What missing link?

Reports of huge gaps in the fossil record have been greatly exaggerated, says geologist **Donald Prothero**

WHEN Charles Darwin published *On the Origin of Species* in 1859, there was relatively little evidence in the fossil record of evolutionary change. Darwin spent two chapters of his book apologising for the paucity of the fossil record, but predicted that it would eventually support his ideas.

What Darwin was bemoaning was the lack of "transitional" fossils – those with anatomical features intermediate between two major groups of organisms. At the time, such fossils were conceived as "missing links" in the "great chain of being" from lowly corals through higher organisms such as birds and mammals to humans (and ultimately to God).

We now know this is a misconception. Life does not progress up a hierarchical ladder from "low" to "high" but is a branching bush with numerous lineages splitting apart and coexisting simultaneously. For example, apes and humans split from a common ancestor 7 million years ago and both lineages are still around. Similarly, corals and sponges did not vanish when more advanced lineages of worms branched out 600 million years ago.

For this reason the concept of "missing link" is a misleading one. A transitional form does not need to be a perfect halfway house directly linking one group of organisms to another. It merely needs to record aspects of evolutionary change that occurred as one lineage split from another. They don't even have to be fossils: many living lineages have transitional features.

Darwin's 1859 prediction that transitional forms would be found was quickly confirmed. In 1861 the first specimen of *Archaeopteryx* – a classic transitional form between dinosaurs and birds – was discovered, and in the 1870s the iconic sequence of fossil horses was documented. By the time of Darwin's death in 1882 there were numerous fossils and fossil sequences showing evolutionary change, especially among invertebrates.

Evidence of evolution in the fossil record has vastly increased since then. Yet the idea still persists that the fossil record is too patchy to provide good evidence of evolution. One reason for this is the influence of creationism. Foremost among their tactics is to distort or ignore the evidence for evolution; a favourite lie is "there are no transitional fossils".

This is manifestly untrue. We now have abundant evidence for how all the major groups of animals are related, much of it in the form of excellent transitional fossils.

Recently palaeontologists have begun to strike back, pointing out the wealth of evidence for evolution in the fossil record and publicising their discoveries when they represent important transitional forms, something that perhaps was lacking in the past. Many examples are provided in my new book, *Evolution: What the fossils say and why it matters* (Columbia University Press). Just a few of these are given on the pages that follow. ▶

IMAGE SOURCE LARRY WILLIAMS/CORBIS

1

Velvet worms

The Cambrian period (542 to 488 million years ago) was a pivotal time in the history of life, an era of rapid evolutionary innovation in which most of the animal phyla we recognise today made their first appearance. One of these was Arthropoda: insects, spiders, scorpions, crustaceans and their relatives – perhaps the most successful group of animals the world has ever known.

A classic example of a transitionary form links the arthropods to the lineage they split from in the Cambrian, namely, the nematode worms. These are the "velvet worms" or Onychophora.

In many respects, the velvet worms resemble nematodes, but they also have key attributes of the arthropods – most notably segmented legs that end in hooked claws. They also have many other features found in arthropods but not nematodes, including an outer layer made of chitin, which they moult on a regular basis, antennae, compound eyes and arthropod-like mouthparts.

Fossilised examples of early velvet worms are known from a handful of amazing fossil deposits that have preserved soft body parts, in particular the middle-Cambrian Burgess Shale in British Columbia, Canada, and the slightly older Chengjiang fauna from Yunnan province in China. There are also around 80 species of velvet worms living today, mostly found in the vegetation of tropical forests.

You could not ask for a better "missing link" between the nematodes and the arthropods, except it's not missing – we've known about velvet worms for over a century in both the living fauna and the fossil record.

Velvet worms both fossilised and living are a classic transitional form

2

Lancelets

Another key transition in animal evolution was the appearance of the vertebrates. For more than a century, evidence has been accumulating from anatomy and embryology that the Chordata phylum (which includes the vertebrates) evolved from the echinoderms – sea urchins, starfish and their kin. This has now been corroborated by molecular biology. We also have an array of fossils and living organisms to tell the story of the transition.

