Life in the Palaeozoic

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Introduction

The Palaeozoic Era was a very important time in the history of life. Using evidence from fossils, we start by looking at the Cambrian explosion, when many forms of animal life first appeared about 545 million years ago. Then we move on to study creatures living in the Ordovician seas, including the extinct trilobites. Next, we'll investigate the invasion of land by plants and invertebrates that occurred in the Silurian Period, and look at life in Silurian seas. You'll also learn about the Devonian Period, when vertebrates first moved onto land. The course finishes with a brief outline of vertebrate evolution.

This OpenLearn course provides a sample of level 1 study in Environment & Development

Learning outcomes

After studying this course, you should be able to:

- describe some key events in the evolution of life during the Palaeozoic Era, such as the first appearance of major groups of invertebrates and vertebrates, and the invasion of the land
- identify some common types of fossil organisms that were living in Palaeozoic seas, and comment on their likely environment and geological age
- make inferences from fossils about the biology and mode of life of some Palaeozoic organisms.

1 The Cambrian explosion

1.1 A burst of evolution

One of the most important events in the history of life began about 545 million years (Ma) ago, i.e. some four billion years after the origin of the Earth, and over 3.3 billion years after the origin of life. The term '**Cambrian explosion**' reflects a sudden burst of evolution, when a wide variety of organisms, especially those with hard, mineralised parts, first appear in the fossil record. Thus began the Phanerozoic Eon - 'the time of visible life' - and the Palaeozoic Era.

As part of this course you will often be referred to a pdf file taken from Douglas Palmer's *Atlas of the Prehistoric World*.

Before going any further, click on 'View document' below and read pages 58-61 from Douglas Palmer's Atlas of the Prehistoric World.

View document

At the start of the Cambrian Period, body fossils with hard shelly parts became abundant for the first time. Actually, the very first evidence of preservable hard parts comes from some tiny fossils, including tubes made of calcium carbonate about 0.2 mm across, found in late Precambrian strata about 550 Ma old. The unknown organisms that produced them were living at the same time as the Ediacaran fauna.

SAQ 1

What, in general, was different about the size of fossils with hard shelly parts in the earliest Cambrian, compared with late Precambrian life such as the Ediacaran organisms?

Answer

The fossils with hard shelly parts were much smaller (*Atlas*, p. 60).

A wide variety of small (1-2 mm) shelly fossils appeared in the earliest part of the Cambrian Period - assorted shapes such as tubes and cones, as well as spines, scales, and knobs (*Atlas*, pp. 58-59). It's often difficult to tell whether a fossil is the complete skeleton of a single organism or an isolated part of some larger creature. The soft tissues associated with these hard parts are almost entirely unknown, and the reconstructions of soft parts shown in the *Atlas* (pp. 60-61) are conjectural.

SAQ 2

What seems likely to have been the main stimulus for the acquisition of hard parts by organisms in the earliest Cambrian?

Answer

The need for protection (*Atlas*, pp. 60-61).

Protection from predation or other damage is certainly consistent with the first appearance of defensive structures such as spines and scales, and tubes and conical shells that could protect vulnerable soft parts inside. There are, however, a number of other possible reasons why hard parts first evolved, as discussed in the *Atlas*, p. 61, some or all of which may have been involved.

SAQ 3

A greatly increased variety of types of trace fossils, especially burrows of soft-bodied animals, are found around the start of the Cambrian Period. What is the significance of this finding?

Answer

It reflects the evolution of more complex patterns of activity and behaviour, some of it probably related to the avoidance of predators.

Although environmental changes were occurring (such as a rise in global sea level (*Atlas*, p. 58), there is, to date, little evidence of special, widespread environmental changes that could have directly triggered the Cambrian explosion. Whatever the causes, once triggered, a wide range of ecological opportunities presumably became available for exploitation, promoting the rapid evolution of new, quite different types of animals. By about 530 Ma, most of the animal phyla that are in existence today had appeared. Not surprisingly, a few entirely soft-bodied phyla living today have no known fossil record, so we don't know when they evolved. Evidence from genetics suggests that some animal phyla had diverged from each other much earlier than the start of the Cambrian explosion, but the timing remains uncertain.

Many of the newly evolved Cambrian phyla show organisation of the body into specialised areas - especially a head end with food-trapping and sensory organs, a tubular gut and limbs. There is no doubt that many Cambrian animals were equipped with adaptations for preying on other animals, and were able to pursue food much more actively than could the Ediacaran fauna - such as by scuttling over the sea floor, swimming actively, and burrowing. Note that all forms of life (except possibly a few algae) were as yet confined to the sea.

Although many types of the small shelly fossils disappear from the fossil record soon after the start of the Cambrian, some are thought to have been molluscs at an early evolutionary stage, in which case they did leave descendants.

1.2 The Burgess Shale

High in the Canadian Rockies is exposed a deposit of middle Cambrian age, about 530 Ma old, called the Burgess Shale. It contains the fossils of animals that lived on a muddy sea floor, and which were suddenly transported into deeper, oxygen-poor water by submarine landslides. Their catastrophic burial has given us an exceptional view of Cambrian life. Not only have animals with hard shelly parts been preserved but entirely soft-bodied forms are also preserved as thin films on the sediment surface.

Before going any further, click on 'View document' below and read pages 62-65 from Douglas Palmer's Atlas of the Prehistoric World.

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Some of the most common Cambrian fossils, which appear immediately after the first shelly fossils, are trilobites. These were a group of exclusively marine arthropods, members of the enormously diverse phylum of animals with jointed, external skeletons that today include forms such as crabs, lobsters, insects and spiders. The trilobite fossils of the Burgess Shale are like many trilobites found elsewhere but exceptional in that not only is the main part of their outer skeleton (or exoskeleton) preserved, but so too are their appendages such as antennae and legs (see, for example, those of *Olenoides, Atlas*, p. 63). Elsewhere, trilobite appendages are extremely rare as they were poorly mineralised. We will study trilobites in more detail shortly. Other types of arthropods, especially ones lacking well-mineralised exoskeletons (such as *Marrella, Atlas*, p. 64), are particularly abundant in the Burgess Shale.

Only about 15 per cent of the 120 genera present in the Burgess Shale are shelly organisms such as trilobites and brachiopods that dominate typical Cambrian fossil assemblages (fossils that occur together) elsewhere. The shelly component was therefore in a minority, and organisms with hard parts probably formed less than 5 per cent of individuals in the living community.

SAQ 4

If the soft-bodied fossils of the Burgess Shale are taken away, all that remains is a typical Cambrian assemblage of hard-bodied organisms. Why is this important to bear in mind when trying to interpret other Cambrian fossil assemblages?

Answer

The other Cambrian assemblages may also have been dominated by soft-bodied animals, even if the only fossils they now contain are of hard-bodied ones.

