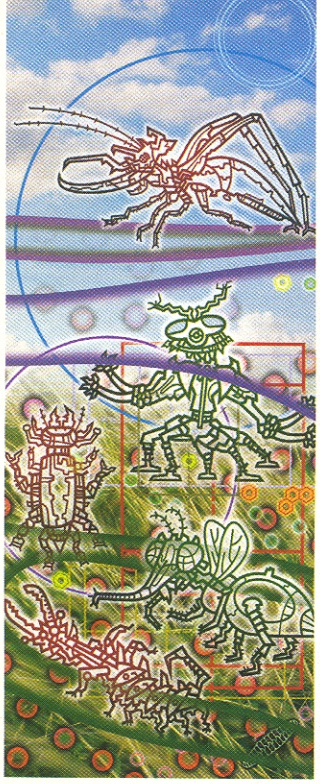


The Fossils Say Yes

The discovery of transitional forms has filled in some of the most talked-about gaps in the fossil record.

By Donald R. Prothero

It has been asserted over and over again, by writers who believe in the immutability of species, that geology yields no linking forms. This assertion . . . is certainly erroneous. . . . What geological research has not revealed, is the former existence of infinitely numerous gradations . . . connecting together nearly all existing and extinct species.
—Charles Darwin, the *Origin of Species*

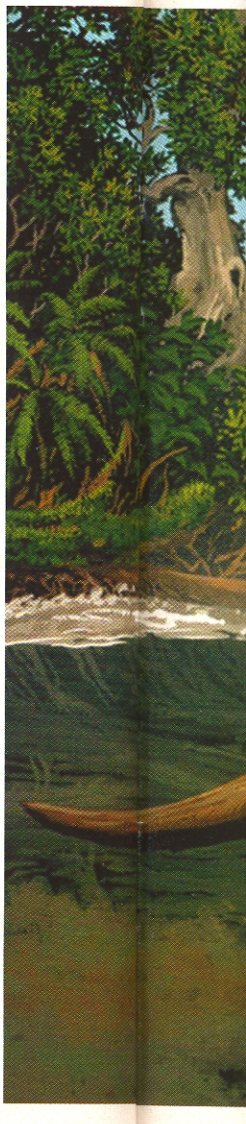
When Darwin first proposed the idea of evolution by natural selection in 1859, the fossil record offered little support for his ideas. Darwin even devoted two entire chapters of the *Origin of Species* to the imperfection of the geologic record, because he was well aware it was one of the weakest links in his arguments. Then, just two years after his book was published, the first specimen of *Archaeopteryx* was discovered, hailed by many as the "missing link" between birds and reptiles. By the late nineteenth century, fossils helped demonstrate how the modern thoroughbred horse evolved from a dog-size, three-toed creature with low-crowned teeth. (The understanding of those fossils has since been much refined.)

Fossil evidence supporting evolution has continued to mount, particularly in the past few decades. DNA analysis, moreover, has helped make sense of how the evidence fits together in the family tree of life on Earth. Unfortunately, many people still think, quite erroneously, that the fossil record shows no "transitional forms." In large part, that misconception is the product of the campaign of misinformation—or disinformation—spread by the creationist movement.

The fossil record is far from perfect, of course. By most estimates, less than 1 percent of all the species that have ever lived are preserved as fossils. The reason for the scarcity is simply that the physical conditions needed to turn a dead organism into a fossil lasting millions of years are unusual.

Nevertheless, there are numerous excellent specimens that reflect transitional stages between major groups of organisms. Many more fossils exhibit how "infinitely numerous gradations" connect the species. The one caveat is that when a sequence of fossils appears to follow a direct line of descent, the chances are slim that they actually bear such precise interrelations. Paleontologists recognize that when one fossil looks ancestral to another, the first fossil is more safely described as being closely related to the actual ancestor.