One of these is the living phylum Hemichordata (the acorn worms and filter-feeding pterobranchs). These are neither echinoderms nor chordates but share features with both. Next up are the sea squirts, or tunicates. Though adult sea squirts are similar to pterobranchs, the larvae look much like primitive fish, with a muscular tail supported by a "backbone" of cartilage, the notochord – the defining feature of the chordates.

The transitional sequence continues with a group of obscure invertebrates called the lancelets. These resemble tunicate larvae, and probably evolved from a tunicate-like creature through "neoteny" – retention of juvenile features in adulthood. With a notochord, muscular tail, gill slits, a digestive tract along the belly and many other chordate features, lancelets are the most fish-like invertebrates known. They have been around since the Cambrian: we have a number of good lancelet fossils such as *Pikaia* from the Burgess Shale and similar fossils from Chengjiang.

Cambrian rocks in China have also yielded fossils of the earliest-known vertebrates, the soft-bodied jawless fish *Haikouella, Haikouichthys*, and *Myllokunmingia*. These creatures did not yet have a hard bony skeleton, but have all the other features of jawless fish supported by a skeleton of cartilage. Placed in sequence, the acorn worms, tunicates, lancelets and soft-bodied jawless fish show the complete set of steps needed to evolve a vertebrate from an invertebrate ancestor.

