

Chapter 10



Origin of the metazoans

Key points

- Relatively few basic body plans have appeared in the fossil record; most animals have a triploblastic architecture, with three fundamental body layers.
- Molecular data show there are three main groupings of animals: the deuterostomes (echinoderm–hemichordate–chordate group), the spiralian (mollusk–annelid–brachiopod–bryozoans–most flatworms–rotifers (platyzoans) group) and the ecdysozoans (arthropod–nematode–priapulid plus other taxa group). Together, the spiralian and ecdysozoans are usually called the protostomes.
- Five lines of evidence (body fossils, trace fossils, fossil embryos, the molecular clock and biomarkers) suggest that the metazoans had originated prior to the Ediacaran, 600 Ma.
- Snowball Earth by coincidence or design was a pivotal event in metazoan history; bilaterians evolved after the Marinoan glaciation.
- The first metazoans were probably similar to the demosponges, occurring first before the Ediacaran.
- The Ediacaran biota was a soft-bodied assemblage of organisms largely of uncertain affinities, reaching its acme during the Late Proterozoic, which may represent the earliest ecosystem dominated by large, multicellular organisms.
- The Tommotian or small shelly fauna was the first skeletalized assemblage of metazoans; this association of Early Cambrian microfossils contains a variety of phyla with shells or sclerites mainly composed of phosphatic material.
- The Cambrian explosion generated a range of new body plans during a relatively short time interval.
- The Ordovician radiation was marked by accelerations in diversification at the family, genus and species levels together with increased complexity in marine communities.

Consequently, if my theory be true, it is indisputable that before the lowest Silurian [Cambrian of modern usage] stratum was deposited, long periods elapsed, as long as, or probably far longer than, the whole interval from the Silurian age to the present day; and that during these vast, yet quite unknown, periods of time, the world swarmed with living creatures.

Charles Darwin (1859) *On the Origin of Species*

ORIGINS AND CLASSIFICATION

When did the first complex animals, the metazoans, appear on Earth and what did they look like? How could complex, multicelled animals evolve from the undifferentiated single-celled organisms of most of the Precambrian? Why did they take almost 4 billion years to appear? These questions have puzzled scientists, including Charles Darwin, for over two centuries. In the last few decades a range of multidisciplinary techniques, from molecular biology to X-ray tomography, has helped generate new testable hypotheses regarding the origins of our early ancestors. Apart from the fossil evidence of metazoan body and trace fossils, the investigation of minute fossil embryos, carefully calibrated molecular clocks and more recently biomarkers have placed the investigation of Precambrian life at the top of many scientific agendas.

The first metazoans: when and what?

Life on our planet has been evolving for nearly 4 billion years. Molecular data suggest metazoans have probably been around for at least 600 myr (Fig. 10.1), during which time, according to some biologists, as many as 35 separate phyla have evolved. Five lines of evidence have figured prominently in the search for the earliest metazoans: body fossils, trace fossils, fossil embryos, the molecular clock and biomarkers.

Much controversy still surrounds the timing of their origin. Was there a long cryptic interval of metazoan evolution prior to the Ediacaran – a time when we do not find fossils preserved, either because the animals lacked preservable bodies, or they were small, or perhaps a combination of both? Or, as the recalibrated molecular clocks suggest, can animal origins be tracked back only to the Ediacaran, when there was also a sudden rise

