pain, fever, cough, vomiting and anxiety, are actually neither diseases nor design defects but rather are evolved defenses. Second, conflicts with other organisms—*Escherichia coli* or crocodiles, for instance—are a fact of life. Third, some circumstances, such as the ready availability of dietary fats, are so recent that natural selection has not yet had a chance to deal with them. Fourth, the body may fall victim to tradeoffs between a trait's benefits and its costs; a textbook example is the sickle cell gene, which also protects against malaria. Finally, the process of natural selection is constrained in ways that leave us with suboptimal design features, as in the case of the mammalian eye.

Evolved Defenses

Perhaps the most obviously useful defense mechanism is coughing; people who cannot clear foreign matter from their lungs are likely to die from pneumonia. The capacity for pain is also certainly beneficial. The rare individuals who cannot feel pain fail even to experience discomfort from staying in the same position for long periods. Their unnatural stillness impairs the blood supply to their joints, which then deteriorate. Such pain-free people usually die by early adulthood from tissue damage and infections. Cough or pain is usually interpreted as disease or trauma but is actually part of the solution rather than the problem. These defensive capabilities, shaped by natural selection, are kept in reserve until needed.

Less widely recognized as defenses are fever, nausea, vomiting, diarrhea, anxiety, fatigue, sneezing and inflammation. Even some physicians remain unaware



JOHNNY JOHNSON

MUCH SUFFERING is unnecessary but inevitable because of the smoke-detector nature of our defenses. The cost of a false alarm—a strong reaction such as vomiting in the absence of a true threat to life—is temporary unpleasantness. But the cost of no alarm in the presence of a true threat, such as a food toxin, could mean death. A lack of defensive response during pregnancy, for example, could kill the fetus.

of fever's utility. No mere increase in metabolic rate, fever is a carefully regulated rise in the set point of the body's thermostat. The higher body temperature facilitates the destruction of pathogens. Work by Matthew J. Kluger of the Lovelace Institute in Albuquerque, N.M., has shown that even cold-blooded lizards, when infected, move to warmer places until their bodies are several degrees above their usual temperature. If prevented from moving to the warm part of their cage, they are at increased risk of death from the infection. In a similar study by Evelyn Satinoff of the University of Delaware, elderly rats, who can no longer achieve the high fevers of their younger lab companions, also instinctively sought hotter environments when challenged by infection.

A reduced level of iron in the blood is another misunderstood defense mechanism. People suffering from chronic infection often have decreased levels of blood iron. Although such low iron is sometimes blamed for the illness, it actually is a protective response: during infection, iron is sequestered in the liver, which prevents invading bacteria from getting adequate supplies of this vital element.

Morning sickness has long been considered an unfortunate side effect of pregnancy. The nausea, however, coincides with the period of rapid tissue differentiation of the fetus, when development is most vulnerable to interference by toxins. And nauseated women tend to restrict their intake of strong-tasting, potentially harmful substances. These observations led independent researcher Margie Profet to hypothesize that the nausea of pregnancy is an adaptation whereby the mother protects the fetus from exposure to toxins. Profet tested this idea by examining pregnancy outcomes. Sure enough, women with more nausea were less likely to suffer miscarriages. (This evidence supports the hypothesis but is hardly conclusive. If Profet is correct, further research should discover that pregnant females of many species show changes in food preferences. Her theory also predicts an increase in birth defects among offspring of women who have little or no morning sickness and thus eat a wider variety of foods during pregnancy.)

Another common condition, anxiety, obviously originated as a defense in dangerous situations by promoting escape and avoidance. A 1992 study by Lee A. Dugatkin of the University of Louisville evaluated the benefits of fear in guppies. He grouped them as timid, ordinary or bold, depending on their reaction to the presence of smallmouth bass. The timid hid, the ordinary simply swam away, and the bold maintained their ground and eyed the bass. Each guppy group was then left alone in a tank with a bass. After 60 hours, 40 percent of the timid guppies had survived, as had only 15 percent of the ordinary fish. The entire complement of bold guppies, on the other hand, wound up aiding the transmission of bass genes rather than their own.

