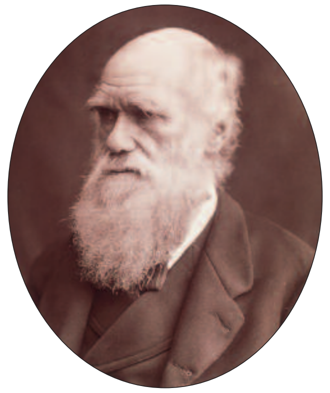
ORIGIN AND BEYOND



During a long life, Charles Darwin wrote numerous scientific papers, monographs, and some seven books. Apart from *The Origin of Species*, these included such topics as the biology of coral reefs and the ancestry of human beings (*above*).

DESPITE THE INSPIRATION AND WEALTH OF DATA HE HAD GATHERED DURING HIS YEARS ABOARD THE BEAGLE, DARWIN TOOK MANY YEARS TO FORMULATE HIS THEORY AND READY IT FOR PUBLICATION – SO LONG, IN FACT, THAT HE WAS ALMOST BEATEN TO PUBLICATION. NEVERTHELESS, WHEN IT EMERGED, DARWIN'S WORK HAD A PROFOUND EFFECT.

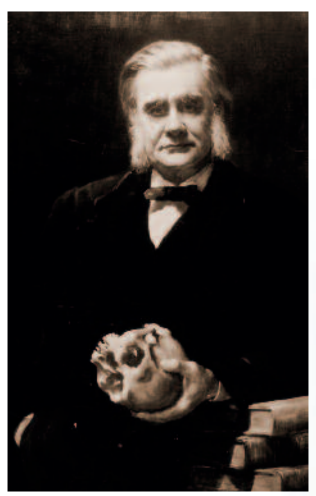
After his five-year round the world voyage, Darwin arrived back at the family home in Shrewsbury on 5 October 1836. The following year he moved to London, dispersed his collections to appropriate experts, and, in 1838, was appointed Secretary to the Geological Society of London, one of the most dynamic scientific societies of the day. He published the first edition of his Journal of researches, married his cousin Emma Wedgwood in January 1839, and later in the year their first child was born. The young naturalist was quickly transformed into an established family man and junior member of a London elite that led the world in newly developing academic sciences such as geology, zoology, and botany. Between 1842 and 1846 Darwin saw himself largely as a geologist, and published books on coral reefs, volcanic islands, and geological observations on South America.

DEVELOPING THE IDEA

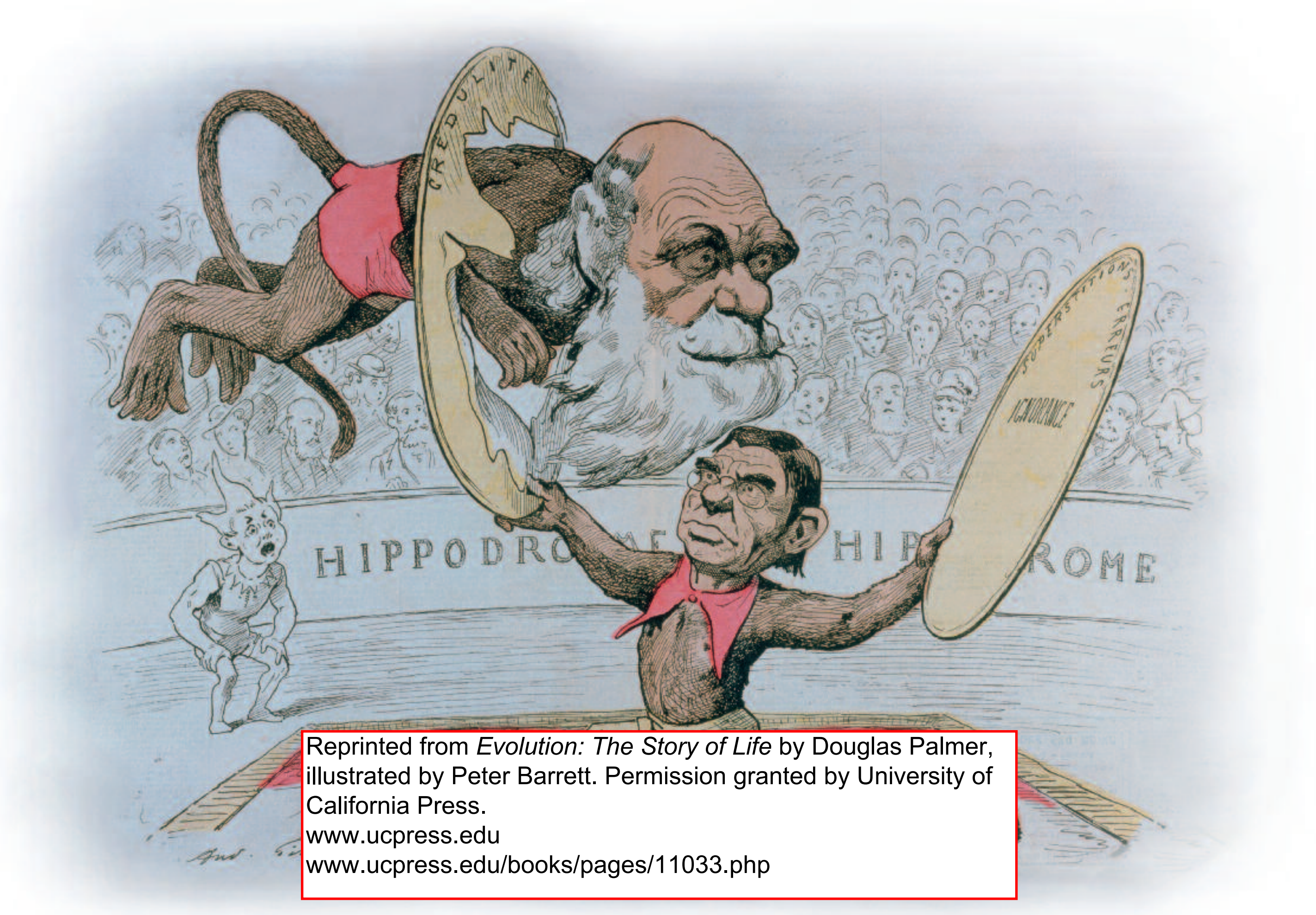
Meanwhile, however, Darwin was also developing his own ideas through a series of notebooks on species transmutation, biological evolution, and the implication of such ideas for mankind. In 1839 he wrote to Henslow, his Cambridge mentor, "I keep on steadily collecting every sort of fact, which may throw light on the origin & variation of species". He also began to receive important information about his specimens from experts such as the ornithologist John Gould, who alerted him to the fact the Galapagos finches were distinct but closely related species. Darwin investigated the breeding and artificial selection of domesticated animals, and learned about species, time, and the fossil record from the anatomist Richard Owen, who had worked on many of Darwin's vertebrate specimens and, in 1842, had "invented" dinosaurs as a separate category of reptiles.

By 1842, Darwin's evolutionary ideas were sufficiently advanced for him to produce a 35-page sketch and, by 1844, a 250-page synthesis, a copy of which he sent in 1847 to the botanist, Joseph Dalton Hooker. This trusted friend was sympathetic to his approach and was one of the first converts to 'Darwinian evolutionism'. By the 1850s, Darwin's following was extended to include the dynamic young zoologist Thomas Henry Huxley (1825–95). Meanwhile, the results of an 8-year study of barnacles, both living and fossil, were published between 1851 and 1854, establishing Darwin's credentials as a very able zoologist.

This research helped him develop the principle of divergence in speciation, which is most active with intense competition for limited resources. In other words, Darwin recognized that competition is a constant presence in nature and, as there is always some variation in populations, the result is natural selection of those adaptations that best fit the circumstances. Geographical isolation was just one of several possible conditions for speciation, with ecological pressures being equally if not more important.

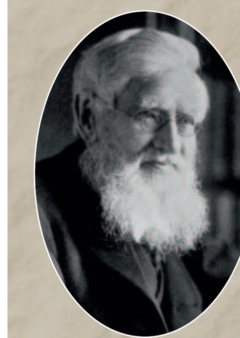


Thomas Henry Huxley's vehement support for the Darwin–Wallace theory of evolution through his writing and popular lectures helped the idea to gain more general acceptance and earned him the nickname of "Darwin's bulldog" (*above*).

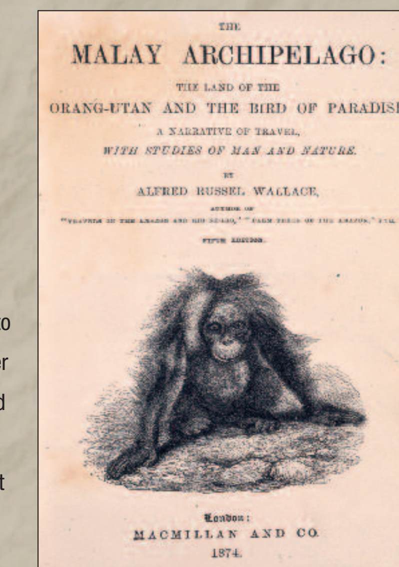


Because of his ideas about the descent of man, Darwin was frequently caricatured as a monkey – as in this 19th-century French cartoon where he is seen leaping through hoops of credulity, superstition, and ignorance. Philosopher and physician Émile Littré (1801–81), a well-known French supporter of Darwin's supposedly "irreligious" ideas, holds the hoops (*opposite*).