Another important revelation of the Burgess Shale lies in the wide diversity of animal types that were around in middle Cambrian time, about 530 Ma ago. There are representatives of about a dozen of the phyla that persist to the present day. One form closely related to early arthropods was *Anomalocaris*, the largest known Cambrian animal, some individuals of which may have reached two metres in length. Its extraordinary jaw (*Atlas*, p. 65) consisted of spiny plates encircling the mouth, which probably constricted down on prey in much the same way that the plates of an iris diaphragm cut down the light in a camera. This fearsome mouth is seen in place in the reconstruction of the closely related *Laggania (Atlas*, pp. 64-65). Note that the colours of organisms shown in this and other such reconstructions are conjectural.

About a dozen types of Burgess Shale fossils have been said to be so unlike anything living today and so different from each other that, had they been living now, each would have been placed in a separate phylum. With further study, however, the relationships of these puzzling animals (such as *Hallucigenia, Atlas*, p. 63) are becoming clearer. It seems that some Burgess Shale forms are hard to classify simply because the boundaries between major categories of animal life were still blurred shortly after the Cambrian explosion. In other words, by mid Cambrian time, there still had not been enough time for some groups to have diverged sufficiently from their recent common ancestors to be distinctly different.

Burgess Shale-type faunas have been found in about 30 sites ranging from North America and Greenland, to China and Australia. The wide range of animals they contain seems to reflect an unpruned 'bush of diversity' resulting from the Cambrian explosion. Not long after, though, extinction lopped off some of the branches, leaving phyla with the relatively distinct features that have remained to this day.

1.3 An overview of animal phyla

We have already met quite a few different animal phyla, and it's useful to get an overview of all the ones commonly found in the fossil record and their mode of life before studying some in more detail. Except for a few soft-bodied phyla with very poor fossil records, it is clear that all the animal phyla had appeared by the Ordovician Period.

Modes of life

The following terms are very useful for describing the mode of life and the environmental setting of organisms. The terms are explained here as they are applied to marine organisms, but they are also sometimes applied to organisms living in lakes.

benthic - animals and plants that live on the sea floor; collective noun: **benthos.**

pelagic - animals and plants that live above the sea floor. They may be either **nektonic** (animals only) or **planktonic** (animals and plants).

nektonic - animals that swim actively (e.g. fish, squid); collective noun: **nekton.**

planktonic - animals and plants that drift passively or swim feebly, mainly in the surface waters of seas; collective noun: **plankton.** The term includes **phytoplankton** (photosynthetic organisms, mostly algae) and **zooplankton** (mostly microscopic animals, including larvae of larger ones, but also some macroscopic animals that are readily visible with the naked eye, e.g. jellyfish).

epifaunal - animals that live on the sea floor, either on soft sediment, or attached to rocks, seaweed, etc. (**sessile**), or that move over the sea floor (**vagrant**); collective noun: **epifauna.**

infaunal - animals that live within sediment, often in burrows or borings into harder material; collective noun **infauna.**

Like most classifications involving living organisms, some invertebrates do not fit neatly into these categories, e.g. the common prawn buries itself in sediment during the day (i.e. is infaunal), but at night emerges to join the epifauna as it feeds. Other epifaunal animals bury themselves during low tide.

The following text gives some key points about the important animal phyla most commonly found in the fossil record. The age range and mode of life of some common groups are given, and phyla that are microscopic throughout life are excluded. Figure 1 shows typical fossil representatives of some of the phyla.

Porifera. Sponges. Cambrian to Recent. Mainly marine; some freshwater. Sessile. The simplest multicellular animals, sponges lack definite tissues and organs, e.g. they have no nervous system. They have a skeleton of calcium carbonate, silica, or, as in some bath sponges, horny organic material. Water passes in through the sponge's many surface pores, often to the central cavity of a sack-like body, and out through a large hole at the top. Some have a stalk (Figure 1a), others are encrusting and irregular in shape. Sponges feed by filtering off minute organic particles from the water. Sponges are locally abundant fossils, especially in Cretaceous rocks, where they are very commonly enclosed in flint nodules in the Chalk.

Cnidaria (pronounced with a silent 'C': 'nigh-dare-ee-a'). Late Precambrian (Ediacaran) to Recent. Almost entirely marine. Cnidarians have a central mouth around which are stinging tentacles for catching prey. By far the most important fossil group are the entirely marine, generally benthic, **corals**, which secrete a skeleton of calcium carbonate below the soft, anemone-like parts at the top. Corals may be either colonial (with many genetically identical, linked individuals sharing a skeleton) or solitary individuals. There are three main groups of corals: rugose corals (solitary, Figure 1b, or colonial), Ordovician to Permian; tabulate corals (always colonial), Ordovician to Permian; and scleractinian corals, sometimes also called hexacorals (solitary or colonial), Triassic to Recent. **Sea anemones** and **jellyfish** are also cnidarians, but being soft-bodied these groups are much less common in the fossil record.

Bryozoa. Bryozoans. Ordovician to Recent. Sometimes called 'moss animals'. Normally marine, rarely freshwater. Sessile, tiny animals which live in colonies, with a skeleton usually of calcium carbonate. The colonies vary in shape; some are encrusting sheets ('sea mats'), others may be delicate net-like fronds (Figure 1c) or branching twigs. Each colony consists of a few to thousands of interconnected individuals. When feeding, tentacles filter microorganisms from the water. Bryozoans often occur as fossils among the diverse fauna of reefs. Some bryozoans look rather like small corals; a few species can look a little like graptolites (see below).

Brachiopoda. Brachiopods (pronounced 'bracky-o-pods'). Cambrian to Recent. Entirely marine, benthic animals. Sometimes called 'lamp-shells' (after their resemblance to Roman oil lamps). Brachiopods are typically 2-5 cm long, but they range in size from a few mm to as much as 30 cm. The shell, which encloses the soft tissues, has two parts, called valves. One valve is almost always larger than the other. Many brachiopods are attached to the sea floor by a stalk of horn-like or fleshy material, the pedicle; in fossil brachiopods the presence of this pedicle is indicated by a hole passing through the larger of the two valves (Figure 1d). Some are free-lying on the sea floor, and a few are cemented or attached by spines. In most brachiopods the shell is composed of calcium carbonate, though some are phosphatic. They feed by drawing water into the shell and filtering off food particles with a complex feeding device called a lophophore. Brachiopods are much less abundant and diverse today than during the Palaeozoic and Mesozoic. They are the commonest fossil in many Palaeozoic shallow marine limestones and shales. About 20 species occur today off the British Isles, mostly in deeper waters, and are rarely seen.

Mollusca. Molluscs. Cambrian to Recent. Mainly marine. A very diverse phylum, perhaps numerically the most abundant large invertebrates in the fossil record. There are shelled and unshelled forms. Although at first the six or so living classes may seem unrelated, they represent evolutionary variations on the same theme - the molluscan bodyplan. Three classes, each of which range from Cambrian to Recent, are particularly important, both as fossils and today: the Bivalvia - **bivalves** (e.g. cockles, mussels and oysters) (Figure 1e); the Gastropoda - **gastropods** (e.g. slugs and snails); and the nektonic Cephalopoda - **cephalopods** (e.g. squid, cuttlefish, octopus and nautilus). Most bivalves are marine (vagrant to sessile benthos), though some are freshwater. The majority of gastropods are aquatic, and most of these live in shallow seas, but they are also widespread in freshwater and on dry land. Cephalopods are (and have been) entirely marine, and are the most highly evolved molluscs. The most important fossil cephalopod groups are all forms with chambered shells - the **nautiloids** (Cambrian to Recent), the familiar spiral-shelled **ammonites** (Triassic to Cretaceous), and the bullet-shaped **belemnites** (Jurassic to Cretaceous).