The classic story of the evolution of the horse is a good example. The various known fossils were once arranged—simplistically, it turns out—into a single lineage leading from *"Eohippus"* to *Equus.* When more fossils became available, paleontologists revised that simple lineage. The fossils now give a branching and very bushy picture of equine evolution, with numerous now-extinct lineages living side by side. One quarry in Nebraska has yielded a dozen distinct species of fossil horses, in rock about 12 million years old. The earliest horses, such as *Protorohippus* (from early in the Eocene epoch, about 53 million years ago), are virtually indistinguishable from *Homogalax,* the earliest member of the lineage, which also gave rise to tapirs and rhinoceroses. Very early in my career, when I was taking an undergraduate paleontology class, I discovered just how tough it is to sort out those two ancient genera.



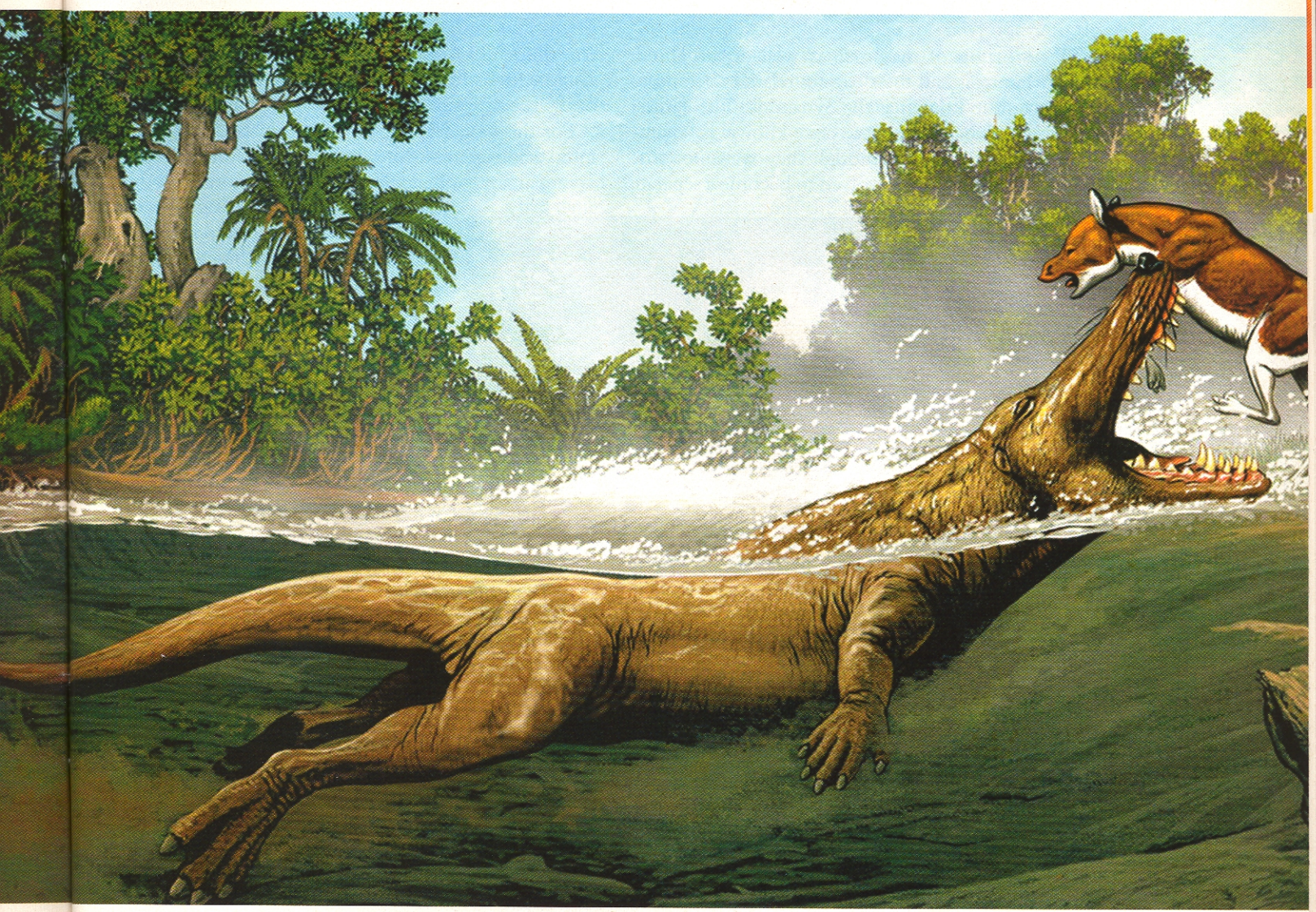
Ambulocetus natans, *a whale the size of a sea lion that could probably walk on land as well as swim, may have been an ambush predator that trolled freshwater streams. Its fossil bones, dating to about 49 million years ago, were discovered in Pakistan in 1994.* A. natans *was a mammal, and is thought to be intermediary between early land carnivores and the more recent, fully aquatic whale. The painting is by Carl Buell.*