Selection for genes promoting anxious behaviors implies that there should be people who experience too much anxiety, and indeed there are. There should also be hypophobic individuals who have insufficient anxiety, either because of genetic tendencies or antianxiety drugs. The exact nature and frequency of such a syndrome is an open question, as few people come to psychiatrists complaining of insufficient apprehension. But if sought, the pathologically nonanxious may be found in emergency rooms, jails and unemployment lines.

The utility of common and unpleasant conditions such as diarrhea, fever and anxiety is not intuitive. If natural selection shapes the mechanisms that regulate defensive responses, how can people get away with using drugs to block these defenses without doing their bodies obvious harm? Part of the answer is that we do, in fact, sometimes do ourselves a disservice by disrupting defenses.

Herbert L. DuPont of the University of Texas at Houston and Richard B. Hornick of Orlando Regional Medical Center studied the diarrhea caused by *Shigella* infection and found that people who took antidiarrhea drugs stayed sick longer and were more likely to have complications than those who took a placebo. In another example, Eugene D. Weinberg of Indiana University has documented that well-intentioned attempts to correct perceived iron deficiencies have led to increases in infectious disease, especially amebiasis, in parts of Africa. Although the iron in most oral supplements is unlikely to make much difference in otherwise healthy people with everyday infections, it can severely

Evolution of Virulence

Changes in virulence relate to the life history of the infectious agent and its mode of transmission. As elucidated by Paul W. Ewald of Amherst College, infection requiring direct contact will ordinarily drive a pathogen toward a state of lowered virulence, because the host must remain mobile enough to interact with others. But intermediaries that spread disease-causing agents, even from totally incapacitated hosts, can cause a change toward more virulence. Behavioral choices, such as safer sex, can also alter the makeup of the pathogen.

SELECTION FACTORS FAVORING HIGHER VIRULENCE	SELECTION FACTORS FAVORING LOWER VIRULENCE
Intermediary disease vectors (Mosquitoes, health care workers' hands, unsanitary water supplies)	Casual human-to-human transmission (Sneezing, coughing, touch)
Unprotected and/or promiscuous sex	Protected and/or monogamous sex

New Environments Bring New Health Threats

Common Threats to Health from 20,000 B.C. to Modern Times

- Accidents
- Starvation
- Predation
- Infectious diseases

Common Threats to Health Today (in Technologically Advanced Cultures)

- Heart attack, stroke and other complications of atherosclerosis
- Cancer
- Other chronic diseases associated with lifestyle and longevity
- Noninsulin-dependent diabetes
- Obesity
- New infectious diseases

harm those who are infected and malnourished. Such people cannot make enough protein to bind the iron, leaving it free for use by infectious agents.

On the morning-sickness front, an antinausea drug was recently blamed for birth defects. It appears that no consideration was given to the possibility that the drug itself might be harmless to the fetus but could still be associated with birth defects, by interfering with the mother's defensive nausea.

Another obstacle to perceiving the benefits of defenses arises from the observation that many individuals regularly experience seemingly worthless reactions of anxiety, pain, fever, diarrhea or nausea. The explanation requires an analysis of the regulation of defensive responses in terms of signal-detection theory. A circulating toxin may come from something in the stomach. An organism can expel it by vomiting, but only at a price. The cost of a false alarm—vomiting when no toxin is truly present—is only a few calories. But the penalty for a single missed authentic alarm—failure to vomit when confronted with a toxin—may be death.

Natural selection therefore tends to shape regulation mechanisms with hair triggers, following what we call the smoke-detector principle. A smoke alarm that will reliably wake a sleeping family in the event of any fire will necessarily give a false alarm every time the toast burns. The price of the human body's numerous "smoke alarms" is much suffering that is completely normal but in most instances unnecessary. This principle also explains why blocking defenses is so often free of tragic consequences. Because most defensive reactions occur in response to insignificant threats, interference is usually harmless; the vast majority of alarms that are stopped by removing the battery from the smoke alarm are false ones, so this strategy may seem reasonable. Until, that is, a real fire occurs.