Echinodermata. Echinoderms. Cambrian to Recent. Entirely marine. Most are benthic. Many are vagrant, some are sessile, and a few are free-swimming (nektonic). Most echinoderm skeletons are made of many porous plates of calcite (calcium carbonate) which are very thinly covered with soft tissue. Multipurpose, extendible tentacles called tube feet emerge to the outside, and are used especially in feeding, respiration and locomotion. In many forms there is a distinctive five-rayed arrangement of plates and tube feet. Echinoderm means 'spiny skin', referring to the fact that some groups have spines or hard, warty bumps projecting from the surface. The most common fossil groups are **sea urchins** (**echinoids**), Ordovician to Recent, and **sea lilies** (**crinoids**), Cambrian to Recent. Two other well-known living groups, both Ordovician to Recent, are **starfish** (**asteroids**) and **brittle stars** (**ophiuroids**). There are also several extinct groups.

Arthropoda. Arthropods. Cambrian to Recent. The largest phylum of animals, with a great diversity of morphology and mode of life; living forms are found in most possible habitats in water and on land. A partial list of groups includes **crustaceans** (**crabs, lobsters, barnacles** and **shrimps**), **insects, millipedes, centipedes, spiders, king crabs, scorpions, mites** and several extinct groups, of which the entirely marine, extinct **trilobites** (pronounced 'try-lo-bites') are the most important. The most characteristic features of the phylum are the hard outer coating (exoskeleton) which is divided into segments, and the paired, jointed appendages which vary in number and function. The exoskeleton, usually of chitin (a strong, lightweight organic material), may be further strengthened by calcium carbonate or calcium phosphate, increasing the preservation potential. Growth occurs during periodic moulting when the exoskeleton is shed and a new, larger one is formed.

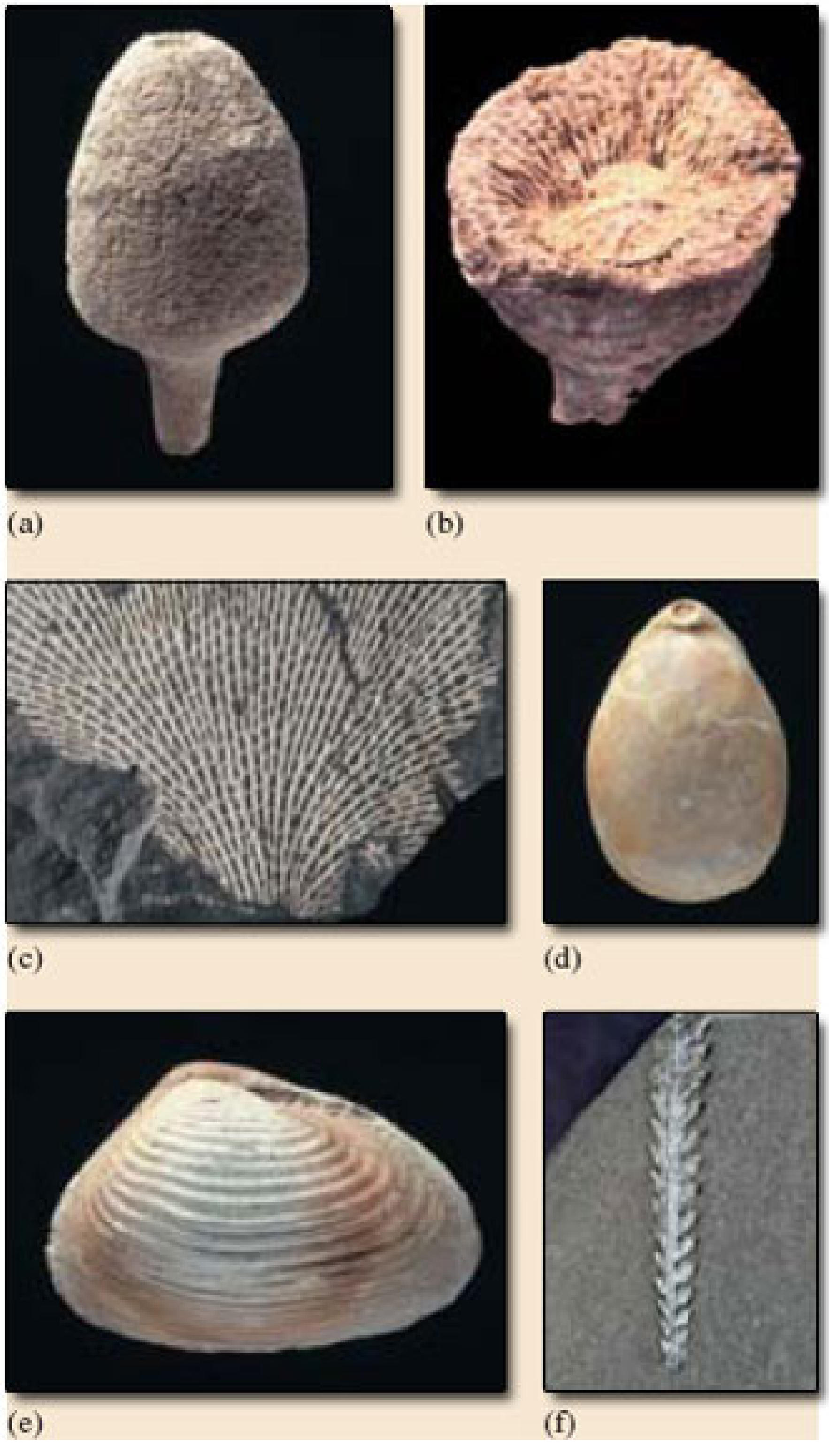

Figure 1 Representative fossils of some of the phyla mentioned above. (a) A sponge, *Siphonia tulipa*, Cretaceous (5.5 cm). (b) A cnidarian, the solitary rugose coral *Clisiophyllum*, Carboniferous (3.5 cm), (c) A bryozoan, *Fenestella plebeia*, Carboniferous (field of view 3 cm). (d) A brachiopod, *Terebratula gigantea*, Cretaceous (4 cm). (e) A mollusc, the bivalve *Pleuromya costata*, Jurassic (4.5 cm). (f) Ahemichordate, the graptolite *Hustedograptus teretiusculus*, Ordovician (2.5 cm)

Hemichordata*. Hemichordates. Cambrian to Recent. By far the most important fossil group are the **graptolites** - extinct, entirely marine colonies confined to the Palaeozoic Era, particularly abundant in Ordovician and Silurian rocks where they are very useful zone fossils. Many look like saw blades a few centimetres long on the rock, with 'teeth' on one or both sides of the 'saw' (Figure 1f). The 'teeth' were actually tiny cups that housed individuals which made up the colony and possessed filter-feeding tentacles. Some graptolites were benthic and sessile, but most were pelagic, either drifting or possibly swimming feebly as part of the zooplankton.