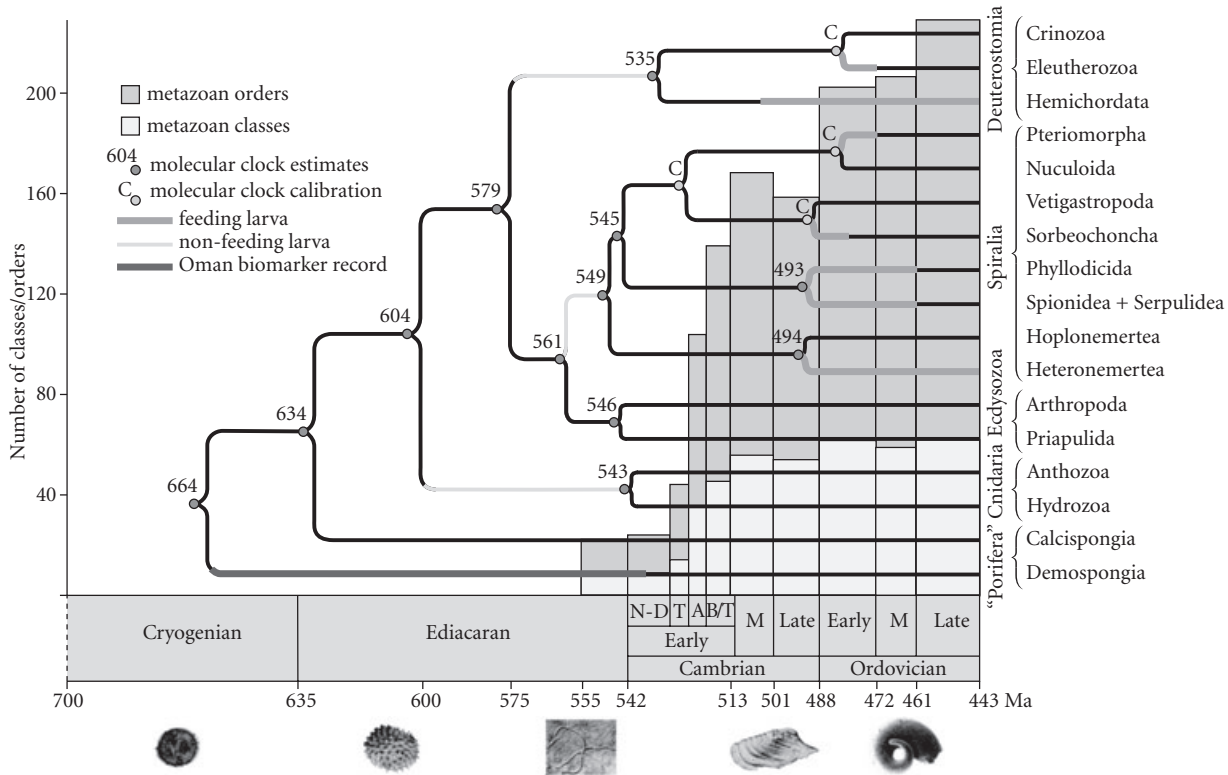


Figure 10.1 Time scale and tempo of early animal evolution: the key metazoan groups are shown with the putative age of their last common ancestor, together with an estimate of the respective numbers of classes and orders indicated against a stratigraphy indicating key biological and chemical events. N–D, Nemakit-Daldynian; T, Tommotian; A, Atdabanian; B/T, Botomian. (Courtesy of Kevin Peterson.)

in oxygen levels in the deep ocean (Canfield et al. 2007).

Body fossil evidence

Body fossils of basal metazoans in the Ediacaran Period are few and far between. The morphology of an early metazoan fossil must be clearly described and convincingly illustrated, different organs and tissues identified, and comparisons drawn with other extant and fossil organisms. Many Upper Precambrian successions have been subjected to intense metamorphism and tectonism (see p. 48) and are now located in some of the Earth's mountain belts. The chances of finding adequately preserved fossils are slight. Nevertheless, the earliest undoubted metazoans occur within the widespread Ediacara biota (see p. 242) dated at approximately 600–550 Ma. Moreover the fact that a relatively advanced metazoan, the mollusk *Kimberella*, possibly equipped with a foot and radula (see p. 330), occurs within the Ediacara biota from southern Australia and Russia could suggest a history of metazoan evolution prior to the Ediacaran. But although a strong case can be made for a significant Proterozoic record for the cnidarians and sponges and perhaps some other metazoans, the Cambrian explosion still marks the arrival, center stage, of the bilaterians (Budd 2008).

Trace fossil evidence

Trace fossils are the behavior of organisms recorded in the sediment (see p. 510). By their very nature they occur in place and thus cannot be transported or reworked by currents. Nevertheless these too must be convincingly demonstrated as biogenic and the age of their enclosing sediments accurately determined. If and when metazoans developed locomotory organs, such as the molluskan foot, and digestive systems, we might expect to find burrows and trails together with fecal pellets. Records of trace fossils from rocks older than 1 Ga in India (Seilacher et al. 1998) and over 1.2 Ga in the Stirling biota of Australia (Rasmussen et al. 2002) generated considerable excitement (Fig. 10.2). Both suggested metazoan life older than 1 Ga but both are now considered questionable (Jensen 2003). The oldest undoubted locomotory



Figure 10.2 Putative trace fossils from the Precambrian of Australia, showing *Myxomitodes*, a presumed trail of a mucus-producing multicellular organism about 1.8–2 billion years old from Stirling Range, Western Australia. (Photo is approximately 65 mm wide.) (Courtesy of Stefan Bengtson.)

trace fossils are from about 550 Ma (Droser et al. 2002) from northwest Russia, whereas fecal strings have been reported from rocks some 600 Ma (Brasier & McIlroy 1998) suggesting the existence of an ancient digestive system. In fact no convincing trace fossils are known from successions older than the **Marinoan glaciation** (635 Ma), the second main icehouse event associated with snowball Earth (see p. 112).