3

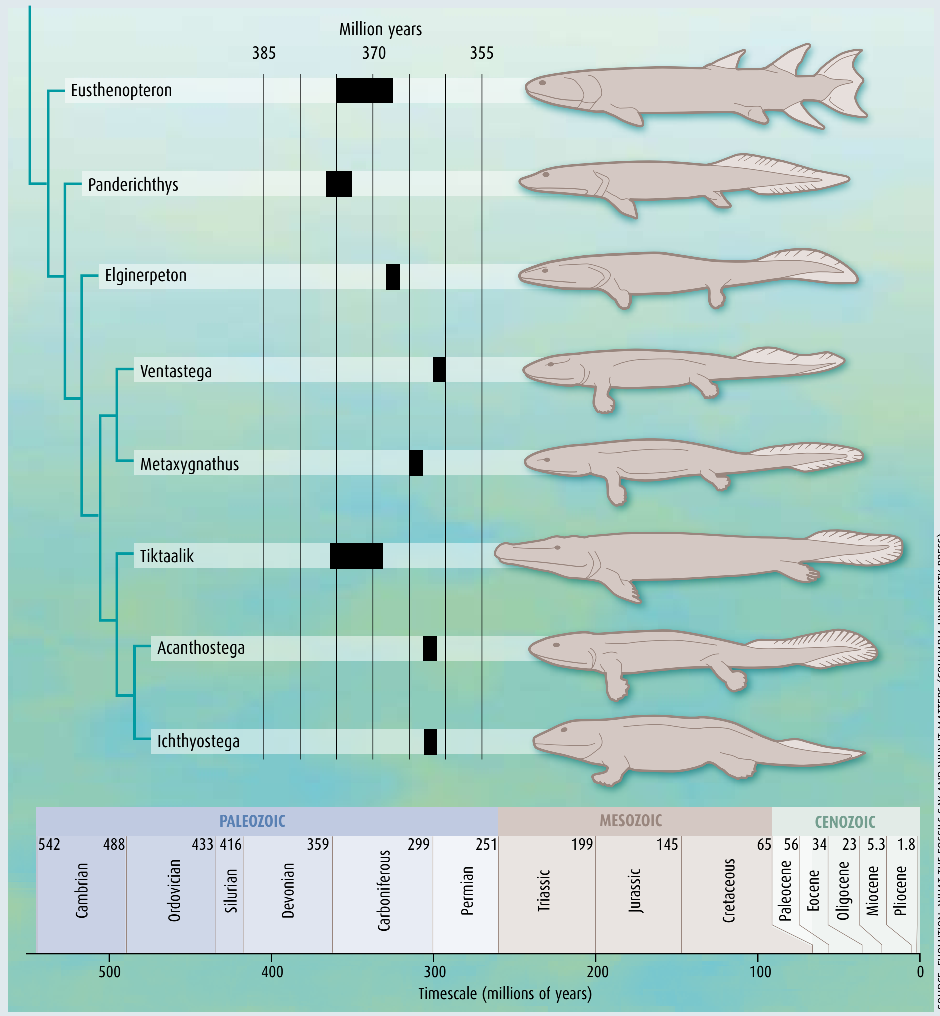
Fishibians

Perhaps the most complete set of transitional fossils is the so-called "fishibian" sequence showing the steps by which fish crawled out of the water and onto the land during the Devonian period (see Illustration, right). The first of these to be discovered was *Ichthyostega*, in 1932, though it was not properly described until 1996. Its limbs and skull were amphibian-like, but it had a fish-like tail and gill coverings, as well as a classic fish characteristic: a lateral-line sensory system for detecting currents in water. Since then an incredible array of fishibians has been found spanning the entire transition, from the distinctly fish-like *Eusthenopteron* to the four-legged amphibian *Hynerpeton*.

The latest fishibian is *Tiktaalik* from Ellesmere Island in the Canadian Arctic (*New Scientist*, 9 September 2006, p 35). It had fish-like scales, jaws and palate, but – like amphibians – it had a mobile neck and head, an ear capable of hearing in air, and bones in the fins that were intermediate between those of fish and *Acanthostega*. The fossil record of the fish-to-amphibian transition is now among the best documented of all.

FROM FISH TO TETRAPOD

The "fishbian" sequence is one of the most complete in the fossil record



SOURCE: EVOLUTION: WHAT THE FOSSILS SAY AND WHY IT MATTERS (COLUMBIA UNIVERSITY PRESS)

"You couldn't ask for a better missing link – except that it's not missing. We've known about it for more than a century"

4

Synapsids

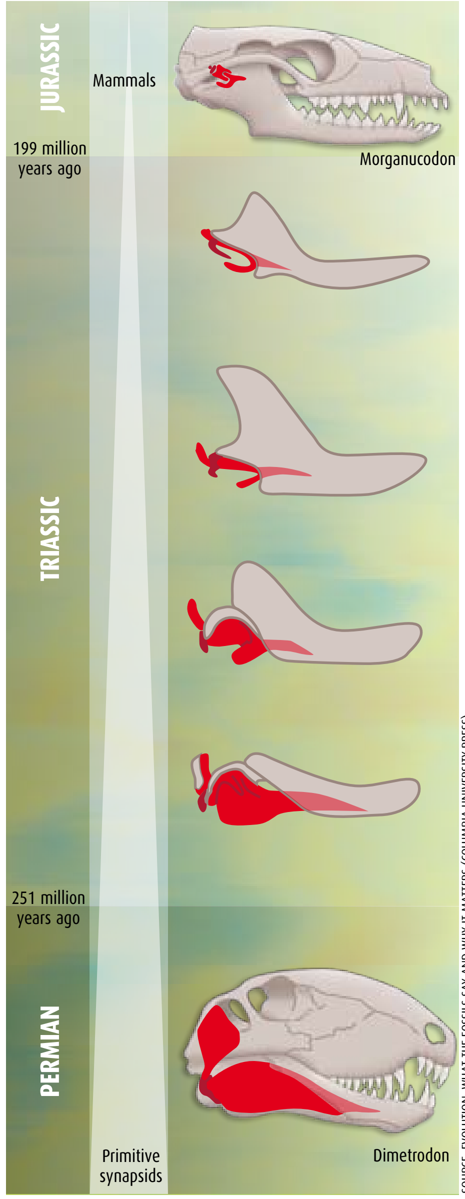
Another excellent example of a transitional sequence is the evolution of mammals from their ancestors, the synapsids. These were once called "mammal-like reptiles", but that term is no longer used because synapsids are not reptiles – the two groups evolved in parallel from a common ancestor.