*Some biologists place the hemichordates as a subphylum within the Phylum Chordata.

Chordata. Chordates. Cambrian to Recent. All chordates possess a notochord (a flexible rod running along the length of the body). Minor living chordate groups, lacking a vertebral column (backbone), include sea squirts and the lancelet. The major group are the **vertebrates**, which have bony or cartilaginous skeletons and a head. Today, vertebrates include five classes: **fish** (Cambrian to Recent), **amphibians** (Devonian to Recent), **reptiles** (Carboniferous to Recent), **mammals** (Triassic to Recent) and **birds** (Jurassic to Recent). Important extinct reptile groups include the land-dwelling **dinosaurs** (Triassic to Cretaceous), the marine **ichthyosaurs** (Triassic to Cretaceous) and **plesiosaurs** (Jurassic to Cretaceous), and the flying **pterosaurs** (Triassic to Cretaceous). Vertebrate fossils are relatively rare compared with invertebrates, and are usually only fragments.

1.4 The origin of the vertebrates

Vertebrates such as ourselves are by definition animals with a backbone (or vertebral column, paired limbs, a skull and various other structures. Until recently vertebrates were thought to extend back only into late Ordovician times, some 450 million years ago. At this time fossils of strange-looking fish with bony headshields, such as *Sacabambaspis (Atlas*, pp. 70-71), appear in the fossil record. These jawless fish (called **agnathans**) are only very distantly related to the sole living agnathans, the lampreys and hagfish. However, these Ordovician creatures are already highly evolved and clearly had yet more ancient ancestors.

To understand what such ancestors might have been like we need to consider the backbone - the fundamental vertebrate feature - in a bit more detail. The precursor to the backbone is a stiffening rod, called the **notochord**, details of which we know from the study of developing vertebrate embryos and the few surviving animals which have retained a notochord, such as the lancelet *Branchiostoma*.

Before going any further, click on 'View document' below and read pages 66-67 from Douglas Palmer's Atlas of the Prehistoric World.

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SAQ 5

What is the main function of the notochord?

Answer

It lengthens and stiffens the body, allowing the blocks of muscles to flex the body sideways into zigzag bends for swimming (*Atlas*, p. 66).

The fundamental chordate characteristic of a notochord (Section 1.3) has now been identified in various Cambrian fossils, such as *Pikaia* from the Burgess Shale (Section 1.2).

SAQ 6a

Why is *Pikaia* classified as a chordate but not a vertebrate?

Answer

It has a notochord but not a backbone, nor other vertebrate features such as paired limbs (*Atlas*, pp. 66-67).

The extinct **conodonts** (late Cambrian to end Triassic in age) have been shown to possess not only a notochord but also tooth structures and paired eyes, which seem to suggest that they were more advanced than chordates such as *Pikaia* and close to the earliest vertebrates. (You will read about conodonts shortly on pp. 70 of the *Atlas.)* Some early Cambrian fossils recently found in China are thought to preserve all the basic chordate features plus some more advanced vertebrate ones, namely gills as well as paired eyes. If so, then it is clear that some animals close to the vertebrate bodyplan had already appeared by early Cambrian times, and chordate ancestry probably reaches back into the late Precambrian.

SAQ 6b

Humans belong to the vertebrate group known as mammals. Using Section 1.3, place mammals and the other four main vertebrate groups in order of their evolutionary appearance.

Answer

The earliest generally recognised group of vertebrates to appear in the fossil record are fish, followed by amphibians, reptiles, mammals and finally birds.

2 The Ordovician seas

Before going any further, click on 'View document' below and read pages 68-71 from Douglas Palmer's Atlas of the Prehistoric World.

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Collecting seashells on an Ordovician beach would have been a rather curious experience. Whilst most shells were made of similar materials to those found on a modern beach, the detailed form of many would have been quite unfamiliar, and all the species have long been extinct.

Have a look at the panoramic illustration on pp. 70-71 of the *Atlas*. From this and the *Atlas*, pp. 68-71, think about which organisms appear most unfamiliar to you.

There are many organisms that probably seem unfamiliar, and when reading about them you may want to refer to Section 1.3. Brachiopods, e.g. *Strophomena*, are superficially clam-like animals, and although not extinct, are much rarer now than in the Palaeozoic; most people have never seen a living one. Graptolites, e.g. *Orthograptus*, are extinct colonial animals that mostly drifted in the ocean currents (Figure 2). Trilobites, e.g. *Triarthrus*, are extinct marine arthropods. Conodonts, e.g. *Promissum*, are extinct, and jawless (agnathan) fish, e.g. *Sacabambaspis*, are extinct except for hagfish and lampreys (see Section 1.4). The straight-shelled nautiloid cephalopods, e.g. *Endoceras*, are extinct and only distantly related to today's *Nautilus*, which has a spiral shell. The groups still very much with us include horseshoe crabs, snails (gastropods), e.g. *Cyclonema*, and corals (although Palaeozoic corals were significantly different from modern corals). Bivalves (not shown) were much rarer in the Ordovician seas than they are today.

All this fauna was marine. Very little, if any, animal life had made it out of the sea onto dry land by the end of the Ordovician. Trace fossils of an unknown, possibly millipede-like animal (*Atlas*, p. 71) are rare evidence that invertebrates were exploring the edge of the land by a freshwater route. There is fossil evidence that bryophyte-like plants and fungi had begun to colonise land environments back in Ordovician times. Apart from a small advance guard, however, the main invasion of freshwater and land environments by plants and animals did not really get going until the Silurian Period.

Figure 2 Specimens of the graptolite *Diplograptus* in Ordovician shales (field of view 3.5 cm). Graptolites often look like tiny saw blades lying on the rock surface

3 The Silurian Period and the invasion of the land

Before going any further, click on 'View document' below and read pages 72-75 from Douglas Palmer's Atlas of the Prehistoric World.

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SAQ 7

What global event had reduced global sea level at the end of Ordovician times, drastically affecting shallow marine organisms, and leaving the diversity of early Silurian life severely curtailed?

Answer

The global climate descended into an ice age, locking up ocean water in the polar ice caps, exposing much of the continental shelves above sea level, eliminating many shallow marine habitats and driving many species to extinction (*Atlas*, p. 69). (Sea level probably fell by about 100 m, not 330 m as stated in the *Atlas*.)

Recent research shows that minor glaciations continued into the early Silurian, but after a while the oceans became warmer again and sea levels rose. It took several million years for marine life to recover. At first, stromatolites were relatively common, apparently because the organisms that normally suppressed them had suffered severely, but by mid Silurian times, vast coral reefs were established in tropical waters, promoting a rich diversity of organisms. The growth of corals with their tough, mineralised skeletons turns flat sea beds into complex 3-D topographies, baffling ocean currents, and providing sheltered surfaces and new ecological niches. We will soon study some of the organisms that thrived in such environments.