ALFRED RUSSEL WALLACE (1823–1913)



Alfred Russel Wallace was a school teacher and naturalist who gave up teaching to earn his living as a professional collector of exotic plants and animals from the tropics. He collected extensively in South America, and from 1854 in the islands of the Malay archipelago. From these experiences, Wallace realized that species exist in variant forms and that changes in the environment could lead to the loss of any ill-adapted variants with the continuing success and survival of those that were adapted. In other words, he had independently come to the same conclusions as Darwin over a key aspect of the theory of evolution. Early in 1858 Wallace sent his paper to the Linnean Society in London, and it was published under the title "On the tendency of species to form varieties: and on the perpetuation of varieties and species by natural selection", alongside an extract from Darwin's manuscript on evolution and part of a letter sent by Darwin to the American botanist Asa Gray in 1857 outlining his ideas.



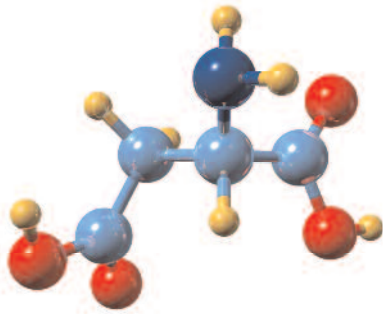
THE
MALAY ARCHIPELAGO:
THE LAND OF THE
ORANG-UTAN AND THE BIRD OF PARADISE
A NARRATIVE OF TRAVEL,
WITH STUDIES OF MAN AND NATURE.
BY
ALFRED RUSSEL WALLACE,
AUTHOR OF
FIFTH EDITION.
London:
MACMILLAN AND CO.
1874.

UNEXPECTED COMPETITION

In 1855, Darwin read with interest a theoretical paper by Alfred Russel Wallace, a young naturalist working in south east Asia, who argued that new species tend to arise in areas already occupied by a related species. By this time Darwin's friends were encouraging him to publish his theory before someone else came up with a similar one, and by spring of 1858 he had completed ten chapters of a projected two-volume work entitled *Natural Selection*. In June 1858, however, Darwin received a bombshell with the arrival of a new manuscript from Wallace, outlining his theory that continuance of certain varieties of species might be perpetuated by processes of natural selection.

To Darwin's dismay Wallace had independently come up with a key aspect of his evolutionary theory. Luckily, Darwin's network of scientific friends arranged a compromise co-publication by the Linnean Society, ensuring that Darwin's independent and earlier formulation of the idea was recognized. Although the Linnean Society papers were largely ignored by the scientific community, the emergence of Wallace as a competitor in the field of evolutionary theory shocked Darwin into action. In July 1858 he set to work on a book-length 'abstract' of his ideas, in preference to the longer work that he had planned. By May 1859 he was working on proofs, and on 24 November the 500-page *The Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life* was published. All 1250 copies of the initial print run sold on the first day.

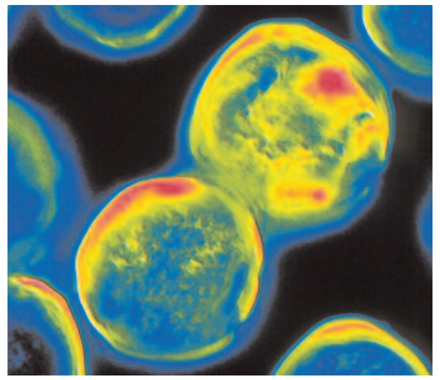
Darwin had been forewarned about the hostile reception his book would receive by the criticism that had been heaped on the evolutionary ideas contained in *Vestiges of the Natural History of Creation*, an anonymous work published in 1844. He deliberately avoided discussing the sensitive topic of human evolution, save only to predict that "Light will be thrown on the origin of man and his history". However, since he also concluded that 'all organic beings which have ever have lived on this earth have descended from some one primordial form, into which life was first breathed', his readers could easily draw their own conclusions. It was not until 1871, when the initial battles had largely been fought and won, that Darwin outlined his detailed views on human origins and the importance of sexual competition in all evolutionary stories.



THE PATTERN OF LIFE

DARWIN DEVELOPED HIS IDEAS ABOUT EVOLUTION BASED ALMOST ENTIRELY ON THE STUDY OF LIVING SPECIES – AT THE TIME, THE STUDY OF LIFE'S LONG HISTORY AND THE FOSSIL RECORD WAS IN ITS INFANCY, AND IT WAS SOME TIME BEFORE THE FOSSILS ULTIMATELY PROVED HIS THEORY RIGHT.

Amino acids are the building blocks of proteins that are, in turn, the essential ingredients of organic life (*above*).



The idea that all life, no matter how complex, has descended from microscopic single-celled microbes that live in the sea was revolutionary and disturbing for many Victorian minds (*above*).

Museums built to house the wealth of new discoveries were conceived as "cathedrals", where the public could worship the newly emerging "gods" of science and technology (*right*).

By the mid-19th century, when Darwin was developing his theory of evolution, it was clear that there was some pattern to the distribution of fossils throughout the rock record. The earliest fossiliferous strata were Cambrian in age, and dominated by sea-living invertebrates, including extinct groups such as trilobites and graptolites. The first fish and land plants appeared in the Devonian, and reptiles and amphibians arrived in the Carboniferous "coal measures" – remains of the first extensive forests.

The Mesozoic Era was seen as the Age of Reptiles, following the discovery of extinct marine forms such as the ichthyosaurs and plesiosaurs, the flying pterosaurs, and finally the dinosaurs, which were not recognized as an independent fossil group until 1842. By this time, it was also known that primitive mammals had been around in Jurassic times, and by the 1860s birds were known to have first appeared in the Late Jurassic. The one group that did not seem to turn up in the fossil record were humans.

In the 1820s the eminent French anatomist Georges Cuvier had debunked earlier claims regarding the existence of human remains (thought to be victims of Noah's Flood), although he had also discovered and named the first fossil primates from Cenozoic strata in France. Consequently, it was still possible to claim that humanity was the result of some act of special creation by a deity. However, by the mid-19th century there was mounting archaeological and fossil evidence that human-like remains occurred alongside those of the extinct animals of the Ice Age. By 1868, the first extinct human-related species – *Homo neanderthalensis* – was named, but it was not for another 20 or so years that the fossil antiquity of humans and the growing evidence for human evolution was generally accepted by the academic community.

MISSING LINKS

Darwin was well aware of the nature of the fossil record in the first half of the 19th century. His theory of evolution required that there should be fossil evidence for ancestral forms shared by descendent groups, because ultimately all life has diverged and descended from a common ancestor. But he knew only too well that such common ancestral forms for major groups had not been found, and he blamed their absence primarily on the incompleteness of the rock and fossil record.

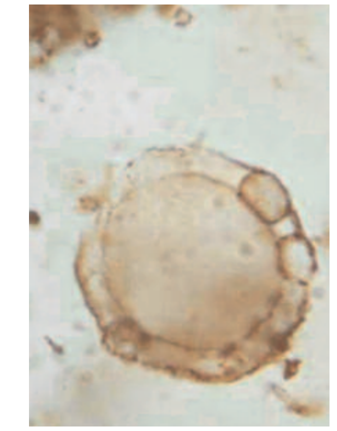
His other major problem was the lack of fossils from Precambrian strata. Since several different invertebrate groups, such as brachiopods and trilobites, appeared in early Cambrian strata, they must have had ancestors that lived in Precambrian times. Darwin admitted that their absence was a problem for his theory, but predicted that Precambrian fossils would turn up eventually, He was right, though it was not until the 1950s that the first convincing evidence of Precambrian life was found in Russia and Canada. Since then, the record has been extended back to at least 3500 million (3.5 billion) years ago, providing indications that the sudden diversity of Cambrian life is more apparent than real.

Among the most ancient remains of life are chemical fossils, so called because all that remains of the original cellular material are complex organic molecules that can be distinguished from inorganic molecules. These are preserved as particles of graphitic carbon within metamorphosed shales from Greenland, over 3.7 billion years old .