Conflicts with Other Organisms

Natural selection is unable to provide us with perfect protection against all pathogens, because they tend to evolve much faster than humans do. *E. coli,* for example, with its rapid rates of reproduction, has as much opportunity for mutation and selection in one day as humanity gets in a millennium. And our defenses, whether natural or artificial, make for potent selection forces. Pathogens either quickly evolve a counterdefense or become extinct. Amherst College biologist Paul W. Ewald has suggested classifying phenomena associated with infection according to whether they benefit the host, the pathogen, both or neither. Consider the runny nose associated with a cold. Nasal mucous secretion could expel intruders, speed the pathogen's transmission to new hosts or both [see "The Evolution of Virulence," by Paul W. Ewald; Scientific American, April 1993]. Answers could come from studies examining whether blocking nasal secretions shortens or prolongs illness, but few such studies have been done.

Humanity won huge battles in the war against pathogens with the development of antibiotics and vaccines. Our victories were so rapid and seemingly complete that in 1969 U.S. Surgeon General William H. Stewart said that it was "time to close the book on infectious disease." But the enemy, and the power of natural selection, had been underestimated. The sober reality is that pathogens apparently can adapt to every chemical researchers develop. ("The war has been won," one scientist more recently quipped. "By the other side.")

Antibiotic resistance is a classic demonstration of natural selection. Bacteria that happen to have genes that allow them to prosper despite the presence of an antibiotic reproduce faster than others, and so the genes that confer resistance spread quickly. As shown by Nobel laureate Joshua Lederberg of the Rockefeller University, they can even jump to different species of bacteria, borne on bits of infectious DNA. Today some strains of tuberculosis in New York City are resistant to all three main antibiotic treatments; patients with those strains have no better chance of surviving than did TB patients a century ago. Stephen S. Morse of Columbia University notes that the multidrug-resistant strain that has spread throughout the East Coast may have originated in a homeless shelter across the street from Columbia-Presbyterian Medical Center. Such a phenomenon would indeed be predicted in an environment where fierce selection pressure quickly weeds out less hardy strains. The surviving bacilli have been bred for resistance.

Many people, including some physicians and scientists, still believe the outdated theory that pathogens necessarily become benign after long association with hosts. Superficially, this makes sense. An organism that kills rapidly may never get to a new host, so natural selection would seem to favor lower virulence. Syphilis, for instance, was a highly virulent disease when it first arrived in Europe, but as the centuries passed it became steadily more mild. The virulence of a pathogen is, however, a life history trait that can increase as well as decrease, depending on which option is more advantageous to its genes.

For agents of disease that are spread directly from person to person, low virulence tends to be beneficial, as it allows the host to remain active and in contact with other potential hosts. But some diseases, like malaria, are transmitted just as well—or better—by the incapacitated. For such pathogens, which usually rely on intermediate vectors like mosquitoes, high virulence can give a selective advantage. This principle has direct implications for infection control in hospitals, where health care workers' hands can be vectors that lead to selection for more virulent strains.

In the case of cholera, public water supplies play the mosquitoes' role. When water for drinking and bathing is contaminated by waste from immobilized patients, selection tends to increase virulence, because more diarrhea enhances the spread of the organism even if individual hosts quickly die. But, as Ewald has shown, when sanitation improves, selection acts against classical *Vibrio cholerae* bacteria in favor of the more benign El Tor biotype. Under these conditions, a dead host is a dead end. But a less ill and more mobile host, able to infect many others over a much longer time, is an effective vehicle for a pathogen of lower virulence. In another example, better sanitation leads to displacement of the aggressive *Shigella flexneri* by the more benign *S. sonnei.*

Such considerations may be relevant for public policy. Evolutionary theory predicts that clean needles and the encouragement of safe sex will do more than save numerous individuals from HIV infection. If humanity's behavior itself slows HIV transmission rates, strains that do not soon kill their hosts have the long-term survival advantage over the more virulent viruses that then die with their hosts, denied the opportunity to spread. Our collective choices can change the very nature of HIV.