Meanwhile, the animals and plants that were invading the land faced all sorts of environmental challenges to which they had to adapt. For example, if a marine plant cell is directly surrounded by fresh water, the water tends to flow into it by the process of osmosis, causing it to burst. Alternatively, if the cell is directly surrounded by air, it loses all its water, just as seaweeds become hard and crisp when stranded above high tide and exposed to the wind and the sun. So, to survive in air, plants had to acquire an effective outer coat to keep the right amount of water in. They also had to evolve small, controllable pores to enable gases to be exchanged through this coat. Expressed this way, it is all too easy to give the impression, quite wrongly, that such innovations could be achieved intentionally, almost as if by some directed effort. On the contrary, as in all evolutionary explanations, natural selection would have favoured those organisms that were, *by chance*, better adapted to these new environmental challenges.

Without the buoyancy provided by immersion in water, adaptations in both plants and animals were needed to support a body on land against the pull of gravity. The relatively high density of water provides much greater support for the bodies of marine organisms than does less dense air - hence the expression 'like a fish out of water'. To grow up off the land surface, plants had to develop groups of special plumbing cells to conduct water, nutrients and the products of photosynthesis around their bodies. Only about 4 cm tall, *Cooksonia* (see Figure 3a and illustration, *Atlas*, p. 75) lacked leaves, and sent short, forking shoots upward to capture sunlight and release **spores** (reproductive cells) into the wind. These first true **vascular land plants** with specialised cells for carrying fluids around an upright plant were still dependent on water for reproduction, and lived in swamps and on riverbanks and floodplains. The earliest movement onto land, for both plants and animals, seems to have been through the medium of fresh, as opposed to saline, water.

Air, being a gas, has a low capacity to store heat compared with seawater and, to survive, life on land must be able to withstand relatively large temperature fluctuations as well as higher amounts of ultraviolet radiation from the Sun. Exchange of gametes during reproduction is also much easier in water where male gametes can swim to fertilise the female ones. The animals that, by chance, were best adapted to life on land were the arthropods. They were very strong for their size, and already had an almost waterproof outer skeleton that was resistant to damage by ultraviolet light. Numerous paired and jointed limbs with internal muscles helped overcome gravity and allow movement over uneven terrestrial surfaces. However, the arthropods could not have invaded the land if there had not already been some supply of food there.

SAQ 8

According to the *Atlas* (p. 74), what are the first arthropods believed to have eaten?

Answer

The first arthropods were probably eating the decaying remains of plants such as *Cooksonia*.

Once the greening of the land had begun, small millipedes and wingless insects were apparently tempted onto it to eat the rotting plant debris, and they and their remains were eaten in turn by predatory or scavenging carnivorous arthropods such as centipedes, scorpions and small spider-like creatures (Figure 3b).

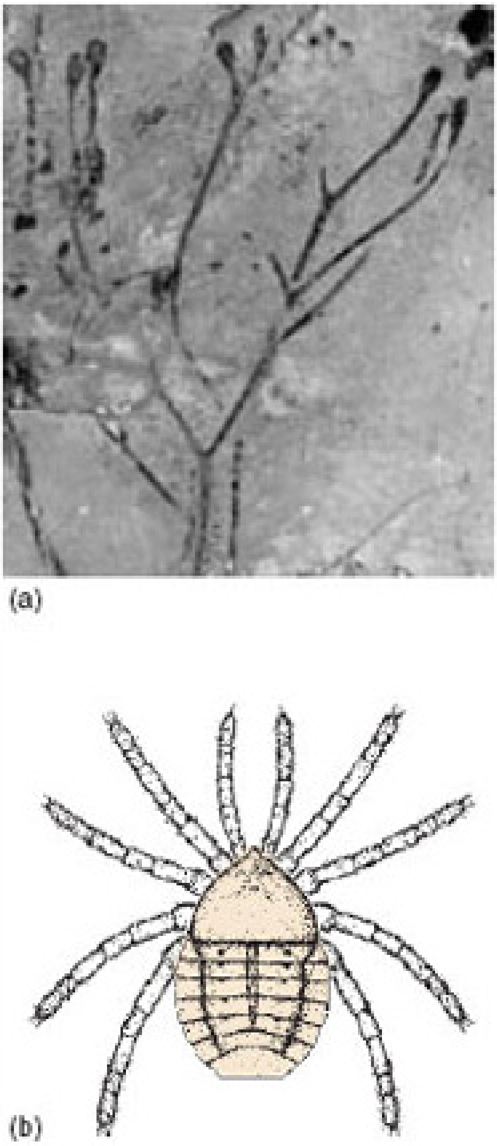

Figure 3 (a) Early life on land. *Steganotheca*, a very early land plant (a close relative of *Cooksonia*) from Silurian rocks in Wales, about 4 cm tall. Notice the spore-bearing structures at the end of each simple-branching stem. (b) One of the earliest known land animals - a spider-like creature (4 mm long including legs) from Silurian rocks in Shropshire, England

4 Life in the Silurian sea

4.1 Trilobites

As we've seen, the Cambrian explosion left the seas teeming with a huge variety of animals. In the following activity you will study some of the marine life at one particular time in the Palaeozoic Era - the middle part of the Silurian Period, 430 Ma ago. You'll look in detail at some fossils which come from a deposit in the UK called the Wenlock Limestone, famous for its many beautiful fossils. The Wenlock Limestone crops out mainly around Birmingham and the borders of Wales.

Figure 4 shows a trilobite from the Wenlock Limestone, called *Calymene* ('kal-iminny').