In this instance, we have hundreds of beautiful fossils of skulls as well as many complete skeletons that document the transition over 100 million years from the late Carboniferous to the early Jurassic.

The earliest synapsids would have looked just like lizards to most people, but they already had the characteristic feature of synapsids – a lower temporal opening on the back part of the skull, which allowed for the attachment of, and gave room for, increasingly large and complex jaw muscles. By the early ▶

FROM JAWBONES TO EAR BONES

As mammals evolved from reptile-like synapsids, part of their lower jaw migrated into the ear to become the hammer and anvil. The sequence of events is preserved in the fossil record



SOURCE: EVOLUTION: WHAT THE FOSSILS SAY AND WHY IT MATTERS (COLUMBIA UNIVERSITY PRESS)

Permian, we find more mammal-like synapsids, such as the finback *Dimetrodon* (familiar from children's dinosaur books, but it's not a dinosaur). Although it was primitive in most respects, it had several advanced mammalian features, including specialised canine teeth for stabbing.

The late Permian was dominated by a wide array of dog- and bear-sized synapsids. Some of these were very mammal-like, with highly specialised teeth and a larger temporal opening to accommodate larger jaw muscles, and eventually muscles that would have given them the ability to chew. They also had the beginnings of a "secondary palate", which separates the mouth from the nasal passages and allows simultaneous eating and breathing. These late Permian synapsids had a much more upright, mammal-like posture than the sprawling *Dimetrodon*.

Among the striking evolutionary changes occurring in the synapsids was in their lower jaws. Most reptiles have several bones in the lower jaw, and *Dimetrodon* shares this characteristic. But mammals have only a single lower jawbone, the dentary. Throughout synapsid evolution, we see the gradual reduction of the non-dentary elements of the jaw as they are crowded towards the back and eventually lost. The dentary bone, in contrast, gets larger and takes over the entire jaw. In the final stage of evolution, the dentary bone expands until it makes direct contact with the skull and develops a new articulation with it (see Illustration, left). The old reptilian jaw articulation is lost, but there is one amazing transition fossil, *Diarthrognathus* from the early Jurassic of South Africa, that has both jaw articulations in operation simultaneously.

Where did the rest of the non-dentary bones go? Most were lost, but the articular bone and the corresponding quadrate bone of the skull are now the malleus ("hammer") and incus ("anvil") bones in your middle ear. This may seem bizarre until you realise that most reptiles hear with their lower jaws, transmitting sound from this to the middle ear through the jaw articulation. In addition, during embryonic development, the middle ear bones start in the lower jaw, and then eventually migrate to the ear.

In the Triassic and early Jurassic, the protomammal story culminated in the most advanced of all the synapsids, the cynodonts. They had a mammal-like posture, a fully developed secondary palate, a large temporal opening for multiple sets of jaw muscles allowing complex chewing movements, and highly specialised molars and premolars for grinding and chewing. Some of them probably had hair. Many of the later species of cynodonts are so mammal-like that it has long been controversial as to where to draw the line between true mammals and the rest of the synapsids.

The oldest fossils that palaeontologists now agree are mammals come from the late Triassic. They were shrew-sized, with a fully developed joint between the dentary bone and the skull, and three middle-ear bones. Thanks to the fossil record, we have a full picture of how they evolved from synapsids.

5 Ceratopsians

Of all the lies about transitional fossils told by creationists, none are as egregious as the claim that there are no intermediate forms among the dinosaurs. The dinosaur fossil record is actually good, with transitional fossils connecting all the iconic dinosaur groups to the earliest dinosaurs of the Triassic and, ultimately, to the common ancestor of all dinosaurs.