Conflicts with other organisms are not limited to pathogens. In times past, humans were at great risk from predators looking for a meal. Except in a few places, large carnivores now pose no threat to humans. People are in more danger today from smaller organisms' defenses, such as the venoms of spiders and snakes. Ironically, our fears of small creatures, in the form of phobias, probably cause more harm than any interactions with those organisms do. Far more dangerous than predators or poisoners are other members of our own species. We attack each other not to get meat but to get mates, territory and other resources. Violent conflicts between individuals are overwhelmingly between young men in competition and give rise to organizations to advance these aims. Armies, again usually composed of young men, serve similar objectives, at huge cost.

Even the most intimate human relationships give rise to conflicts having medical implications. The reproductive interests of a mother and her infant, for instance, may seem congruent at first but soon diverge. As noted by biologist Robert L. Trivers in a now classic 1974 paper, when her child is a few years old, the mother's genetic interests may be best served by becoming pregnant again, whereas her offspring benefits from continuing to nurse. Even in the womb there is contention. From the mother's vantage point, the optimal size of a fetus is a bit smaller than that which would best serve the fetus and the father. This discord, according to David Haig of Harvard University, gives rise to an arms race between fetus and mother over her levels of blood pressure and blood sugar, sometimes resulting in hypertension and diabetes during pregnancy.

Coping with Novelty

Making rounds in any modern hospital provides sad testimony to the prevalence of diseases humanity has brought on itself. Heart attacks, for example, result mainly from atherosclerosis, a problem that became widespread only in this century and that remains rare among hunter-gatherers. Epidemiological research furnishes the information that should help us prevent heart attacks: limit fat intake, eat lots of vegetables, and exercise hard each day. But hamburger chains proliferate, diet foods languish on the shelves, and exercise machines serve as expensive clothing hangers throughout the land. The proportion of overweight Americans is one third and rising. We all know what is good for us. Why do so many of us continue to make unhealthy choices?

Our poor decisions about diet and exercise are made by brains shaped to cope with an environment substantially different from the one our species now inhabits. On the African savanna, where the modern human design was fine-tuned, fat, salt and sugar were scarce and precious. Individuals who had a tendency to consume large amounts of fat when given the rare opportunity had a selective advantage. They were more likely to survive famines that killed their thinner companions. And we, their descendants, still carry those urges for foodstuffs that today are anything but scarce. These evolved desires—inflamed by advertisements from competing food corporations that themselves survive by selling us more of whatever we want to buy—easily defeat our intellect and willpower. How ironic that humanity worked for centuries to create environments that are almost literally flowing with milk and honey, only to see our success responsible for much modern disease and untimely death.

Increasingly, people also have easy access to many kinds of drugs, especially alcohol and tobacco, that are responsible for a huge proportion of disease, health care costs and premature death. Although individuals have always used psychoactive substances, widespread problems materialized only following another environmental novelty: the ready availability of concentrated drugs and new, direct routes of administration, especially injection. Most of these substances, including nicotine, cocaine and opium, are products of natural selection that evolved to protect plants from insects. Because humans share a common evolutionary heritage with insects, many of these substances also affect our nervous system.

This perspective suggests that it is not just defective individuals or disordered societies that are vulnerable to the dangers of psychoactive drugs; all of us are susceptible because drugs and our biochemistry have a long history of interaction. Understanding the details of that interaction, which is the focus of much current research from both a proximate and evolutionary perspective, may well lead to better treatments for addiction.

The relatively recent and rapid increase in breast cancer must be the result in large part of changing environments and ways of life, with only a few cases resulting solely from genetic abnormalities. Boyd Eaton and his colleagues at Emory University reported that the rate of breast cancer in today's "nonmodern" societies is only a tiny fraction of that in the U.S. They hypothesize that the amount of time between menarche and first pregnancy is a crucial risk factor, as is the related issue of total lifetime number of menstrual cycles. In hunter-gatherers, menarche occurs at about age 15 or later, followed within a few years by pregnancy and two or three years of nursing, then by another pregnancy soon after. Only between the end of nursing and the next pregnancy will the woman menstruate and thus experience the high levels of hormones that may adversely affect breast cells.