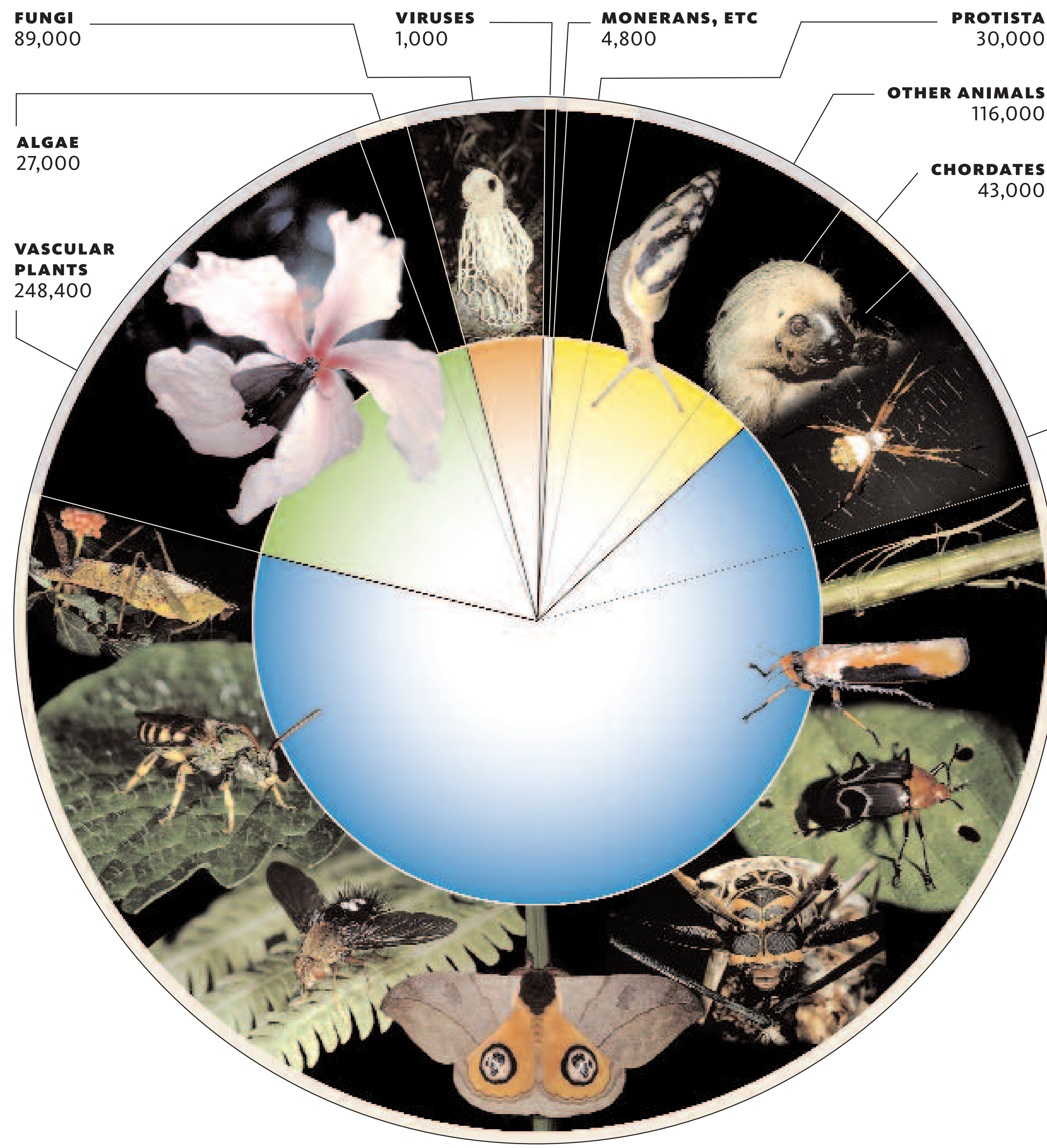
BRIDGING THE GAPS

Modern genetic analyses of the simplest known living organisms show that life can be separated into three major domains. The Bacteria are the most ancient and primitive, followed by the Archea from which the Eukaryota evolved less than 2 billion years ago. The eukaryotes include all the more familiar organisms, from single-celled amoebae to multicellular plants, animals, and fungi.

Today, Darwin's problem with the incompleteness of the fossil record has been largely resolved with the discovery of many extinct fossil groups. These amply demonstrate many major evolutionary innovations such as the development of the tetrapod limb with the transition from aquatic fish to land-living tetrapods, the appearance of feathers and wings in dinosaurs and their flying descendants the birds, and the evolution of upright bipedal walking in our own primate ancestors.



Darwin's evolutionary expectations that fossils of primitive organisms would eventually be found in Precambrian strata were not confirmed until the 1950s, when microbial fossils were found in 2-billion-year-old chert from Canada's Lake Superior (*above*).



As this chart of known present-day species demonstrates (*left*), much of life's variety is concentrated in a few groups of organisms – notably arthropods and vascular plants. However, when more is known about the total diversity of life today, it is possible that microbial organisms will outnumber even these groups. While life in the past probably followed a similar pattern, the fossil record is heavily skewed in other directions – towards organisms with preservable hard parts, such as shelled molluscs.

THE VARIETY OF FOSSILS

WHILE THE TRADITIONAL IMAGE OF A FOSSIL MAY BE THAT OF AN ANCIENT BONE OR TOOTH TURNED TO STONE, THE TRUE DIVERSITY OF FOSSILS IS FAR GREATER, SINCE A FOSSIL CAN BE ANY TRACE LEFT BY FORMER LIFE AND SOMEHOW PRESERVED – THIS INCLUDES A VARIETY OF DIFFERENT MEANS OF PRESERVATION, AND ALSO EXTENDS TO TRACES OF THE WAY ANIMALS INTERACTED WITH THEIR ENVIRONMENTS.

The long history of the interdependence between insects and plants is revealed by this bee, preserved complete with orchid pollen in 15- to 20-million-year-old Miocene amber from the Dominican Republic (*above*).

The cadaver of "Otzi", a Neolithic hunter, found freeze-dried in a glacier in the Tyrolean Alps, preserves not only soft tissues, but also DNA. However, the long-term survival of such "protofossils" depends on the persistence of permafrost, which is much more ephemeral than rock (*below*).

Fossils provide the main evidence for the history and evolution of life on Earth. But this simple statement hides a more complex reality that has taken centuries to resolve. Essentially, fossils are the toughest and least destructible parts of organisms, although occasionally more delicate structures and tissues are preserved, such as when an entire body is freeze-dried in frozen ground.

Fossils vary in composition from mineralized bones and shells, to organic molecules preserved as blobs of bitumen, and the compressed, carbonized plant remains that we know as coal. However, they can generally be separated into just a few different kinds.

Chemical fossils are residual organic chemicals, such as the bituminous biomolecules recovered from Archean strata more than three billion years old. Generally, their true organic nature and chemical composition can only be resolved by sophisticated analytical equipment.

Body fossils, the remains of original tissues, are the most common fossils, represented by countless shells and bones, and their impressions left in the rock. Some have been chemically altered, and a rare few preserve soft tissues. This fossilized skin and muscle is usually preserved in ancient sediment when it has been replaced by inorganic minerals, such as the apatite (a phosphate) or pyrite (an iron sulphide).

Trace fossils are the marks left by a living organism on or within the sediment substrate – for example footprints, burrows and tooth or cutmarks. Most common are the burrows, and root traces of organisms that live or grow within sediment. Rarely is the maker of the trace preserved, but trace fossils provide very important evidence of certain environments such as tidal sandflats, and can prove the existence of ancient behaviours such as herding among certain plant-eating dinosaurs and the meat preparation techniques of Neanderthal hunters.

As we have seen, fossils preserved in the rock record are usually the most robust parts of an organism, especially mineralized skeletal materials such as shell, bones, and the tough woody tissues of plants, which can survive long after death of an organism. As a result, the fossil record is heavily biased towards organisms that have such tissues, and does not fully represent the diversity of life, especially among soft-bodied organisms that range from viruses and bacteria to giant squid.

These trilobite arthropods, perhaps buried alive while breeding in shallow water, were preserved by internal sediment moulds even as their mineralized exoskeletons dissolved away (*above*).

The bulk of body tissue in most organisms is composed of water and organic compounds that degrade rapidly following death. This organic matter also represents potential food for other organisms. In most natural environments any dead body is scavenged, consumed, and biologically degraded to some degree, leaving just the hard parts as potential fossils. Occasionally, however, a body may come to rest in a naturally preservative medium or location before it has deteriorated to any great extent. Fortunately for paleontologists there are many excellent media and circumstances under which soft tissues can and have been preserved. These range from freeze-drying in subzero temperatures to soaking in oil, salt, or resin.

HOW ARE FOSSILS PRESERVED?

While it is true that an entire mammoth or human can be freeze-dried in glacial sediments with their soft tissues and even some DNA preserved, such events are exceedingly rare. Frozen mammoths and humans such as the 5200-year-old Tyrolean Ice-man "Otzi" are not, strictly speaking, true fossils, since their enclosing icy sediments are themselves ephemeral on a geological timescale. Fossils preserved in amber can survive for much longer, but while organisms trapped in this ancient tree resin may seem perfectly preserved, appearances are deceptive. During the 1990s, attempts were made to recover DNA from amber insects, but claims of success were unfounded and did not pass the critical scientific test of consistently reproducible results. However, other proteins have been recovered from fossil remains, most recently collagen from the 68-million-year-old bones of a *Tyrannosaurus rex* dinosaur.

Our everyday experience of terrestrial environments shows why it is difficult to preserve any remains of land-living animals or plants. Our landscapes are full of animal and plant life, but what happens when they die? How often do we come across the bones of a bird, or even leaves buried in soil? Deciduous plant leaves may cover the ground in autumn, but over weeks and months they are degraded by fungi or bacterial decay and a variety of animals from snails to myriapods and earthworms. The bones may survive for a year or so, but acids in the soil and oxidation of the organic matrix soon weaken them – only teeth, with their tough dentine and enamel, last longer.