Perhaps the most remarkable recent discoveries are the numerous fossils that connect whales with their four-legged terrestrial ancestors. If you look at dolphins, orcas, and blue whales, all fully aquatic animals, you would have a hard time imagining them walking on land. Yet even living whales retain vestiges of their hips and thighbones, deeply buried in the muscles along their spines. Paleontologists have known for a long time, on the basis of detailed features of the skull and teeth, that whales are closely related to hoofed mammals. But creationists long touted the absence of transitional fossils for whales as evidence against evolution.

The balance has now changed. In 1983 specimens of *Pakicetus* were discovered Pakistan in early Eocene beds about 52 million years old. Although the body of *Pakicetus* was primarily terrestrial, it had the skull and teeth of the ancient archaeocetes, the earliest family of whales—which swam the world's oceans in the Middle Eocene epoch, about 50 million years ago.

Then, in 1994, *Ambulocetus natans* (literally, the "walking whale that swims") was discovered, also in Pakistan [*see illustration below*]. The animal was the size of a large sea lion, with broad webbed feet on both fore- and hind limbs, so it could both walk and swim. Yet it still had tiny hooves on its toes and the primitive skull and teeth of the archaeocete. *Ambulocetus* apparently swam much like an otter, with an up-and-down motion of the spine, the precursor to the motion of the flukes of a whale's tail. In 1995 yet a third transitional creature was discovered, *Dalanistes,* with shorter legs than *Ambulocetus*, webbed feet, a longer tail, and a much larger and more whalelike skull.

Today more than a dozen transitional whale fossils have been unearthed—an excellent series for such rarely fossilized animals. DNA from the living species suggests that whales are descended from even-

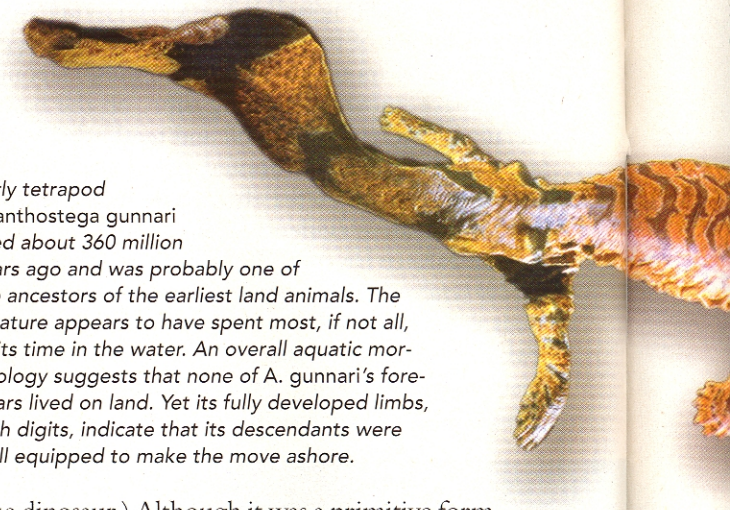


toed hoofed mammals known as artiodactyls and, in particular, are most closely related to the hippopotamus. That hypothesis was dramatically confirmed by the discoveries in 2001 of the "double-pulley" anklebone, which is characteristic of artiodactyls, in two kinds of primitive whales.