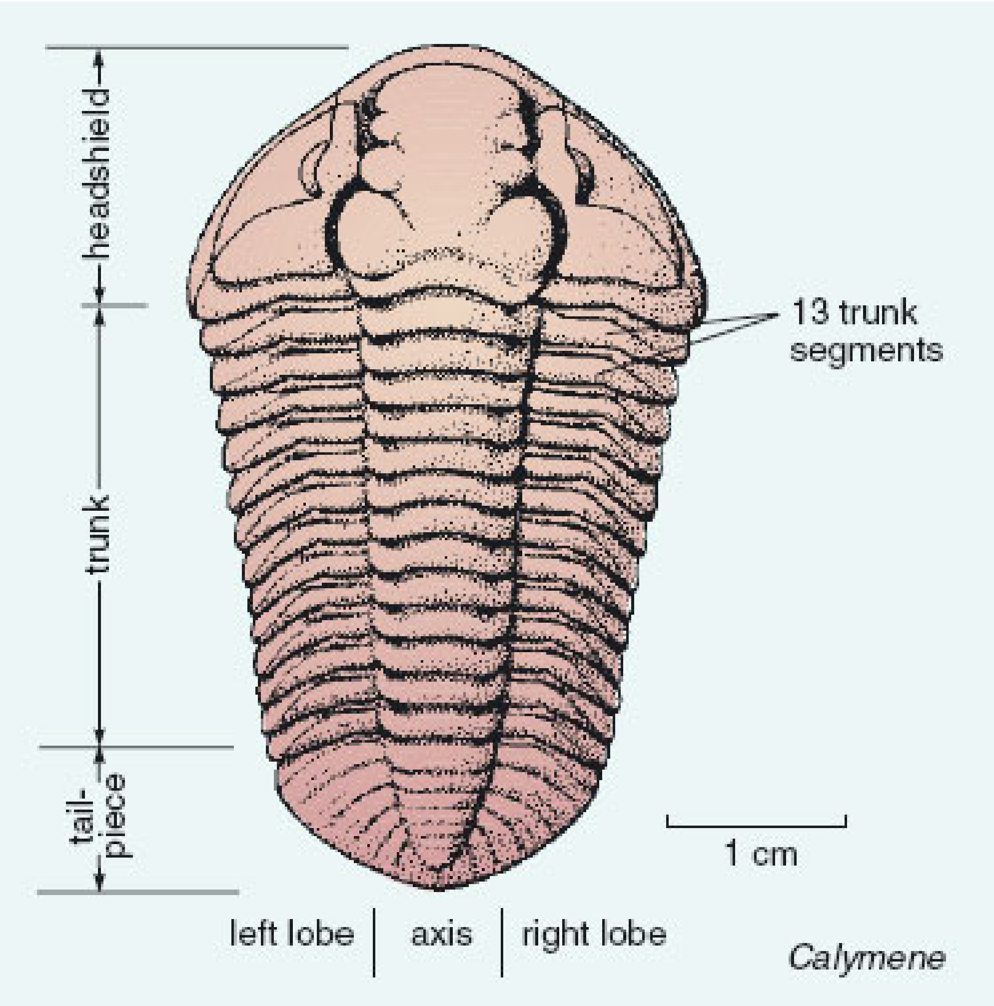

Figure 4 *Calymene*, a trilobite from the Wenlock Limestone

Trilobites were a major group of entirely marine arthropods that thrived in the seas of the Palaeozoic Era and eventually became extinct in the Permian Period. The arthopods are an immensely diverse phylum (see Section 1.3). Their external jointed skeleton (exoskeleton) forms a robust armour-plating for the body, though it is flexible at the joints to allow movement.

SAQ 9

Being arthropods, how did trilobites get around the problem of ytheir growth being constrained by an external skeleton?

Answer

Trilobites, like other arthopods, grew by moulting, i.e. periodically casting off their rigid shell, and secreting a new, larger one.

Trilobites are so named because they have three lobes running up and down their length - a central axis, and two lobes: one on either side. They are also divided cross-ways into a **headshield**, a **trunk**, and a **tailpiece**. Have a preliminiary look at the fossil in Figure 4 to see if you can identify these divisions. The trunk has a number of separate segments, and the tailpiece is made of a single plate. The more formal names for the three main divisions of the trilobite body, often used elsewhere, are as follows:

headshield = cephalon; trunk = thorax; tailpiece = pygidium.

Trilobites also had appendages such as antennae and legs, but these are extremely rarely found. An example where legs are preserved is shown on p. 63 of the *Atlas*.

SAQ 10

What does the rarity of trilobite appendages suggest about their structure?

Answer

They were not so durable, being less mineralised than the components normally found (headshield, trunk and tailpiece), and soon decayed like other soft tissues.

Because trilobites cast off their shell during moulting, most trilobite fossils are actually shed shells, rather than carcasses (dead animals). The trilobite's hard outer shell needed places of weakness along which it could break apart during moulting, a bit like having weak areas between the pieces of a bar of chocolate. There were lines of weakness between the headshield and the front of the trunk; between any two trunk segments; and between the end of the trunk and the front of the tailpiece. Trilobites also had one or more lines of weakness within the headshield. Figure 4 shows these lines of weakness for *Calymene;* they allowed two side pieces to detach from the larger, central part of the headshield.

Many trilobites had eyes. In *Calymene* (Figure 4), they are at the cresent-shaped areas on the detachable side pieces either side of the central part of the headshield. The eyes were rather like the compound eyes of a modern fly (another arthropod) in having many lenses. Each trilobite lens was made of calcite, and its preservation potential was as good as the rest of the skeleton (also made mostly of calcite). Trilobites had the earliest recorded eyes in the animal world.

The presence of well-developed eyes suggests that wherever the trilobites were living there was enough light to see by, and, as light fades with depth, the water is unlikely to have been very deep.

It is likely that *Calymene* spent more time scuttling around on the sea floor than swimming high up in the water. It probably rested on the sea floor, stretched out in the same way as in Figure 4. These trilobites probably ate small organisms and organic debris on or near the sea floor.

Some trilobites could roll up, tucking the tail snugly underneath the head. Figure 5 shows a specimen of *Calymene* that has rolled itself up into a ball, like a pill bug (a type of woodlouse, another arthropod) can do. The flat, outer edges of the trunk segments had to slide over each other to enable the trilobite to roll up.

SAQ 11

Why might the ability to roll up be useful?

Answer

It would protect any soft parts underneath the hard external skeleton from attack by predators, damage during storms, etc.

By studying fossils one can observe various features of the morphology of an extinct organism, and infer aspects of its mode of life and environment. We can do this by comparing observed features with what is known of living relatives and similar fossils. In practice, when studying fossils one would also take other information into account, such as evidence from the sediment enclosing the fossil, and so on. The result is always an *interpretation* that reflects the balance of probabilities from the available information, rather than the certain truth.

Figure 5 A specimen of *Calymene blumenbachi* from the Wenlock Limestone that rolled

itself up into a ball (2.5 cm)

4.1.1 More on trilobites

Many thousands of trilobite species are known, mostly from Cambrian to Silurian rocks, and all were confined to the Palaeozoic Era. By the time trilobites became extinct in the late Permian, their diversity had dwindled to a small number of species, and the group was long past its peak. The variation in trilobite form is enormous, but the basic three-lobed division of the exoskeleton is always present. The number of trunk segments varies from 2 to 40. Not all have eyes. Most are about 2-10 cm in length but some are 1-2 mm and a few species grew to nearly 1 m long. The majority of trilobites lived on or near the floor of shallow seas, but some trilobites swam in the surface waters of the open ocean, and some were adapted to low concentrations of oxygen in water hundreds of metres deep. How they reproduced is not clear. Figure 6 shows a range of trilobites from the Ordovician Period.