Some biological structures do survive well in soil – tough coated spores, seeds, and pollen that are adapted for survival in such conditions. Indeed, such structures may last long enough to be fossilized. Preservation of the soil and other surface sediments requires special conditions such as rapid burial instead of the normal processes of surface weathering, and erosion.

FLUKES OF PRESERVATION

So how is it that any fossil record of terrestrial life survives? And how come there are significant global reserves of terrestrial deposits such as coal, the compressed remains of ancient tropical forests, swamps, and bogs? The answer to both questions is that a combination of geological conditions has made it possible. Deposition of sediments and their organic remains in a generally subsiding landscape has buried them to such a depth that they survive subsequent erosion.

However, the bulk of the fossil record consists of the shells and bones of marine organisms that lived in shallow seas on the continental margins, and within their waters. Yet even ocean-floor sediments and their organic remains are ultimately destroyed by another inexorable geological process – subduction as a result of tectonic movements.

More than 99.9 per cent of all the life that has existed is extinct, but fossils can give us some idea of what life was like in the past, and how it evolved.

A MOUSE CADAVER

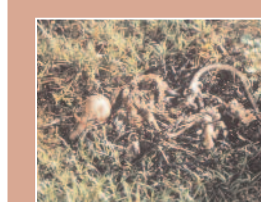
Decomposition after 3 days

Decomposition after 5 days

Decomposition after 7 days

Decomposition after 9 days

Decomposition after 15 days



Decomposition after 23 days

This sequence of photos shows how processes of decomposition and scaveng-ing rapidly destroy organic remains in most conditions.

RECONSTRUCTING THE PAST

Millimetre-sized shells of single-celled organisms, such as this foraminiferan, are abundant in the fossil record. They can be used as proxy measures of past climates, since the shells record ocean water chemistry at the time they were built (*above*).

IN ORDER TO UNDERSTAND THE PROCESSES OF EVOLUTION, WE MUST LOOK AT PLANTS AND ANIMALS WITHIN THEIR WIDER CONTEXT – THE ENVIRONMENT IN WHICH THEY EXISTED, THE FOOD SOURCES THAT WERE AVAILABLE TO THEM, AND THE COMPETITORS AND THREATS THEY FACED. PIECING TOGETHER A COMPLETE PICTURE OF SUCH ANCIENT ECOSYSTEMS CALLS FOR A VARIETY OF TECHNIQUES.

Today we take for granted scenes of the deep past populated with dinosaurs and other extinct fossil animals and plants. And, with the use of computer graphics, such images are getting more and more superficially realistic. However, they often use modern land and seascapes for the background and even modern plants that are not usually appropriate. In this book we rely on the more traditional art techniques that give a greater degree of flexibility, detail, and accuracy.

Even so, all such reconstructions are to some degree imaginative fictions, since there are no visual records beyond the 30,000-year-old artworks made by early modern humans who saw and depicted extinct animals such as the woolly mammoth, woolly rhinoceros, and giant deer. Beyond this in time, we know little of the coloration of extinct animals and plants apart from some indications of camouflage patterning. Detailed body shapes can be equally problematic, except through indirect inference and reconstruction of soft tissues, using our understanding of comparative anatomy. However, a few spectacular new finds of soft tissue preservation, dating back as far as Cambrian times, do provide some accurate information about body shapes.

Over the last 200 years, enormous progress has been made in our understanding of the life of the geological past. Most, but by no means all, fossil organisms can now be reconstructed with some degree of certainty as to their general appearance. The main exceptions are the plants and some of the larger vertebrates, because their entire body form is so rarely preserved in the sedimentary rock record. Plants are especially difficult because their numerous anatomical parts, such as pollen, leaves, woody tissues, and roots, tend to be separated one from another both during life and following death, and may be deposited widely in different sedimentary environments.

Fortunately, interpretation of the rock record and the associations of fossils from specific sites and stratigraphic levels is now sophisticated enough to allow reconstruction

William Buckland (1784–1856), (*above*), was one of the first people to attempt the reconstruction of life in the past – in this case an Ice Age hyena den discovered in Yorkshire in 1821. His conclusions inspired his friend William Conybeare's cartoon (*right*) showing Buckland himself entering the cave.

Catastrophic events such as the eruption of Vesuvius in AD79 preserve some of the most complete records of past life – even if they show the victims' dying moments (*far left*).

Delicate tissues such as those of angiosperm flowers are normally lost to the fossil record. Rare preservations, such as this 34-million-year-old *Florissantia*, from Eocene deposits in Colorado, USA, require special conditions in fine-grained sediments (*left*).

of some past environments and the inter-relationships of the various organisms that lived in them. Most fossil environments are waterlain, although in certain circumstances low-lying terrestrial environments may be preserved, but uplands are exceedingly rare. And there are still many problems of temporal resolution that make it impossible to determine whether the organisms actually lived together, died together, or simply had their remains jumbled together long after their death.

PIECING TOGETHER THE EVIDENCE

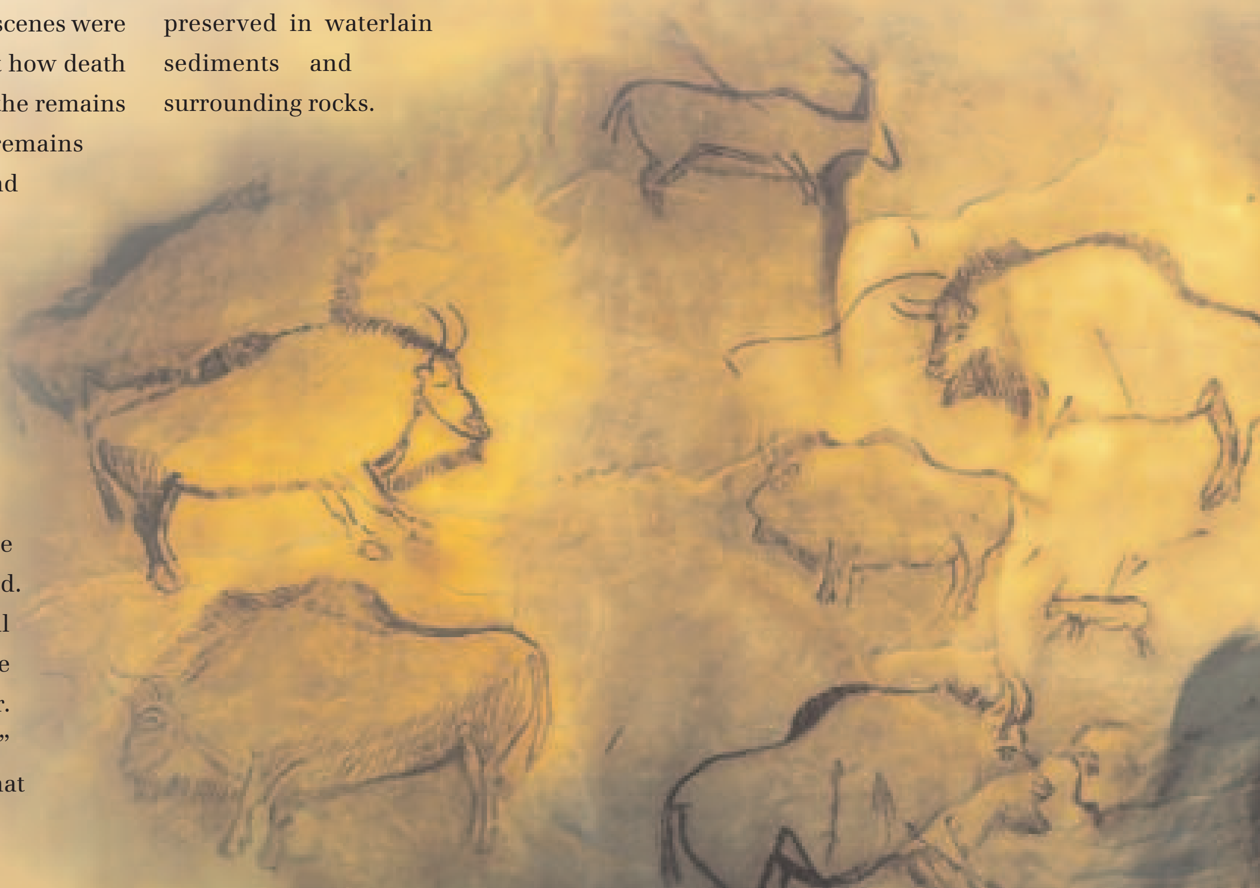
To understand all these factors, scientists have made detailed studies of the ecological relationships between living organisms and their environments. Over the 170 years since the first reconstructions of ancient scenes were attempted, we have learned a great deal about how death occurs in the natural world, what happens to the remains of plants and animals following death, how remains may be lost or recruited to the rock record, and what happens to them after burial, during the often complicated and destructive processes of fossilization.