Whales are not the only aquatic mammals with terrestrial ancestors. Modern sirenians (manatees and dugongs) are large, docile, aquatic herbivores that have flippers for forelimbs and no hind limbs. In 2001 Daryl Domning, a marine mammal paleontologist at Howard University in Washington, D.C., described a remarkably complete skeleton of *Pezosiren portelli* from Jamaican deposits about 50 million years old. That animal had the typical skull and teeth of a sirenian, and even the thick sirenian ribs made of dense bone, which serve as ballast. Yet it had four legs as well, all with feet, not flippers. Strong transitional fossils also link seals and sea lions to bearlike ancestors.

The origin of mammals is well documented. Mammals and their extinct relatives belong to a larger group known as the Synapsida. The earliest members of the group were once known as "mammal-like reptiles," even though they were not true reptiles but had already evolved to become a separate branch of animals. Among them was *Dimetrodon*, the largest predator on Earth about 280 million years ago. (Its sail-shaped back is familiar from toy-dinosaur kits for children, even though it was not a true dinosaur.) Although it was a primitive form, *Dimetrodon* had large, stabbing canine teeth and some of the specialized skull features of mammals.

Meat-eating dinosaur Sinornithosaurus millenia, *depicted in this artist's conception, could flap its forelimbs, which were covered in feathers. This species' fossil remains were unearthed in the Liaoning beds of northeastern China, along with several other birdlike dinosaurs. The animal was a transitional species, indicating that certain dinosaurs evolved to become birds.*



Early tetrapod Acanthostega gunnari *lived about 360 million years ago and was probably one of the ancestors of the earliest land animals. The creature appears to have spent most, if not all, of its time in the water. An overall aquatic morphology suggests that none of* A. gunnari*'s forebears lived on land. Yet its fully developed limbs, with digits, indicate that its descendants were well equipped to make the move ashore.*

For the next 80 million years, synapsids evolved into various wolflike and bearlike predators, as well as into an array of peculiar piglike herbivores. Along the way, they acquired progressively more mammalian features: additional jaw muscles that enabled complex chewing motions; a secondary palate covering the old reptilian palate and nasal region, which enabled them to breathe and eat at the same time; multicusped molars for chewing rather than gulping their food; enlarged brains; relatively upright (rather than sprawling) posture; and a muscular diaphragm in the rib cage for efficient breathing. There are even signs that they had hair, a quintessentially mammalian feature. The story of the synapsids culminates in the appearance of the earliest true mammals—shrew-size creatures—in fossil beds about 200 million years old in China, South Africa, and Texas.

Among the most remarkable transformations that took place as the mammals emerged are the ones that can be observed in fossils of the lower jaws. In reptiles and primitive synapsids, the right and left lower jaws are each made up of a number of bones, one of which is the dentary, or tooth-bearing, bone. As synapsids

evolved, the dentary bone grew progressively larger until it took over the role of hinging the jaw to the skull. One of the other reptilian jawbones shrank until it vanished, whereas the other two shifted to the middle ear. There they became the anvil and the hammer, minute bones that transmit sound from the eardrum to the stirrup bone and, ultimately, to the inner ear. The shift in function seems bizarre until you realize that in reptiles, sound vibrations from the lower jaw travel through the skull bones to the inner ear, and that, along with the vibrations that travel from the eardrum, those vibrations are important sources of sensation.

Excellent "missing links" now exist for other major groups as well. Many fossil species show the transition from dinosaurs to birds. *Archaeopteryx,* for instance, discovered in Europe in Late Jurassic fossil beds about 150 million years old, had teeth. Slightly younger fossils, from the Chinese Lower Cretaceous, about 140 million years ago, had more birdlike features. *Sinornis,* for instance, had wings it could fold against its body, grasping feet with an opposable toe, and tailbones fused into a single element. *Confuciusornis* sported the first toothless beak. Lower Cretaceous rocks in Spain, about 130 million years old, have yielded *Iberomesornis,* which had a large, keeled breastbone to which powerful flight muscles were anchored. Still, the creature had the primitive long backbone of a dinosaur.