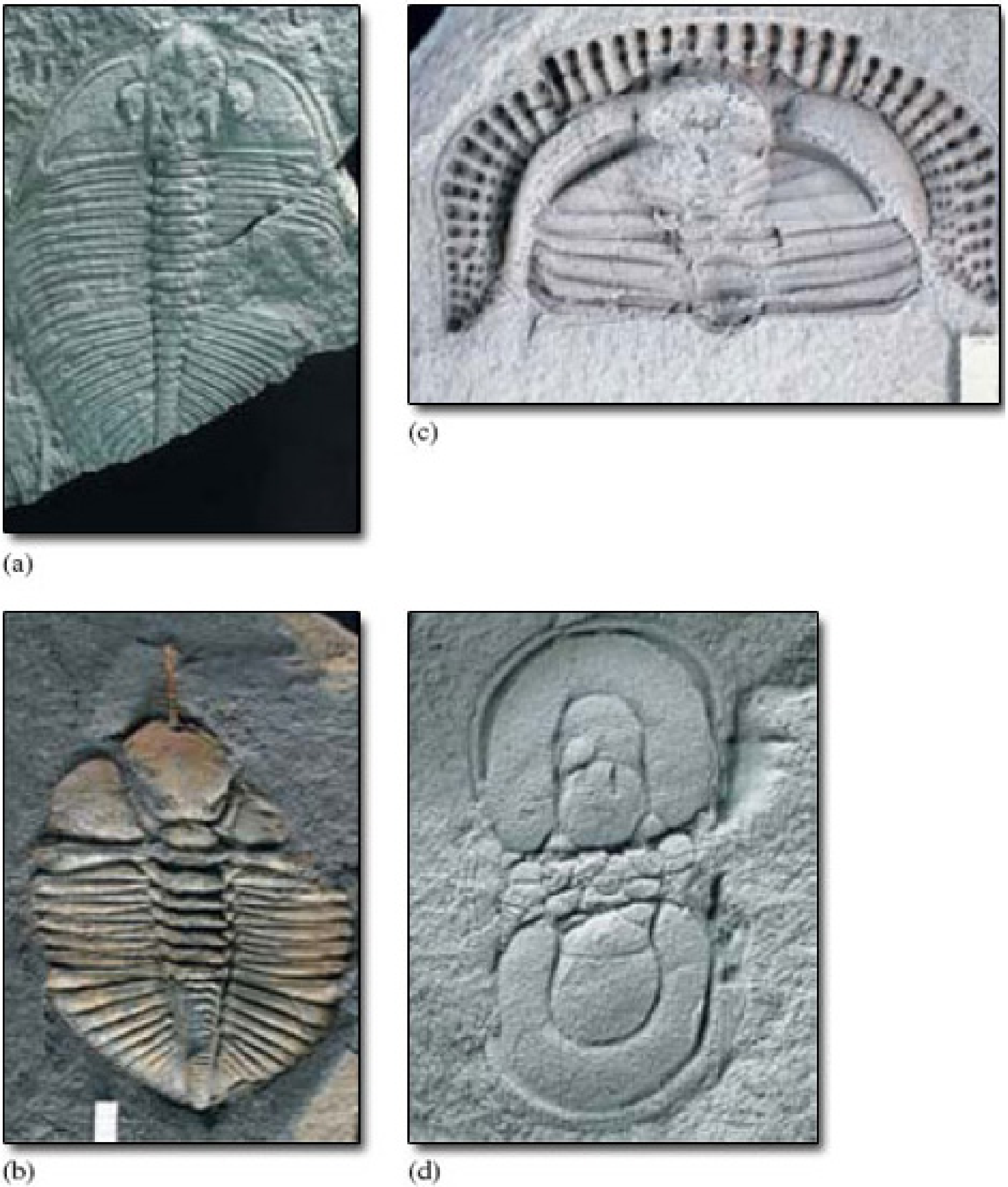

Figure 6 A selection of Ordovician trilobites from central Wales. (a) *Oygiocarella* (7.5 cm). (b) *Cnemidopyge* (3 cm). (c) *Telaeomarrolithus* (2 cm). Trilobites like this with a pitted fringe around the head are called trinucleids. The main function of the fringe, which has tiny holes at the centre of each little pit, may have been to allow water to pass out from a feeding chamber underneath the head after the animal had strained off small food particles. This specimen is enrolled - the tailpiece, along which the specimen has partly split, is tucked up underneath the headshield. (d) *Segmentagnostus*. This trilobite, about 1 cm long, belongs to a group of small trilobites called agnostids, which have only two or three trunk segments and a headshield and tailpiece of similar size and shape

4.2 Crinoids

Figure 7 shows the fossilised remains of a type of echinoderm called a crinoid ('cry-noyed'). Although crinoids occur today, they were far more common in the Palaeozoic and Mesozoic Eras. Most crinoids feed by bending their umbrella-like arrangement of flexible appendages (called '**arms**') downstream so as to catch a current, rather as in an umbrella being caught in the wind. Tube feet (multipurpose tentacles) on the arms gather food particles suspended in the water, which are then wafted by small hair-like threads in grooves along the arms to the central mouth. Most ancient crinoids lived gregariously in shallow, current-swept areas, free of muddy sediment that would otherwise have tended to kill them by clogging their feeding mechanism.

Figure 7 *Marsupiocrinites*, a Silurian crinoid from the Wenlock Limestone. The lower part of the stem is broken off. The length of the part of the specimen shown here is 9 cm

Most ancient crinoids were attached to the sea floor by a stem or stalk with a root-like holdfast. The mouth and gut were situated in an enclosed cup at the top of the stem. In life, the stem was fairly flexible, like the arms. The majority of living crinoids do not have a stem, and are capable of creeping around or even swimming. The few surviving stemmed forms generally live in deep water. Although they are animals, crinoids with stems look at first so like plants that they are often informally called 'sea lilies'. Shortly after death, the tiny organic fibres that alone hold the calcite plates together rot away, often causing the crinoid to disintegrate into separate plates that can be readily dispersed by currents or the movement of other organisms. In some ancient environments where crinoids were abundant, rocks have formed that are largely composed of isolated plates and stem fragments (Figure 8).

Crinoids have an arrangement of five '**rays**', each of which carries one or more arms that together form an efficient food-gathering structure. Attached to each arm are many fine side-branches called **pinnules**, each made of tiny plates, which are also part of the food-gathering apparatus.

Figure 8 A limestone of Carboniferous age composed of crinoid debris, especially stem plates. The stems are in varying degrees of disarticulation. Field of view 8 cm

4.3 Corals

Corals are especially abundant in the Wenlock Limestone.

SAQ 12

According to Section 1.3, which two main groups of corals, each confined to the Palaeozoic Era, might you expect to find in the Silurian Period?

Answer

Rugose corals and tabulate corals.

SAQ 13

Which of these two coral groups only forms colonies?

Answer

The tabulate corals are always colonial (whereas the rugose corals may be either colonial or solitary).

Figure 9 shows two rugose corals. When alive, the *Acervularia* colony in Figure 9a would probably have looked like a bunch of sea anemones, with each of them sitting in one of the bowl-shaped hollows of their calcite skeletons. The skeleton secreted by an individual, whether part of a colony or not, is called a **corallite.** In rugose corals, each corallite is usually divided by a series of conspicuous radial partitions, called septa (Figure 9). The corallites in a colony such as *Acervularia* share adjacent walls. In the centre of many corallites of *Acervularia* is a single, bowl-shaped hollow. Within some corallites there are one or more smaller hollows. These little hollows have the same basic arrangement of septa as in the larger corallites: they represent *new* individuals formed by the splitting up of their parent, enabling the coral colony to grow upward and outward by a process of asexual reproduction.