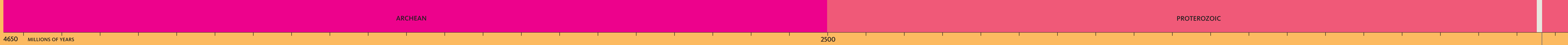
There are a few situations that tend to preserve organic remains particularly well. For body form and soft tissue preservation rapid entombment in a mummifying medium, such as cold dry air, ice, amber resin, or salt is necessary, but these are relatively rare in the geological record. Catastrophic and near-instantaneous natural burial processes can entomb a whole range of organisms that lived and died together. Such circumstances are known as "Pompeii" scenarios, after the pyroclastic erupion that engulfed the Roman town in AD79, preserving much of the structure, artefacts, and some of the inhabitants.

Volcanic eruptions, avalanches of sediment, dust-storms, and floods are common catastrophic events in the natural world, both on land and in water. They can overwhelm living communities and potentially preserve much of their life. And, if the post-mortem environment lacks oxygen – for example the fine sediments of a lake bottom, they may even preserve some soft tissues.

As will be seen from the reconstructions in this book, most marine fossil locations were in shallow waters and lagoons, and most of the terrestrial locations were in lake and river deposits, so the actual land environments are largely reconstructed from indirect information preserved in waterlain sediments and surrounding rocks.

Rock art, such as these engravings from North Africa, records an abundance and diversity of life forms that are not now present because of climate change and extinction aided by human hunting (*below*).





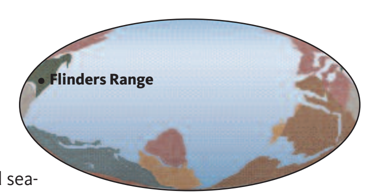
SNOWBALL EARTH
FLINDERS RANGE, SOUTH AUSTRALIA

Climate: widespread glaciation
Biota: low-diversity marine micro-organisms (eg acritarchs)

Common organisms: cold-tolerant micro-organisms

647–635 million years ago
Cryogenian Period of the Neoproterozoic Era

Latitude then: *c.*8°N
Latitude now: 31°S
Sea level: falling until end of glaciation, then rising rapidly
Original environment: global terrestrial ice sheets and sea-ice perhaps as far as the equator
Deposits: "Elatina formation" glacial deposits
Status: numerous accessible exposures of Elatina strata occur around Adelaide, South Australia
Preservation: the glacial deposits are devoid of fossils



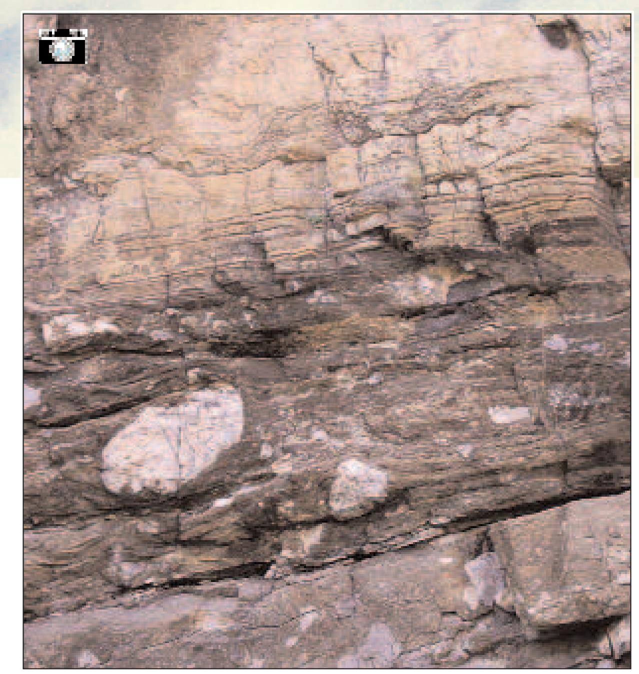
Earth *c.*640MA

Fossil site today

One of the most extraordinary phenomena in Earth's early history is that of repeated and extensive glaciation. According to the "Snowball Earth" theory, at least two, and perhaps four or more, glacial phases encompassed the Precambrian world from pole to pole. Theoretically, growing polar ice sheets reflected so much solar energy back into space that even the tropics were cooled sufficiently to ice over, with temperatures plummeting to -50°C, freezing the world's oceans.

The first glacial event occurred around 2.3 billion years ago, but the best known events are all late Proterozoic, dating to around 710, 640, and perhaps 580MA – known as the Sturtian, Marinoan, and Varangian glaciations.

Supposedly, the impact on environment and life was such that, in this frozen "icehouse" state, ocean productivity and the weathering of the land were shut down. Unable to photosynthesize, marine phytoplankton died off and the oceans became anoxic. Biological activity only revived in brief, hot interglacials. Such stop–start, "freeze–fry" processes were precursors to the subsequent explosion of Ediacaran life, and may be responsible in some way for that event. At least, that is the theory, but it is still far from proven.



1 dropstone

DROPSTONE (1) This metre-wide boulder – one of many found 'floating', surrounded by finer grained sediment – is a dropstone, formed when a melting iceberg released it to fall into soft sediment on the sea floor. No other natural mechanism can carry such large and heavy rocks out to sea, so the presence of dropstones is a useful indicator of glacial activity. This spectacular specimen occurs within the Late-Proterozoic (Sturtian) glacial strata of Namibia's Skeleton Coast, close to Narachaamspos. Carbonate rocks in the overlying strata lack dropstones: they show that, following the glacial event, the environment quickly returned to its normal hot subtropical phase.

CAMBRIAN | ORDOVICIAN | SILURIAN | DEVONIAN | CARBONIFEROUS | PERMIAN

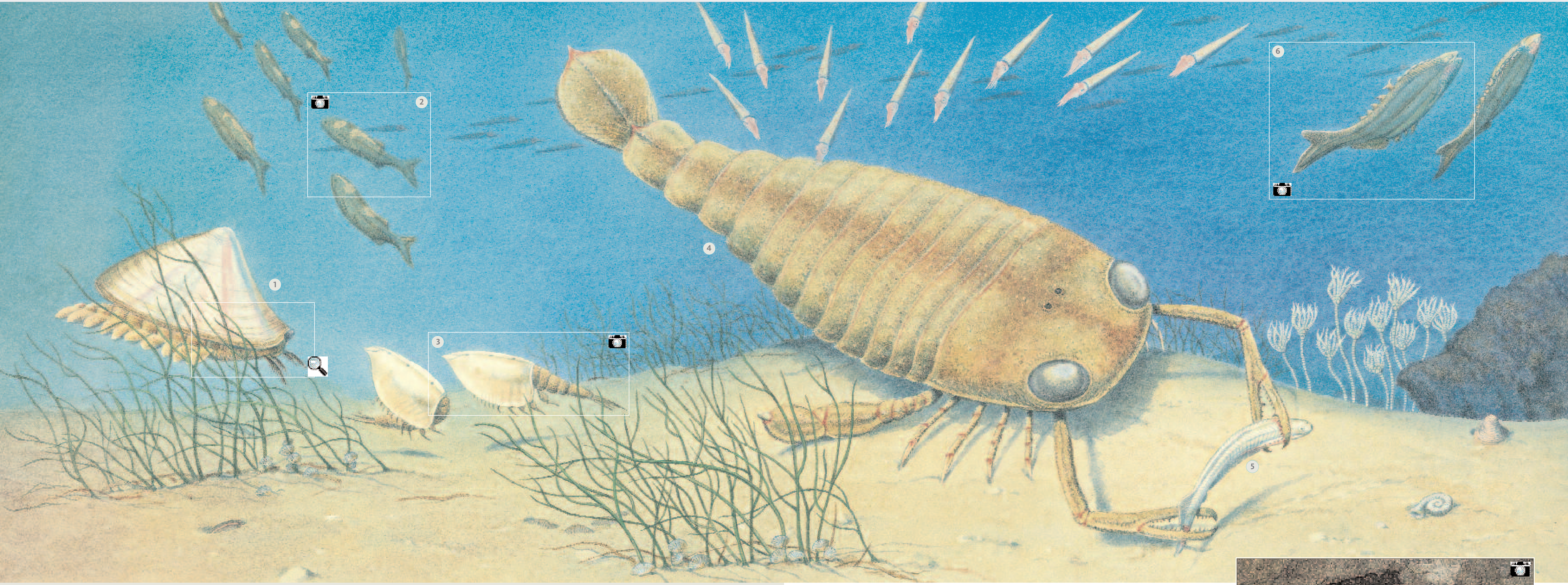
542 MILLIONS OF YEARS | 488.3 | 443.7 | 416 | 359.2 | 299 | 251

SEA SCORPIONS AND JAWLESS FISH
LESMAHAGOW, SCOTLAND

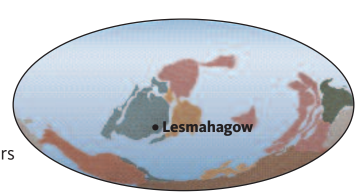
430 million years ago
Telychian Stage of the Llandovery Epoch

Common organisms: agnathans, eurypterids, phyllocarids, brachiopods, sponges, sea lilies, trilobites, nautiloids

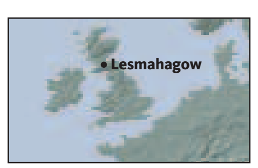
Climate: warm-water tropical marine
Biota: euryhaline shallow sea dwellers



Latitude then: 17°S
Latitude now: 56°N
Sea level: high
Original environment: shallow marine to brackish waters
Deposits: mud carbonates
Status: several protected historic sites throughout the Midland Valley of Scotland
Preservation: fossils flattened but mostly well preserved with some fossilized soft tissues



Earth c.430MA



Fossil site today

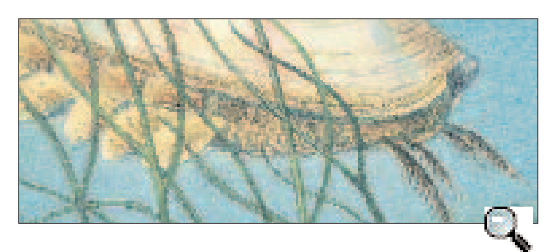
By Silurian times the agnathan fish were flourishing in the oceans of the world and extending their range into shallow waters with fluctuating salinities. At least 15 different kinds of agnathans are known from Silurian strata in Scotland's Midland Valley, where they range from sluggish bottom-dwelling and heavily armoured forms to more active non-armoured swimmers (such as *Loganellia*, *Jamoytius* and *Birkenia*) that probably fed on a variety of microbial and planktonic food. Some of the best specimens of these later swimmers have been found in the fine-grained sediments of localities such as Lesmahagow.