In modern societies, in contrast, menarche occurs at age 12 or 13—probably at least in part because of a fat intake sufficient to allow an extremely young woman to nourish a fetus—and the first pregnancy may be decades later or never. A female hunter-gatherer may have a total of 150 menstrual cycles, whereas the average woman in modern societies has 400 or more. Although few would suggest that women should become pregnant in their teens to prevent breast cancer later, early administration of a burst of hormones to simulate pregnancy may reduce the risk. Trials to test this idea are now under way at the Uni-

Selected Principles of Darwinian Medicine

A Darwinian approach to medical practice leads to a shift in perspective. The following principles provide a foundation for considering health and disease in an evolutionary context:

DEFENSES and **DEFECTS** are two fundamentally different manifestations of disease

BLOCKING defenses has costs as well as benefits

Because natural selection shapes defense regulation according to the **SMOKE-DETECTOR PRINCIPLE**, much defensive expression and associated suffering are unnecessary in the individual instance

Modern epidemics are most likely to arise from the mismatch between **PHYSIOLOGICAL DESIGN** of our bodies and **NOVEL ASPECTS** of our environment

Our **DESIRES**, shaped in the ancestral environment to lead us to actions that tended to maximize reproductive success, now often lead us to disease and early death

The body is a bundle of **COMPROMISES**

There is no such thing as "the **NORMAL** body"

There is no such thing as "the **NORMAL** human genome"

Some **GENES** that cause disease may also have benefits, and others are quirks that cause disease only when they interact with novel environmental factors

GENETIC SELF-INTEREST will drive an individual's actions, even at the expense of the health and longevity of the individual created by those genes

VIRULENCE is a trait of the pathogen that can increase as well as decrease

SYMPTOMS of infection can benefit the pathogen, the host, both or neither

Disease is **INEVITABLE** because of the way that organisms are shaped by evolution

Each disease needs a **PROXIMATE EXPLANATION** of why some people get it and others don't, as well as an **EVOLUTIONARY EXPLANATION** of why members of the species are vulnerable to it

Diseases are not products of natural selection, but most of the **VULNERABILITIES** that lead to disease are shaped by the process of natural selection

Aging is better viewed as a **TRADE-OFF** than a disease

Specific clinical recommendations must be based on **CLINICAL STUDIES**; clinical interventions based only on theory are not scientifically grounded and may cause harm

versity of California at San Diego.

Trade-offs and Constraints

Compromise is inherent in every adaptation. Arm bones three times their current thickness would almost never break, but *Homo sapiens* would be lumbering creatures on a never-ending quest for calcium. More sensitive ears might sometimes be useful, but we would be distracted by the noise of air molecules banging into our eardrums.

Such trade-offs also exist at the genetic level. If a mutation offers a net reproductive advantage, it will tend to increase in frequency in a population even if it causes vulnerability to disease. People with two copies of the sickle cell gene, for example, suffer terrible pain and die young. People with two copies of the "normal" gene are at high risk of death from malaria. But individuals with one of each are protected from both malaria and sickle cell disease. Where malaria is prevalent, such people are fitter, in the Darwinian sense, than members of either other group. So even though the sickle cell gene causes disease, it is selected for where malaria persists. Which is the "healthy" allele in this environment? The question has no answer. There is no one normal human genome—there are only genes.

Many other genes that cause disease must also have offered benefits, at least in some environments, or they would not be so common. Because cystic fibrosis (CF) kills one out of 2,500 Caucasians, the responsible genes would appear to be at great risk of being eliminated from the gene pool. And yet they endure. For years, researchers mused that the CF gene, like the sickle cell gene, probably conferred some advantage. Recently a study by Gerald B. Pier of Harvard Medical School and his colleagues gave substance to this informed speculation: having one copy of the CF gene appears to decrease the chances of the bearer acquiring a typhoid fever infection, which once had a 15 percent mortality.