Such bird fossils are now joined in the web of ancient life-forms by numerous, recently discovered fossils of nonflying, nonavian dinosaurs, closely related to *Velociraptor* of *Jurassic Park* fame. Those fossils, such as *Microraptor* and *Caudipteryx,* had well-developed feathers, suggesting that feathers originally served other functions, such as insulation, long before they became useful for flight [*see "Bird's-eye View," by Matthew T. Carrano and Patrick M. O'Connor, May 2005*].

Another transition that is now well documented is the conquest of the land by the amphibians. For decades the only good intermediate fossil between fishes and amphibians was *Ichthyostega,* from the Late Devonian epoch (about 360 million years ago) of Greenland and Spitzbergen. Although *Ichthyostega* resembled many amphibians in having well-developed legs, a complete shoulder girdle, and hips fused to the backbone, it still had fishlike gill slits, a sensory system on its face for detecting underwater currents, and a long, fishlike tail fin.

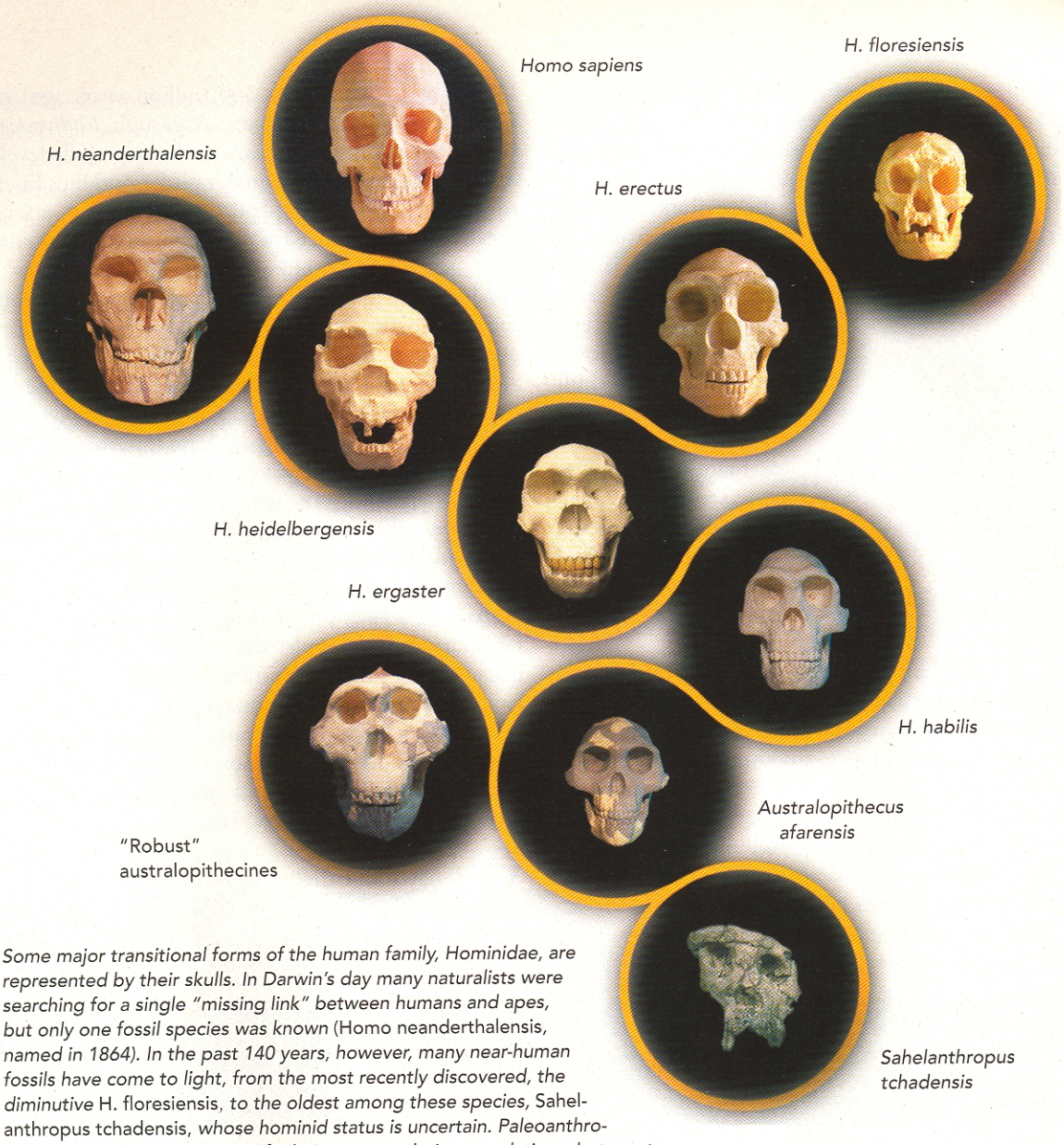
More recent discoveries, such as *Acanthostega* from the same beds, show that the picture is much more complicated and interesting [*see illustration at left*]. *Acanthostega* had ear bones that were still adapted for underwater hearing, a longer tail fin than *Ichthyostega,* and better-developed gills, making it more primitive and aquatic than *Ichthyostega. Acanthostega* also had as many as eight toes on each of its four feet—rather than five, which became the standard in most early four-footed creatures. Apparently, its limbs were primarily adapted for swimming and walking along the bottom of a lake, rather than for crawling on land. Contrary to the popular story that four legs evolved because they enabled animals to crawl out onto the land (to escape drying ponds, chase new food sources, and so forth), it now appears that legs evolved for walking underwater (as most salamanders still do today). They became secondarily useful on land, because they were already in place.