Embryo fossil evidence

Fossil Neoproterozoic embryos are now known from a number of localities, although claims that they represent sulfur-oxidizing bacteria or that they are not embryos at all have their advocates. Some of the best studied examples are from the Doushantuo Formation, South China. The part of the formation yielding the embryos was first dated at approximately 580 Ma, predating much of the Ediacaran but postdating the Marinoan glaciation. Revised dates seem to suggest that the faunas are younger and that they overlap with the older Ediacaran assemblages. Cell division and cleavage patterns are obvious although it is difficult to assign the material to distinct metazoan groups in the absence of juvenile and adult forms. There are, however, a lack of epithelia even in clusters of over 1000 cells

suggesting that the embryos examined are those, at best, of stem-group metazoans (Hagadorn et al. 2006); they could equally well be fungi or rangeomorphs (enigmatic frond-like fossils). Nonetheless the Doushantuo embryos, although unplaced taxonomically, provide our earliest body fossil evidence for probable metazoan life, albeit very basal, and a fascinating insight into embryologic processes in deep time (Donoghue 2007) (Box 10.1).

Molecular evidence

Not only have the morphologies of organisms evolved with time, but so too have their molecules. This forms the basis of the concept of the **molecular clock** (see p. 133). The molecular clock has opened up tremendous possibilities to date, independently of direct fossil evidence, the times of divergence of say the mammals from the reptiles or the brachiopods from the mollusks. Nevertheless, attempts to date the divergences of the various groups of metazoans have proved controver-

sial. For example, the last common ancestor of the bilaterians, the metazoan clade excluding the sponges and cnidarians, has been variously placed at anywhere between 900 and 570 Ma. Why is there such a spread of ages in a seemingly exact science? The rates of molecular evolution in various groups are unfortunately not constant. The vertebrates appear to have reduced their rates of molecular change through time. So, using the slow vertebrate rates of molecular evolution to calibrate the date of origin of Bilateria gives dates that are too ancient (900 Ma). On the other hand, using mean bilaterian rates of molecular evolution gives a date (570 Ma) that is more in keeping with evidence from the fossil record (e.g. Budd & Jensen 2000) and thus makes the Cambrian explosion much more of an explosion of animals rather than fossils (Peterson et al. 2004). Nevertheless the most recent molecular clock data (Peterson et al. 2008) suggest a major phase of metazoan radiation within the Ediacaran, prior to that in the Cambrian. This radiation probably set the agenda for metazoan macroevolution for the rest of geological time.



Box 10.1 Synchrotron-radiation X-ray tomographic microscopy

Fossil embryos from the Upper Neoproterozoic and Cambrian are providing some important clues about the origin and early evolution of the metazoans. They are, however, tiny and notoriously hard to study. Nevertheless Phil Donoghue and his colleagues (2006) are beginning to accumulate a large amount of new information on the composition, structure and cell division within these minute organisms together with their modes of preservation. Synchrotron-radiation X-ray tomographic microscopy (SRXTM) has provided a whole new way of scanning embryos without actually destroying them (Fig. 10.3). The embryos, most of them 1 mm across or smaller, are held steady in a high-energy beam of photons, and multiple “slices” are produced, spaced a few microns apart. Using imaging software, these slices can be combined to create a detailed three-dimensional model of the internal structure of the fossil. Embryos assigned to the bilaterian worm, *Markuelia*, together with *Pseudoooides*, variously show the process of cell cleavage and development of possible blastomeres, clusters of cells produced by cell division after fertilization, rather than yolk pyramids, which are more typical of the arthropods. This high-tech methodology has already demonstrated a real prospect for identifying the animals themselves and charting their early stages of development, some 600 Ma. It also can reject the claims that such fossils were the planula larvae of cnidarians, minute bilaterians or the early stages of gastrulation (see p. 240) of hydrozoans or bilaterians. It has, however, been recently suggested that many of these embryonic structures were created by bacteria (see p. 190). But not all.

Read more about this topic at <http://www.blackwellpublishing.com/paleobiology/>.