Aging may be the ultimate example of a genetic trade-off. In 1957 one of us (Williams) suggested that genes that cause aging and eventual death could nonetheless be selected for if they had other effects that gave an advantage in youth, when the force of selection is stronger. For instance, a hypothetical gene that governs calcium metabolism so that bones heal quickly but that also happens to cause the steady deposition of calcium in arterial walls might well be selected for even though it kills some older people. The influence of such pleiotropic genes (those having multiple effects) has been seen in fruit flies and flour beetles, but no specific example has yet been found in humans. Gout, however, is of particular interest, because it arises when a potent antioxidant, uric acid, forms crystals that precipitate out of fluid in joints. Antioxidants have antiaging effects, and plasma levels of uric acid in different species of primates are closely correlated with average adult life span. Perhaps high levels of uric acid benefit most humans by slowing tissue aging, while a few pay the price with gout.

Other examples are more likely to contribute to more rapid aging. For instance, strong immune defenses protect us from infection but also inflict continuous, low-level tissue damage. It is also possible, of course, that most genes that cause aging have no benefit at any age—they simply never decreased reproductive fitness enough in the natural environment to be selected against. Nevertheless, over the next decade research will surely identify specific genes that accelerate senescence, and researchers will soon thereafter gain the means to interfere with their actions or even change them. Before we tinker, however, we should determine whether these actions have benefits early in life.

Because evolution can take place only in the direction of time's arrow, an organism's design is constrained by structures already in place. As noted, the vertebrate eye is arranged backward. The squid eye, in contrast, is free from this defect, with vessels and nerves running on the outside, penetrating where necessary and pinning down the retina so it cannot detach. The human eye's flaw results from simple bad luck; hundreds of millions of years ago, the layer of cells that happened to become sensitive to light in our ancestors was positioned differently from the corresponding layer in ancestors of squids. The two designs evolved along separate tracks, and there is no going back.

Such path dependence also explains why the simple act of swallowing can be life-threatening. Our respiratory and food passages intersect because in an early lungfish ancestor the air opening for breathing at the surface was understandably located at the top of the snout and led into a common space shared by the food passageway. Because natural selection cannot start from scratch, humans are stuck with the possibility that food will clog the opening to our lungs.

The path of natural selection can even lead to a potentially fatal cul-de-sac, as in the case of the appendix, that vestige of a cavity that our ancestors employed in digestion. Because it no longer performs that function, and as it can kill when infected, the expectation might be that natural selection would have eliminated it. The reality is more complex. Appendicitis results when inflammation causes swelling, which compresses the artery supplying blood to the appendix. Blood flow protects against bacterial growth, so any reduction aids infection, which creates more swelling. If the blood supply is cut off completely, bacteria have free rein until the appendix bursts. A slender appendix is especially susceptible to this chain of events, so appendicitis may, paradoxically, apply the selective pressure that maintains a large appendix. Far from arguing that everything in the body is perfect, an evolutionary analysis reveals that we live with some very unfortunate legacies and that some vulnerabilities may even be actively maintained by the force of natural selection.

Evolution of Darwinian Medicine

Despite the power of the Darwinian paradigm, evolutionary biology is just now being recognized as a basic science essential for medicine. Most diseases decrease fitness, so it would seem that natural selection could explain only health, not disease. A Darwinian approach makes sense only when the object of explanation is changed from diseases to the traits that make us vulnerable to diseases. The assumption that natural selection maximizes health also is incorrect—selection maximizes the reproductive success of genes. Those genes that make bodies having superior reproductive success will become more common, even if they compromise the individual's health in the end.

Finally, history and misunderstanding have presented obstacles to the acceptance of Darwinian medicine. An evolutionary approach to functional analysis can appear akin to naive teleology or vitalism, errors banished only recently, and with great effort, from medical thinking. And, of course, whenever evolution and medicine are mentioned together, the specter of eugenics arises. Discoveries made through a Darwinian view of how all human bodies are alike in their vulnerability to disease will offer great benefits for individuals, but such insights do not imply that we can or should make any attempt to improve the species. If anything, this approach cautions that apparent genetic defects may have unrecognized adaptive significance, that a single "normal" genome is nonexistent and that notions of "normality" tend to be simplistic.