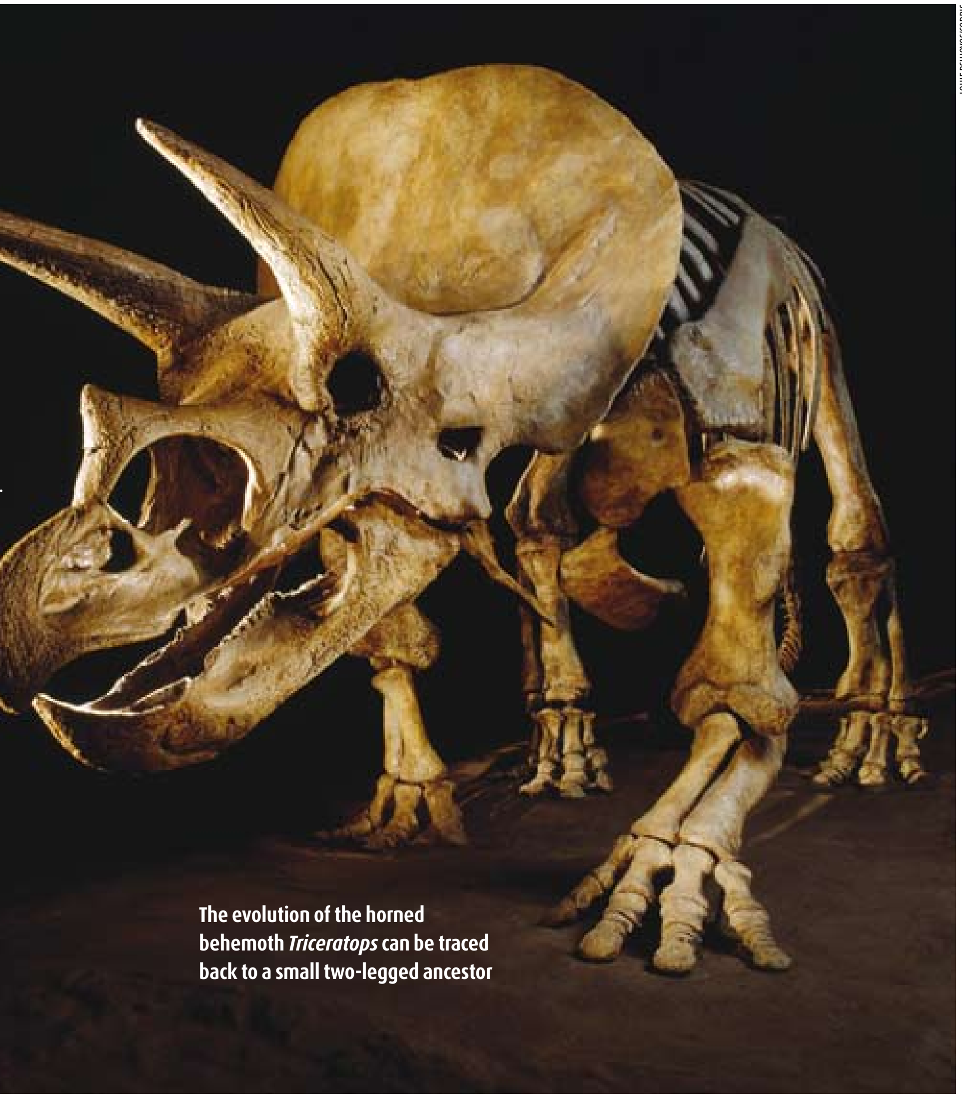
For example, we have fossils showing the evolution of the huge, long-necked sauropods such as *Brachiosaurus* from transitional forms known as prosauropods. Others show the ancestry of the large predatory theropods such as *Tyrannosaurus rex*, the duck-billed dinosaurs, stegosaurs and ankylosaurs.