However, the agnathans were, by this time, facing fierce competition from both the newly evolving jawed fish, and large and active arthropod predators – the eurypterids, some of which grew up to 2m (6.6ft) long. Also known as the sea scorpions, these extinct arthropods were armed with large and powerful pincers for grabbing and pulling apart their prey.

Numerous smaller arthropods are also found, including *Ainiktozoon*, once thought to be a peculiar chordate animal. Turned upside down, it was more easily recognized as a free-swimming, predatory thylacocephalan arthropod, with a protective carapace.

1. *Ainiktozoon*
2. *Loganellia*
3. *Ceratiocaris*
4. *Pterygotus*
5. *Jamoytius*
6. *Birkenia*

AINIKTOZOON (1) This strange thylacocephalan arthropod, about 15cm (6in) long, had large compound eyes for spotting its prey, which it then captured with its grasping clawed appendages.



LOGANELLIA (2) This thelodont agnathan, 15cm (6in) long, has small paired fins and a body covered in naked skin with some very small scales. They are widely found across the Baltic and Germany.

CERATIOCARIS (3) This free-swimming shrimp-like arthropod, up to 12cm (5in) long, had a bivalve carapace for protection. The muscular tail could produce a rapid flick to escape predators.

BIRKENIA (6) Here flattened on it side, the 10cm (4in) *Birkenia* shows numerous thin body scales. The mouth is to the left with a large eye above, and the tail to the right.

CAMBRIAN | ORDOVICIAN | SILURIAN | DEVONIAN | CARBONIFEROUS | PERMIAN

542 MILLIONS OF YEARS · 488.3 · 443.7 · 416 · 359.2 · 299 · 251

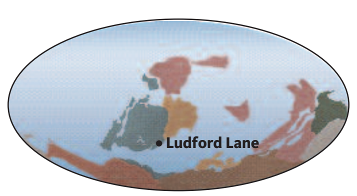
GREENING THE LAND
LUDFORD LANE, SHROPSHIRE, ENGLAND

419 million years ago
Ludfordian Stage of the Ludlow Epoch

Common organisms: *Cooksonia*, *Steganotheca*, trigonotarbids, myriapods

Climate: tropical, with global 'greenhouse' temperatures
Biota: first land plants and animals

Latitude then: 15°S
Latitude now: 52°N
Sea level: high
Original environment: coastal mudflats
Deposits: mud and sand
Status: many protected historic sites scattered over the Welsh Borders
Preservation: fossils are generally flattened but often well preserved in fine-grained strata



Earth c.419 MA

Fossil site today

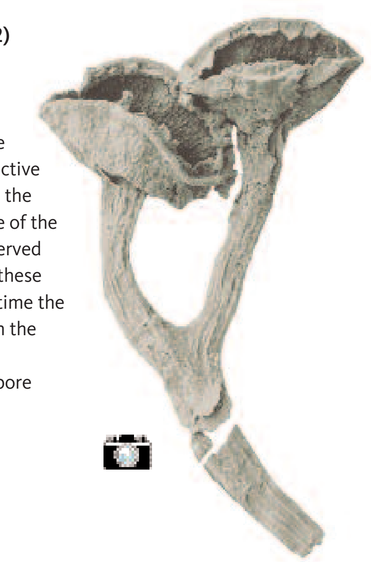
The first land plants were primitive mosses and lichens (bryophytes) that evolved in the Late Ordovician but were very restricted in their growth. Life on land in a relatively dry atmosphere is difficult for all organisms. In colonizing the land, plants had the advantage of securing their energy from sunlight through photosynthesis, while animals were dependent on either plants or other animals for food. However, plant tissue still needed support to grow against gravity, and for protection from oxidation, hydration, and the damaging effect of ultraviolet light. Fossils of early vascular upright land plants, such as *Cooksonia* and *Steganotheca* come from Late Silurian strata in the Welsh Borders. They had short (4cm/1.6in) forked stems ending in spore-bearing capsules. With no leaves, the stomata (cell openings for "breathing") were on stems and branches.

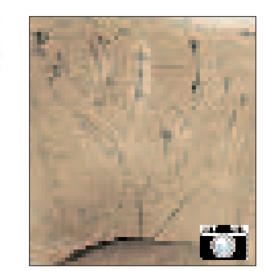
The first animals on land were arthropods, pre-adapted for life in the inhospitable conditions by their tough, waterproof exoskeletal armour. They included myriapod "detritivores" that ate plant material already degraded by soil bacteria, and carnivorous trigonotarbid arachnids. All these early terrestrial fossils are found as river-borne fragments stranded along shorelines.

1. *Lingula*
2. *Cooksonia*
3. *Steganotheca*
4. *Palaeotarbus*
5. *Eoarthropleura*
6. *Strophochonetes*

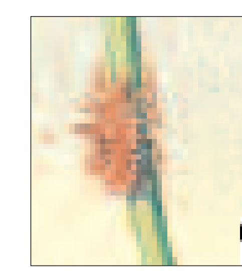
COOKSONIA (2) A highly flattened and carbonized fossil shows the simple forked branches and terminal reproductive structures of this primitive land plant.

COOKSONIA (2) Chemically isolated from the rock, this specimen of *Cooksonia* shows the cap-shaped reproductive structures that bore the plant's spores. Some of the spores are still preserved within the cup, and these proved for the first time the connection between the parent plant and a particular (trilete) spore structure.





STEGANOTHECA (3) This primitive land plant offers an example of more complex, first- and second-order branching. *Steganotheca* grew to around 4.5cm (1.8in) high.



PALAEOTARBUS (4) These tiny (2–3mm/1in long), air-breathing and land-living arthropod predators had paired fangs with which to stab their prey.

TRIASSIC | JURASSIC | CRETACEOUS

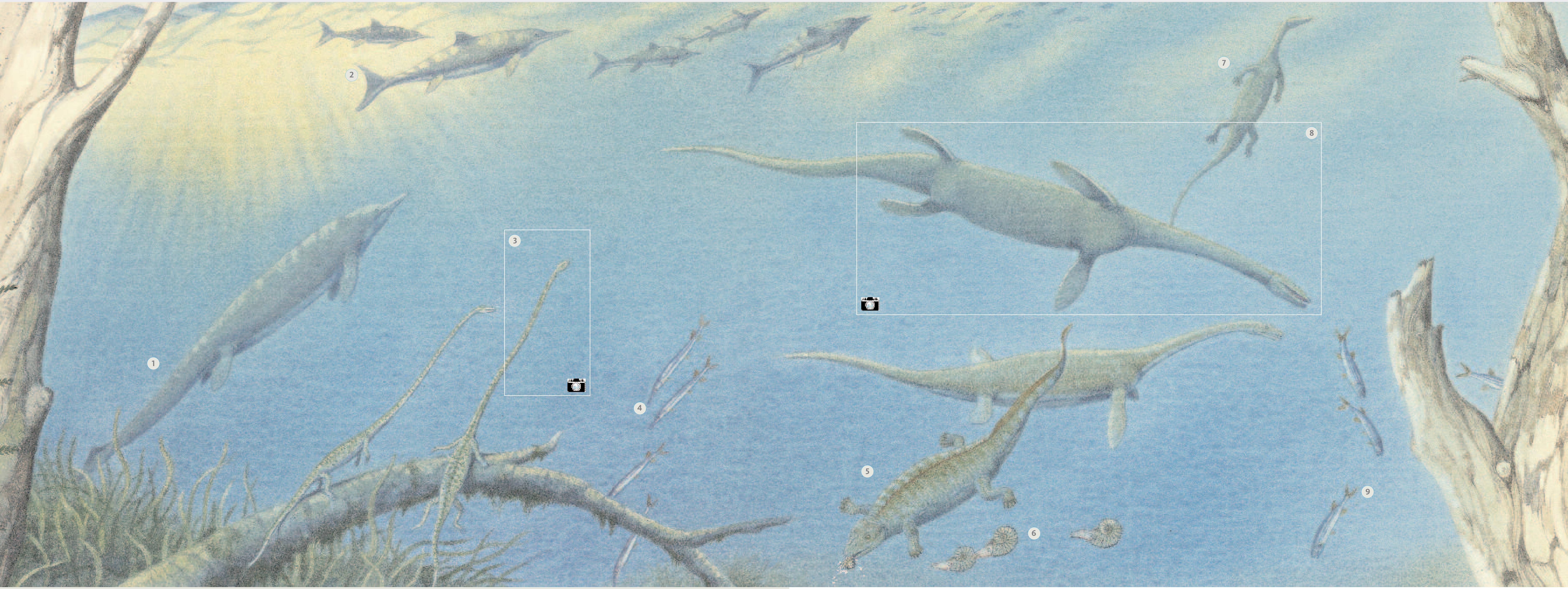
251 | 199.6 | 145.5 | 65.5

MARINE REPTILES DIVERSIFY
MONTE SAN GIORGIO, SWITZERLAND

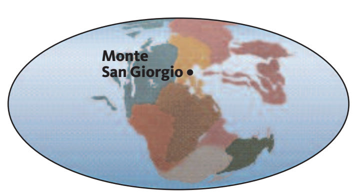
233 million years ago
Ladinian Stage of the Middle Triassic Epoch