The systematic application of evolutionary biology to medicine is a new enterprise. Like biochemistry at the beginning of this century, Darwinian medicine very likely will need to develop in several incubators before it can prove its power and utility. If it must progress only from the work of scholars without funding to gather data to test their ideas, it will take decades for the field to mature. Departments of evolutionary biology in medical schools would accelerate the process, but for the most part they do not yet exist. If funding agencies had review panels with evolutionary expertise, research would develop faster, but such panels remain to be created. We expect that they will.

The evolutionary viewpoint provides a deep connection between the states of disease and normal functioning and can integrate disparate avenues of medical research as well as suggest fresh and important areas of inquiry. Its utility and power will ultimately lead to recognition of evolutionary biology as a basic medical science.

The Authors

RANDOLPH M. NESSE and GEORGE C. WILLIAMS are the authors of the 1994 book *Why We Get Sick: The New Science of Darwinian Medicine.* Nesse received his medical degree from the University of Michigan Medical School in 1974. He is now professor of psychiatry at that institution and is director of the Evolution and Human Adaptation Program at the university's Institute for Social Research. Williams received his doctorate in 1955 from the University of California, Los Angeles, and quickly became one of the world's foremost evolutionary theorists. A member of the National Academy of Sciences, he is professor emeritus of ecology and evolution at the State University of New York at Stony Brook and edits the *Quarterly Review of Biology.*

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Teach the Science

Wherever evolution education is under attack by creationist thinking, Eugenie Scott will be there to defend science—with rationality and resolve

By STEVE MIRSKY

Federal court had just been dismissed in Harrisburg, Pa., on September 26, 2005, the first day of the Dover intelligent design trial. Commentators dubbed it Scopes II or III, depending on how many previous evolution education cases they knew of. The defendants, members of the Dover, Pa., school board, had required that a statement denigrating evolutionary theory be read to ninth-grade biology students and recommended so-called intelligent design be considered a viable and intellectually adequate alternative. Plaintiffs were parents in the school district who alleged that intelligent design, or ID, was in fact a religious construct and that presenting it to their children in a public school science class thus violated the establishment clause of the First Amendment to the U.S. Constitution.

A steady rain forced plaintiffs, defendants, witnesses and media to huddle together under the overhang at the entrance to the Harrisburg Federal Building and Courthouse. Within a few feet of advocates who had minutes before put evolution itself on trial stood Eugenie Scott. As executive director of the National Center for Science Education (NCSE), she is the country's foremost defender of evolution education. She patiently explained to reporters why this trial was so important: “It's the first case that is considering the legality of the two current strategies of the antievolution movement.”

The first strategy is advocacy for intelligent design—the notion that life or certain aspects of life are too complex to have arisen naturally and must therefore be the product of an intelligent designer. “Creation science was the original scientific alternative to evolution,” says Scott, who turned 60 during the trial, “and ID is the scientific alternative to evolution du jour. And it's basically a subset of creation science. ID has never been on trial before.”

The second strategy, casting doubt on evolutionary science, has roots in 1987, when the U.S. Supreme Court in *Edwards v. Aguillard* found by a 7–2 decision that creationism was religious and therefore ineligible for inclusion in public school biology curricula. In his majority opinion, Justice William J. Brennan wrote that teachers had the right to teach scientific alternatives to evolution, “which of course they do,” Scott explains. “If there were any, they would have the right to teach them.”

But Justice Antonin Scalia, joined in his dissent by Chief Justice William H. Rehnquist, wrote that “whatever scientific evidence there may be against evolution” could also be “presented in their schools.” A tactic, then, is to portray the lack of certitude about every last detail of evolution—so-called gaps or honest disagreements between evolutionary biologists about mechanisms—as evidence against it.

The Dover trial involved arguments on both evidence against evolution and intelligent design. To Scott, “it's a dream condition because we can hopefully challenge both of these components.” Scott's dream was apparently the defendant's nightmare. Fellows of the Discovery Institute, a Seattle-based pro–intelligent design group, were to appear as defense witnesses but withdrew, citing their desire to be represented by their own attorneys during depositions. That “they yanked the A team I think suggests that they're cutting their losses,” Scott says.

Dover was just the latest hot spot Scott has visited.