One striking example is the horned dinosaurs, or ceratopsians. The best known is *Triceratops*, but this was only one of a dozen or more horned dinosaurs wandering around in the late Cretaceous with numerous variations including the number and shape of horns, and size and shape of neck frills.

All of these late ceratopsians are descended from earlier dinosaurs that were also large and quadrupedal with a neck frill, but lacked horns, such as *Protoceratops, Leptoceratops* and *Graciliceratops*. These in turn can be traced back to the early Cretaceous *Psittacosaurus*, which was small and bipedal, but still had characteristic ceratopsian features such as a neck frill and a "beak".

The entire ceratopsian lineage can now be traced back to a newly described late Jurassic dinosaur, *Yinlong*. Its name means "hidden dragon" – it hails from the region of the China where *Crouching Tiger, Hidden Dragon* was filmed. It was also small and bipedal, but the bones in the back of the skull are intermediate between those found in all ceratopsians and those in their nearest relatives, the pachycephalosaurs, which had a thick dome of bone over their skulls. You could not ask for finer examples of transitional dinosaurs.

"The fossil record of the dinosaurs is actually good, with transitional forms of all the iconic groups"



The evolution of the horned behemoth *Triceratops* can be traced back to a small two-legged ancestor

LOUIE PSIHOYOS/CORBIS

6 Rhinos

We don't just have a good record of the evolution of early mammals. The entire evolutionary history of mammals is probably better known than that of any group of vertebrates. We have excellent transitional forms that demonstrate the evolution of rodents, rabbits, cats, dogs and others. Horse evolution is well documented, but what is less well known is the excellent fossil record of their relatives, the rhinoceroses and tapirs.

All horses, tapirs and rhinos can be traced back to a common ancestor in the late Paleocene of Asia. In fact, the earliest ones look so similar that only a specialist can tell them apart using subtle differences in the cusps and crests of their teeth, and slight variations in the skull and skeleton.

Through the Eocene, the fossil record shows how the horse, rhino and tapir lineages diverged. Tapirs, for example, develop from animals about half a metre high, such as *Homogalax*, to larger creatures with teeth adapted for leaf eating and a characteristic notch in the nasal region, which indicates the presence of a muscular proboscis. This notch develops gradually until it reaches the advanced stage seen in living forms.

The fossil record of the rhinoceroses is even more complete. Starting with dog-sized creatures, such as the early Eocene *Hyrachyus*, that are barely distinguishable from early tapirs and horses, fossil rhinos gradually diversify into a wide variety of forms. Some became large and hippo-like, others developed long legs and slender bodies for running. Some of these "running rhinos" became gigantic, culminating in the huge indricotheres, which were about 7 metres high at the shoulder and weighed 20 tonnes. None of these early rhinos had horns.

The living rhino family began in the middle Eocene with primitive creatures like *Teletaceras*, which looked much like a running rhino except for the distinct combination of a chisel-like upper tusk and pointed lower tusk, which defines the modern family. Throughout their evolution, modern rhinos show numerous changes in their teeth, size and shape, including two independent cases of evolving horns on the nose, three independent evolutions of dwarfism, and three independent occurrences of fat-bodied, short-legged hippo-like lineages. Most of these lineages vanished during an extinction at the end of the Miocene; those lineages that persisted in Africa and Eurasia were the ancestors of today's five living species. ▶