Jawbones that once functioned only for eating evolved and later became ear bones needed for hearing.

What about the transitional forms that led to our favorite species, *Homo sapiens*? Not long ago, the fossil record of the human family was severely limited, and readily thrown into confusion by a single fraudulent "fossil" such as the 1912 hoax known as Piltdown Man. But in the past three decades new findings have exploded. In Chad, fossils of *Sahelanthropus* were discovered in beds between 6 million and 7 million years old. In Ethiopia, the new genus *Ardipithecus* and two new species of *Australopithecus (A. anamensis* and *A. bahrelghazali)* were unearthed in beds between 2 million and 5 million years old. Several species of our own genus, *Homo,* which goes back at least 2 million years, have now been identified.

In short, the human fossil record has become quite dense and complete, and the newfound samples have led to some surprises. For example, contrary to the expectations of earlier anthropologists, the fossils show that bipedalism arose before enlarged brains, which came quite late in human evolution.

The origin of vertebrates as a whole once also



Some major transitional forms of the human family, Hominidae, are represented by their skulls. In Darwin's day many naturalists were searching for a single "missing link" between humans and apes, but only one fossil species was known (Homo neanderthalensis, *named in 1864). In the past 140 years, however, many near-human fossils have come to light, from the most recently discovered, the diminutive* H. floresiensis, *to the oldest among these species,* Sahelanthropus tchadensis, *whose hominid status is uncertain. Paleoanthropologists are hesitant to specify their exact evolutionary relations, but most agree that there were many human forms living contemporaneously. The thick yellow curves connecting the photographs of the skulls show one rough hypothesis about how the various species might be interrelated. But the illustration is intended only to represent some of the major hominid fossil finds, rather than serve as a definitive family tree.*

presented a frustrating gap in the fossil record. Biologists could examine the many living animals (such as lancelets and sea squirts) that represented stages in the transition from the invertebrates to the earliest jawless fishes. Until recently, however, few good fossils had been identified from beds older than about 480 million years, near the beginning of the Ordovician period. What's more, they were only scattered bony scales and plates.

But recent discoveries in China from the Middle Cambrian epoch, between 510 million and 500 million years ago, have included not only the earliest relatives of the lancelets, but also some soft-bodied specimens that appear to be the earliest vertebrates. Thus, backboned animals can now be traced all the way back to the Cambrian, when most of the modern branches of animals originated.

As the 150th anniversary of Darwin's *Origin* approaches, the fossil evidence now available would make Darwin proud, rather than apologetic. Evolutionary biologists can also look forward to many more discoveries. Some will come as a surprise, like the early small-brained bipedal hominids. Some will force paleontologists to revise their ideas about evolutionary events. But the fossil record is no longer the embarrassment that it was in Darwin's day. □