Common organisms: ammonites and clams

Climate: tropical–equatorial
Biota: marine fish and reptiles



Latitude then: 15°N
Latitude now: 45.5°N
Sea level: +25m (82ft)
Original environment: stratified basin with anoxic bottom waters
Deposits: black bituminous shales and laminated dolomitic limestones
Status: quarrying has been necessary to excavate the fossiliferous strata
Preservation: flattened but often entire skeletons with some fossilized soft tissues



Earth *c.*233 MA

Fossil site today

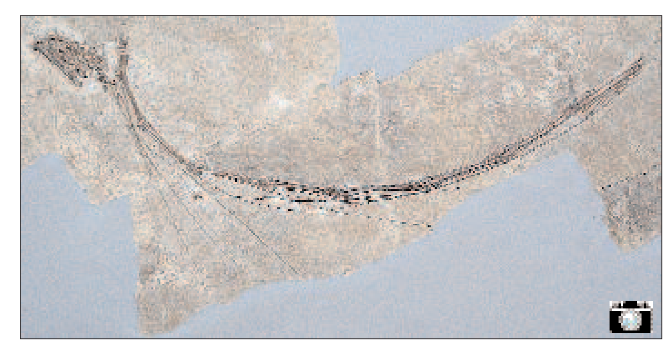
An extraordinary window on the marine life of the tropical Tethys Ocean first opened in the late 19th century, when remarkably well-preserved fossils were discovered in shales and dolomitic limestones near Besano in the southern Alps during quarrying for bitumen.

The outcrop of Middle Triassic strata straddles the Italian–Swiss border, and has surrendered hundreds of complete marine reptile skeletons over the last 150 years, along with thousands of fish (including 30 ray-finned species), clams, and ammonoids.

All these animals lived in the quiet waters of a marine embayment off the main Tethys Ocean. Here abundant fish and ammonoid cephalopods were hunted by a variety of marine reptiles such as ichthyosaurs (eg *Mixosaurus*) and nothosaurs (eg *Ceresiosaurus*). Specialist predators such as the placodonts (eg *Paraplacodus*) had large flat teeth for crushing shellfish.

The strata also contain the skeletons of reptiles such as the bizarre *Tanystropheus*, which grew to 6m (20ft) long with a stiff, elongated neck twice the length of its body. Such an animal must have been essentially marine, but the related *Macronemus* was only 80cm (31.5in) long and may have spent more time on land.

1. *Shastasaurus*
2. *Mixosaurus*
3. *Tanystropheus*
4. *Saurichthys*
5. *Paraplacodus*
6. *Eoprotrachyceras*
7. *Askeptosaurus*
8. *Ceresiosaurus*
9. *Birgeria*



TANYSTROPHEUS (3) Three genera of archosauromorphs have been found at Monte San Giorgio, including the strange *Tanystropheus* with its extremely long neck, produced by elongation of between 12 and 24 individual vertebrae, depending on the species.

CERESIOSAURUS (8) The most abundant reptiles at Monte San Giorgio were the amphibious nothosaurs. They were probably fish feeders, and may have laid eggs on land. They include *Ceresiosaurus* (up to 3m/10ft long), *Paranothosaurus*, *Lariosaurus*, and the tiny *Neusticosaurus* (up to 30cm/12in long), of which several hundred specimens have been found.

SYNAPSIDA

THE SYNAPSIDS INCLUDE ALL THE LIVING MAMMALS AND THEIR EXTINCT RELATIVES EXTENDING BACK TO THE LATE CARBONIFEROUS – GROUPS THAT HAVE IN THE PAST BEEN GIVEN THE MISLEADING NAME OF "MAMMAL-LIKE REPTILES". DESPITE THEIR RANGE AND DIVERSITY, THESE EXTINCT FORMS ARE STILL RELATIVELY UNKNOWN OUTSIDE THE WORLD OF PALEONTOLOGY.

The appearance of the synapsids was a major event in amniote evolution, and can be reconstructed through the fossil record of its various stages. The group was originally defined by the presence of a lower temporal opening behind the eye, which provided space for the passage of enlarged jaw muscles. This in turn was connected to improvements in processing food through tooth specialization, which in turn required restructuring of the lower jaw and its articulation. The snout region was extended in the carnivorous forms, but took on a very different shape in some of the plant-eaters, where the front teeth were lost and replaced with a horny, turtle-like beak for shearing through tough plant material.

Synapsids arose in equatorial regions in late Carboniferous times, and were initially lizard-like in appearance. The Permian and Triassic saw the origination and rapid expansion of successively more advanced groups, many of which soon died out to be replaced by new forms.

One of two main groups of early synapsids, the caseasaurians are only known from Permian times. They include two families – the large plant-eating caseids, which grew up to 4m (13ft) long, and the smaller carnivorous eothyridids, which look superficially different but are united by the structure of the snout and nostrils. They were a successful group in early Permian times, but by the middle of the period were challenged by the rapidly evolving therapsids. They ultimately died out in the end-Permian extinction.

As their name suggests, these small- to medium-sized synapsids, which grew up to 1.5m (5ft) long, resemble varanid (monitor) lizards with slender bodies and long limbs. The slender, lightly built skull with large eyes, a long narrow snout, and jaws with specialized sharp, recurved teeth, was adapted for hunting down small but active prey. The varanopseids were probably the most agile predators of the time. They evolved during the late Carboniferous and died out in late Permian times.

This group evolved in the late Carboniferous and died out in mid-Permian times. It includes a number of long-snouted forms up to 3m (10ft) long, and the earliest known pelycosaur – the 50cm (20in) *Archaeothyris*, which was discovered in the bole of a fossil lycopod tree, preserved by late Carboniferous "coal measure" strata at Joggins in Nova Scotia. Its slender snout is armed with sharply pointed teeth, one of which shows a developed canine-like form. The group includes aquatic, semi-aquatic, and fully terrestrial animals.

This group of specialized plant-eaters, up to 3m (10ft) in length, are among the earliest known herbivorous amniotes. They bear a superficial resemblance to the caseids, but differ in skull details. The head was very small in relation to a bulky body, but the jaw had powerful muscles and teeth adapted for cropping vegetation. Elongated neural spines supported a large dorsal "sail". They evolved in late Carboniferous times and became extinct in the middle Permian.

This is the most advanced group of eupelycosaurs and includes the largest of these "sail-backed" lizards, *Dimetrodon*, which grew to 3.5m (12ft) in length. Tooth differentiation is further developed, with enlargement of the upper canines and first incisor, while in the lower jaw the second incisor is enlarged. The group evolved late in the Carboniferous and died out at the beginning of the late Permian.

This group of heavily built animals, up to 4m (13ft) long, were among the first and most primitive therapsids, appearing at the beginning of the late Permian, expanding to become the commonest therapsid group with both carnivorous and herbivorous forms, and disappearing before the end of the Permian. They are defined by their teeth, shortened jaw and thickened skull bones.

This large, diverse group of herbivores evolved in mid-Permian times and radiated to become the most successful terrestrial amniotes of the late Permian and Early Triassic, surviving in Australia until the Early Cretaceous. In size they ranged from a small dog to a large ox. The body is barrel-shaped, with strong limbs, a short tail, and a powerful beaked skull.

This short-lived group of therapsids evolved in the middle Permian and quickly rose to become top carnivores of the late Permian, up to 4m (13ft) long. They are characterized by a skull structure with powerful jaw muscles and tooth differentiation with well-developed incisors and enlarged canines.

This group of predominantly carnivorous therapsids (up to 3m/10ft long) are similar to the gorgonopsians, but survived in Gondwana to the Middle Triassic. Characterized by features of the skull and teeth, they are closely related to the cynodonts.

Evolving in late Permian times, the cynodonts survived the end-Permian extinction and went through several waves of origination and extinction, becoming progressively more mammal-like.

SYNAPSIDA

This very large group is characterized by several features of the skull and teeth, such as the presence of a lower temporal opening and the development of canine-like "caniniforms".