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Giraffes

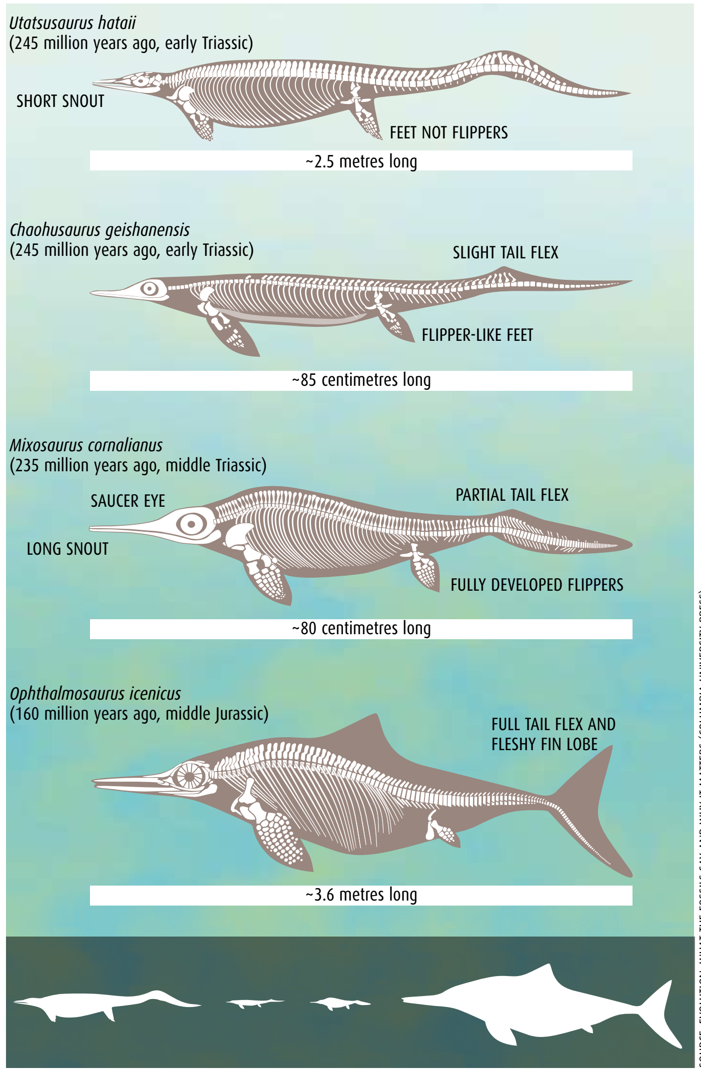
How did the giraffe get its long neck? This question has puzzled biologists as far back as the early 18th century naturalist Jean-Baptiste Lamarck, who famously – and wrongly – speculated that the giraffe's ancestors had stretched their necks in search of food and passed this "acquired characteristic" onto their offspring.

The giraffe fossil record is fairly good, with a wide variety of species known from the Miocene. These sported a range of weirdly shaped horns, but all had short necks rather like that of the only other living species of giraffid, the okapi. Only in the late Miocene do we see the fossils of long-necked giraffes. Like modern giraffes, they have an extra vertebra in the neck – recruited from the back – and lengthened neck vertebrae.

Until recently, there was no fossil evidence linking the long-necked giraffes to their short-necked relatives. But as my book went to press, news emerged that Nikos Solounias of the New York Institute of Technology had described a fossil giraffe from the late Miocene and early Pliocene. Its neck is a perfect intermediate between the short-neck ancestors and their long-neck descendants.

SEAGOING LIZARDS

The marine reptiles called Ichthyosaurs evolved from lizard-like ancestors in the Triassic period. The fossil record shows them becoming progressively more dolphin-shaped over time



SOURCE: EVOLUTION: WHAT THE FOSSILS SAY AND WHY IT MATTERS (COLUMBIA UNIVERSITY PRESS)

Ichthyosaurs

8

During the Mesozoic era, numerous groups of land-dwelling reptiles took to the waters and gradually evolved a fully marine lifestyle. These include the dolphin-like ichthyosaurs, the "Loch Ness monster" plesiosaurs and the giant swimming monitor lizards known as mosasaurs. The fossil record documents each of these transitions. Typical is the story of the ichthyosaurs (see Illustration, left).