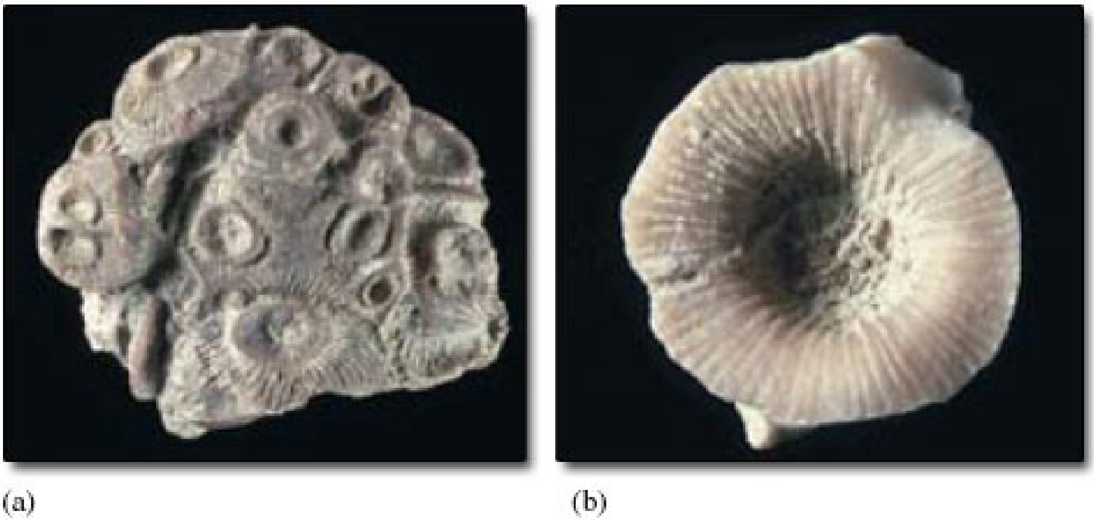

Figure 9 Rugose corals from the Wenlock Limestone. (a) *Acervularia ananas*, a rugose coral colony (5.5 cm); (b) *Kodonophyllum truncatum* (2.5 cm). This is a solitary individual from a species that more often forms colonies. Most other rugose coral species are either always solitary or always colonial

Tabulate corals are distinguished by having much smaller corallites than those of rugose corals, and septa are either absent or short and inconspicuous. Tabulate coral colonies may take various forms, including massive (Figure 10a) or chains (Figure 10b).

Some Wenlock Limestone corals are shown on pp.74 and 75 of the *Atlas;* see if you can distinguish the solitary corals from colonial ones. The coral at the bottom of the group on p. 75 is a tabulate coral called *Heliolites*.

SAQ 14

What sort of environments do corals tend to be associated with today?

Answer

Images of Australia's Great Barrier Reef and tropical islands like the Bahamas probably spring to mind (though not all corals live in shallow waters).

SAQ 15

According to Section 1.3, what is the main group of modern corals, and what is their age range?

Answer

Scleractinian corals; Triassic to Recent.

Figure 11 shows some examples of modern coral skeletons, both solitary and colonial. Like rugose corals, scleractinians usually have conspicuous septa. However, unlike both rugose and tabulate corals, the skeleton of scleractinians is made of aragonite, not calcite. Although it is also a form of calcium carbonate, aragonite tends to alter to calcite or dissolve away, so that Mesozoic and Cenozoic corals (i.e. scleractinians) are often less well preserved than Palaeozoic ones.

Most, but not all, scleractinian corals today grow in warm, clear, shallow seas. The same seems to have been true of many ancient corals, including Palaeozoic ones. The requirement of many of today's corals for clear, shallow water is mostly because within the corals' soft tissues are tiny algae with which they live in an association of mutual benefit. The algae require clear, well-lit water for photosynthesis. By analogy with the preferences of most modern corals, and what is known of ancient ones, it therefore seems very likely that the water of the Wenlock Limestone sea was warm rather than cold. This is supported by palaeomagnetic evidence showing that at this time Britain was about 25° south of the Equator. Palaeozoic and scleractinian corals are, however, unrelated and there is evidence that Palaeozoic corals lacked a special association with algae.

(a)

(b)

Figure 10 Tabulate corals from the Wenlock Limestone. (a) *Favosites* (field of view 8 cm); (b) *Halysites*, the 'chain coral' (field of view 3.5 cm)

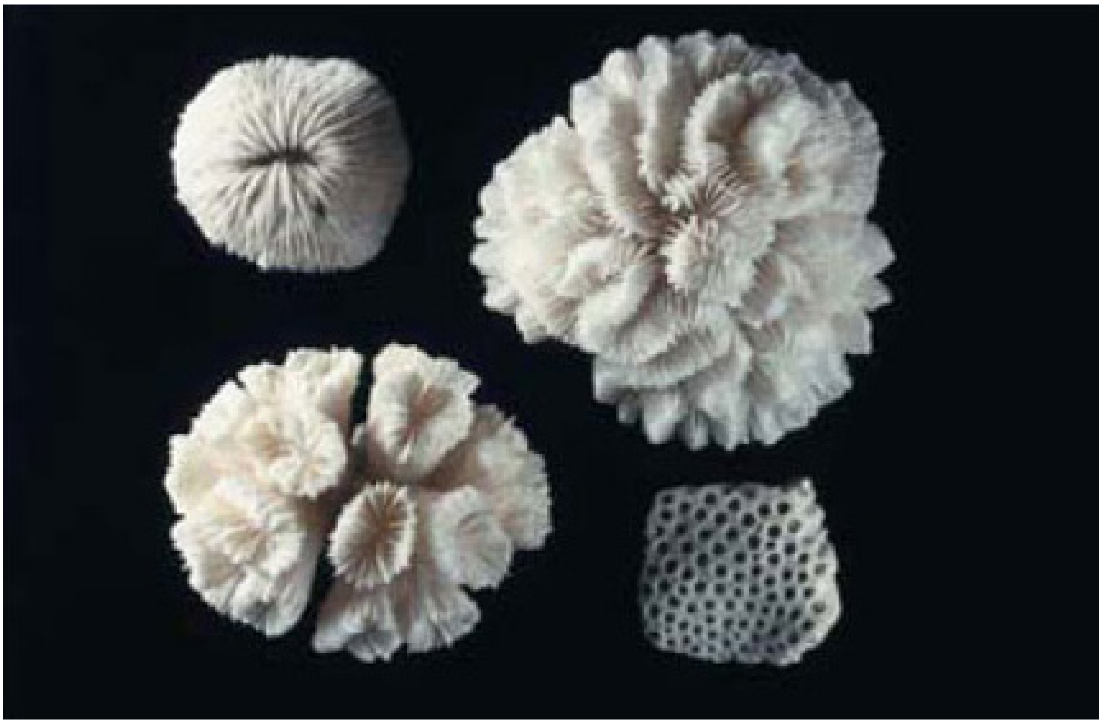

Figure 11 Examples of modern scleractinian coral skeletons. The largest is 9 cm across

4.4 Other Wenlock Limestone fossils

Among the other fossils common in the Wenlock Limestone are brachiopods (Figure 12a and b), gastropods (Figure 12c) and bryozoans (Figure 12d). You may need to reread Section 1.3 to remind yourself about various aspects of these groups.

Figure 13 (the course image) is a reconstruction of a typical scene from a Wenlock Limestone environment. See if you can identify trilobites (alive, dead, or moulted pieces of exoskeleton), corals (colonies and isolated individuals), and crinoids among the various forms of life depicted. The cone-shaped squid-like animals are straight nautiloids (cephalopod molluscs, Section 1.3).