THERAPSIDA

This grouping includes the biarmosuchians, dinocephalians, dicynodonts, and theriodonts. It is characterized by enlarged fenestrae (the typical synapsid holes in the skull), further specialization of the teeth into incisors, canines, and molars, and a more upright posture.

THERIODONTIA

This group is characterized by a number of skull features such as laterally flaring cheek bones, more specialized and mammal-like teeth, and an enlarged jawbone with improved surfaces for muscle attachment. The theriodonts include the gorgonopsians, therocephalians, cynodonts, and all their mammalian descendants. Apart from cynodonts, the last theriodonts became extinct in the Early Triassic.

SAIL-BACKED PELYCOSAURS

Despite being one of the best known synapsid groups, the traditional "Order Pelycosauria" are not featured on this cladogram, since it is a paraphyletic group containing species that are now placed within several groups including Ophiacodontidae, Edaphosauridae, and Spenacodontidae. Some animals within each of these latter groups independently evolved a strange dorsal "sail" or "fin" structure on their backs – a web of skin supported by extreme elongations of the neural spines from the vertebrae. Probably the best known of these "sail-backed" species are the carnivorous sphenacodontid *Dimetrodon* and the herbivorous *Edaphosaurus*. The function of the sail structure has generated a great deal of argument, but the two most popular suggestions are that it may have been used in mating displays, or for heat-exchange (allowing sunlight to warm the animal in cold conditions, and helping the animal to cool down when hot).

Inostrancevia from the Permian of Russia is a member of the short-lived gorgonopsian group of synapsids.

(together known as the Ponginae), and the African apes – chimps and gorillas plus humans and their fossil relatives (together known as the Homininae). Their divergence resulted from the adoption of different modes of locomotion – the orang-utan swings by its arms ("brachiation") and climbs slowly, while the African great apes mostly use all four limbs to climb in a typical quadripedal manner, and humans are bipedal.

The earliest known hominids are fossil forms such as the Miocene age *Kenyapithecus* from eastern Africa and central Europe. There is a reasonable record of fossil Ponginae in Asia from Miocene times onwards, but there is a big gap in the record of African Homininae until around 6 million years ago. At present, the earliest fossil hominin is *Sahelanthropus*, a small ape-like creature from the late Miocene that lies close to the divergence of ape and human branches from their common ancestor.

Some 20 human-related species have diverged over the last 6 million years in Africa, but few of them have spread beyond this continent. One of these African species, *Homo sapiens*, arose some 200,000 years ago to become the most widespread and successful.

• PONGINAE

PONGIN SIVAPITHECINES
Sivapithecus 212–13

• HOMININAE

UNDETERMINED GROUP
Sahelanthropus 214–15

"AUSTRALOPITHECINES"
Australopithecus afarensis 216–17
Australopithecus africanus 218–19

"PARANTHROPINES"
Paranthropus boisei 220–1

HOMININI
Homo habilis 220–1
Homo antecessor 222–3
Homo erectus/ergaster 224–5
Homo sapiens 226–7, 230–1, 236–7, 240–1, 242–3, 244–5
Homo neanderthalensis 228–9
Homo floresiensis 238–9

HOMINOIDEA (APES)

Miocene – Extant

WITHIN *Anthropoidea*
SEE ALSO *Hominidae*

The apes, also known as hominoids, are a group that unites the gibbons (Family Hylobatidae) with the Hominidae (chimps, gorillas, orang-utans, humans, and their ancestors). Although there are few surviving ape species, their distribution in Africa and southeast Asia reflects a much wider diversity and distribution in the past. Unfortunately, the early ape fossil record is sparse, obscuring many details of their origins within the haplorhine primates around 25 million years ago. The best known early fossil representative of the group is the Miocene *Proconsul* from Africa. By late Miocene times, the apes were abundant and widely dispersed across Africa, Asia, and Europe. They were mostly fruit-eating, chimp-sized, and tailless, with short snouts, forward-facing eyes, and highly domed skulls.

◀ **Orang-utan** (*Pongo* sp.). Although these hominid apes are generally solitary, offspring stay with their mothers until the age of six or seven.

Stenopterygius. This relatively small, slender-skulled ichthyosaur from Holzmaden in Germany had a form strongly resembling a modern dolphin, and probably had a similar fish-eating lifestyle.

ICHTHYOSAURIA

Early Triassic – Late Cretaceous

WITHIN *Diapsida*
COMPARE *Lepidosauria, Archosauria, Plesiosauria, Placodontia*

The extinct ichthyosaurs or "fish lizards" were a very successful group of predatory marine diapsid reptiles throughout much of the Mesozoic. Their dolphin-shaped bodies were streamlined for the pursuit of fast-swimming prey, their tetrapod limbs were adapted as seal-like paddles for steering, and the main propulsion came from a muscular tail. Ichthyosaurs grew up to 15m (50ft) long, and had projecting beak-like jaws armed with sharp teeth. Their large eyes suggest that they depended upon sight for hunting.

• ICHTHYOSAURIA

MIXOSAURIDAE
Mixosaurus 116–17

SHASTASAURIDAE
Shastasaurus 116–17

ICHTHYOSAURIDAE
Ichthyosaurus 128–9

STENOPTERYGIIDAE
Stenopterygius 130–1
Platypterigius 164–5

OPTHALMOSAURIDAE
Aegirosaurus 140–1

LAURASIATHERIA (LAURASIATHERIAN MAMMALS)

Early Cretaceous – Extant

WITHIN *Boreoeutheria*
COMPARE *Euarchontoglires*

Extending back to Early Cretaceous times, the first laurasiatherian mammals included the ancestors of living insectivores such as shrews, hedgehogs, moles (lipotyphlans), and bats (chiropterans). Among more advanced members is a large branch known as the ferungulates, whch includes the familiar cetartiodactyls (cattle, pigs, and whales), perissodactyls (horses, rhinoceroses, and tapirs), carnivorans (dogs, cats, weasels, seals, and bears), and the bizarre and less familiar pholidotans (pangolins).

The cetartiodactyls are further subdivided into the even-toed ungulates (artiodactyls) and, according to molecular analysis, the cetaceans. The former include the suiforms (pigs and hippos) and the selenodontids (cattle, deer, giraffes, antelopes, and camels) – their link with the cetatceans, which include whales, dolphins, and porpoises, might seem surprising but is now supported by fossil evidence. The artiodactyls seem to have originated in Eocene times from rabbit-sized plant-eaters such as *Diacodexis*. There is also fossil evidence that the cetaceans arose from a land-living artiodactyls such as *Pakicetus* from Pakistan.

Eocene times also saw the diversification of the perissodactyls, which have odd numbers of toes, to become the dominant browsing plant-eaters (and subsequently grazing plant-eaters once the grasses had evolved in Oligocene times). Two important perissodactyl groups that became extinct but left good fossil records are the chalicotheres and brontotheres. The latter were rhino-like browsers such as the North American *Brontops*, which stood more than 2m (6.6ft) high at the shoulder. The similar sized chalicotheres were strange animals with horse-like heads, long grasping forelimbs, and short back legs all ending in three-hooved digits.

Among the remaining laurasiatherians, the carnivorans are characterized by a pair of enlarged carnassial cheek teeth that work together as effective shears, cutting the flesh off their prey for rapid ingestion. Additionally, the canine "eye" or "dog" teeth have developed into dagger-like fangs, capable of puncturing tough hide to help hold and kill their prey. The pinnipeds (seals, sealions, and walruses) are an aquatic group of carnivorans that probably evolved from a bear-like ancestor in the Oligocene, perhaps similar to *Enaliarctos* from North America.

Finally, molecular analysis has revealed close links between the carnivorans and the strange scaly-skinned, ant-eating, and toothless pangolins. Although living pangolins are restricted to Africa and southeast Asia, they were once more widespread throughout North America and Europe. *Eomanis* is a wonderfully preserved pangolin found in the Eocene shales of Messel in Germany.

▶ **Flying fox** (*Pteropus* sp.). Large "fruit bats" and their smaller, insect-eating relatives show how the Laurasiatheria have evolved enormous variety.

• LIPOTYPHLA

AMPHILEMURIDAE
Pholidocercus 198–9

ERINACEIDAE (HEDGEHOGS)
"Tupaiodon" 206–7
Gymnurechinus 210–1

• CHIROPTERA (BATS)

MICROCHIROPTERA
Archaeonycteris 196–7
Icaronycteris 190–1
Palaeochiropteryx 198–9
Brachipposideros (leaf-nosed bat) 208–9
Hipposideros 238–9

ONYCHONYCTERIDAE
Onychonycteris 190–1

• CETARTIODACTYLA

ARCTOCYONIDAE
Chriacus 180–1

HYOPSODONTIDAE
Hyopsodus 188–9

PHENACODONTIDAE
Phenacodus 188–9

• DINOCERATA

UINTATHERIIDAE
Uintatherium 190–1

• ARTIODACTYLA

DICHOBUNOIDEA
Diacodexis 188–9
Messelobunodon 196–7

• ARTIODACTYL SUIFORMS

SUIDAE (PIGS)
Hippopotamodon 212–13
Nyanzochoerus 214–15
Sus scrofa 222–3