EUGENIE SCOTT: SISYPHUS WITH A SMILE

- **Executive director of the National Center for Science Education, she describes herself as Darwin's golden retriever, for her amiable defense of evolution in the classroom.**
- **Hosts an annual rafting trip through the Grand Canyon to counter one by creationists who use it to teach biblical flood geology.**
- **On who should be concerned about creationism: “Anybody who cares that the U.S. has a biologically literate society, with biotech, biomedicine, agriculture and other related technologies and industries.”**

The NCSE office in Oakland, Calif., includes a wall map of the U.S., with stickpins in the sites of challenges to evolution education. "There's a surprising amount in the midsection and in Maryland, Pennsylvania, Tennessee," she notes. "Then a cluster in California, in Texas and in Kansas, of course." Kansas, which remains a battleground over evolution education, is where Scott first got directly involved in the fight.

Shortly after joining the faculty of the University of Kentucky as a physical anthropologist in 1974, she attended a debate at the University of Missouri between her mentor, Jim Gavan, and Duane Gish, a leader in the then nascent scientific creationism movement. She began to collect creationist literature and to study adherents' methods. As a visiting professor at the University of Kansas in 1976, she was thus prepared to advise two biology professors who debated Gish and fellow creationist Henry Morris. Her "true baptism," as she calls it, came in 1980, when she advised the Lexington, Ky., Board of Education, which ultimately rejected a request to include the "balanced" teaching of origins.

Recognizing that the creationism movement would continue, a group of scientists and educators established the NCSE in 1981. "This was to be an organization that would focus on opposing creationism at the grassroots," explains Scott, who was on the periphery then, "because that's where the problem is. Education is decentralized, so the fight has to be local."

In 1986 she became the NCSE's executive director. Her current career bears strong similarities to an academic one. "I'm still teaching. I'm just teaching on a radio show, or I'm teaching a reporter the details. A lot of the same skills I had as a college professor are involved—taking complicated ideas and bringing them to the level so that whoever you're talking to can understand."

Along with intellectual rigor and stamina, Scott is known for her congeniality. Thomas Huxley was called Darwin's bulldog, leading to other canine analogies for evolution's defenders. Richard Dawkins, elegant and aggressive, has been called Darwin's greyhound. Scott thinks that the fast and focused Brown University biologist Ken Miller, a devout Catholic who was the first witness in the Dover case, is Darwin's border collie. "And I am Darwin's golden retriever," she says. "In my personal relationships with creationists, I have tried very hard to always keep things civil and never personal."

Being a happy warrior is both natural to Scott and probably the best way for her and her side to harness support. "To me, her most impressive accomplishments are the coalitions of very diverse people and organizations she has knit together in support of science education—especially the clergy," says Sean Carroll, a molecular biologist and geneticist at the University of Wisconsin–Madison. "Because when seriously religious people speak up in favor of evolution, people listen."

The Dover trial was a dream condition, Eugenie Scott says—it challenged both intelligent design and doubts about evolution.

Total victory could be long in coming, with thousands of local school boards making curriculum decisions. In fact, the threat to public science education may be growing: astronomy and cosmology can also offend religious fundamentalists. Of her first American Astronomical Society meeting in 2005, she says: "I couldn't get five yards without somebody coming up to me and saying, 'Let me tell you about the problems I'm having teaching big bang, let me tell you about the problems I'm having teaching formation of the solar system, etc.' "

On December 20, 2005, Judge John Jones issued a blistering 139-page decision in favor of the plaintiffs, in which he referred to the "breathtaking inanity" of the school board's decision to require the antievolution disclaimer. He also forcefully noted that intelligent design is not science, "in the hope that it may prevent the obvious waste of judicial and other resources which would be occasioned by a subsequent trial." Scott declares Jones's finding a victory for science and education but also predicts the judge's hope will be dashed. "It's like a water bed," she says of antievolutionism. "You push it down in one place, and it bounces up in another." Indeed, the Kansas State Board of Education recently voted, 6–4, to allow intelligent design to be taught in public schools. Scott, it seems clear, won't be out of a job anytime soon. SA