The earliest known ichthyosaur ancestor is *Nanchangosaurus* (not illustrated) from the early Triassic of China, which looks almost entirely like a lizard except for subtle features of the skull and the snout that connect it to ichthyosaurs. Then comes *Utatsusaurus* from Japan, which had a slightly more ichthyosaur-like body, but a short snout and no signs of flippers. More advanced was *Chaohusaurus*, which had feet that were a little more paddle-like and a slight downward flexure of the spine – indicating the beginnings of a dolphin-like tail fin – but the short snout remained and it had small eyes. *Cymbospondylus* from the Middle Triassic of Nevada also retained the primitive hand and foot structure and short snout, but the downward flexure of the tail vertebrae is more pronounced. Finally, *Mixosaurus* from the middle Triassic of Germany looks almost entirely like an ichthyosaur with a long snout, saucer eyes and fully developed paddles on the front and hind limbs. But it still has a transitional feature – its tail was only slightly flexed downward and is not fully developed into the downward flexed tail fin seen in the classic ichthyosaurs of the late Triassic and Jurassic.

Pinnipeds

As we have seen with fishibians and the marine reptiles of the Mesozoic, transitions from water to land and back again provide some of the best sequences in the fossil record. The same is true of mammals. The evolution of whales from land mammals related to hippos has been much discussed in recent years. A less well-known example is the evolution of pinnipeds, or seals, sea lions and walruses.

For decades, we had good anatomical evidence that the pinnipeds were descended from primitive bears. Recently, the early Miocene fossil *Enaliarctos* has provided a beautiful transitional form between the two groups (*Science*, vol 244, p 60). Although superficially like a seal, *Enaliarctos* lacked most of the specialisations in the skull, ears and nose that modern pinnipeds require for their aquatic lifestyle. In addition, its "flippers" had long toes and claws, halfway between bear paw and pinniped flipper. From *Enaliarctos* there was a great evolutionary radiation of seals and sea lions in the middle and late Miocene, all of which appear in the fossil record.

Even more striking is the fossil record of walruses. The most primitive forms from the early Miocene looked very similar to sea lions, though they are larger and more robust, with the beginnings of the size difference between males and females seen in modern walruses.

Slightly later we have *Imagotaria*, which has the beginnings of tusk-like canines and the simplified peg-like cheek teeth typical of modern walruses. In the late Miocene, there are at least eight kinds of walrus, most of which had tusks on both the upper and lower jaw, as well as peg-like cheek teeth.

Modern walruses appear in the latest Miocene. They include *Alachtherium*, which had large tusks on the upper jaw, no tusks on the lower jaw and reduced molars. Next is *Valenictus*, which had the beginnings of a vaulted palate.

Today, walruses use their vaulted palate and piston-like tongue to create suction for hoovering up molluscs they have levered from the seabed with their tusks. Their peg-like molars then crush the shells. Fossilised walruses record the evolution of all these anatomical adaptations in amazing detail.

NORBERT ROSING/OSF

Today's highly specialised marine-living, mollusc-crunching walruses evolved from a primitive bear

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Manatees

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As our final example, let's return to the sea one last time with the sirenians, those peaceful shallow-water grazers including the manatees, dugongs and extinct relatives such as Steller's sea cow. Where did they come from? Many different primitive sirenian fossils are known, but the most spectacular is a 50 million-year-old manatee from Jamaica called *Pezosiren*.

Described in 2001, it has all the characteristics of a typical manatee, including the signature skull with the downturned snout, and the peculiar teeth that erupt from the back and are shed out the front (as in their close relatives, the elephants). It also has characteristic thick, dense ribs used for ballast. However, instead of flippers, the creature has four completely normal legs with feet for walking on land. One could not ask for a more clear-cut transitional form than *Pezosiren* – every other feature of the skeleton is typical of the manatees, but it was walking. *Pezosiren* probably had a hippo-like, semi-aquatic lifestyle – a clear link between the fully aquatic manatees and their land-living ancestors.

Creationists simply have no answer to such irrefutable evidence. Examples such as these are conclusive proof that evolution has occurred, and is still occurring. ●

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