Continued

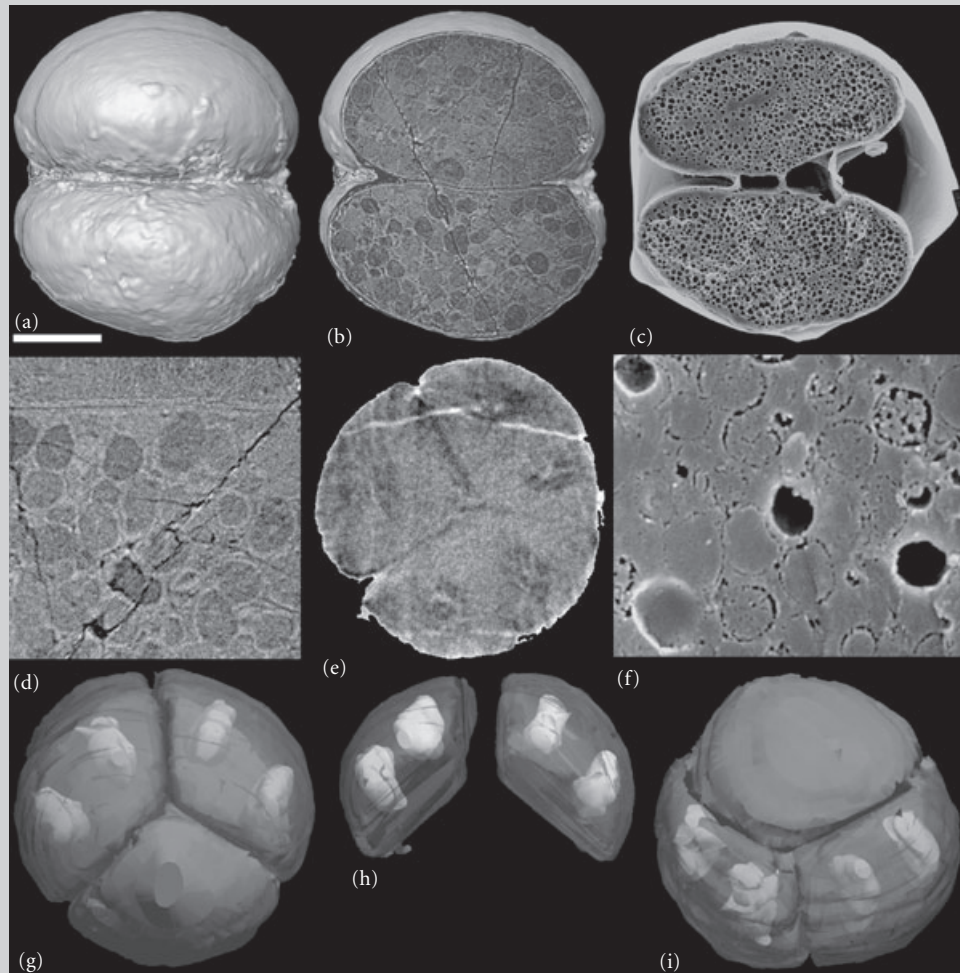


Figure 10.3 Animal embryos from the Doushantou Formation, China. (a) Surface of embryo based on tomographic scans together with (b) an orthoslice revealing subcellular structures analogous to modern lipids and (c) an orthoslice at the boundary between two cells. (c, f) Two-cell embryo of the sea urchin *Heliocidaris* showing lipid vesicles for comparison. (e) Orthoslice rendering of a possible embryo revealing internal structures. (g–i) Models of tetrahedrally arranged cells. Relative scale bar (see top left): 170 μm (a–d, f), 270 μm (e), 150 μm (g–i). (Courtesy of Philip Donoghue.)

Biomarker evidence

Biomarkers, essentially the biochemical fingerprints of life, have become increasingly important in astrobiology, where they have been sought in the quest for extraterrestrial life. But they are also of considerable importance in the investigation of Precambrian life (see p. 188), where other lines of evidence are lacking. Thus amino acids, hopanes, some types of hydrocarbons, evidence of isotopic fractionation in carbon (^{12}C) and biofilms are

strong indicators of life forms. More exciting is the fact that specific biomarkers may be related to particular groups of organisms. Significantly, biomarkers associated with metazoan demosponges (see p. 262) have now been reported from rocks older than the Ediacaran, confirming the presence of basal metazoans at this time. But since the sponges are paraphyletic, biomarkers from the homoscleromorph sponges (see p. 262) would also have to be present to prove the presence of the eumetazoans.

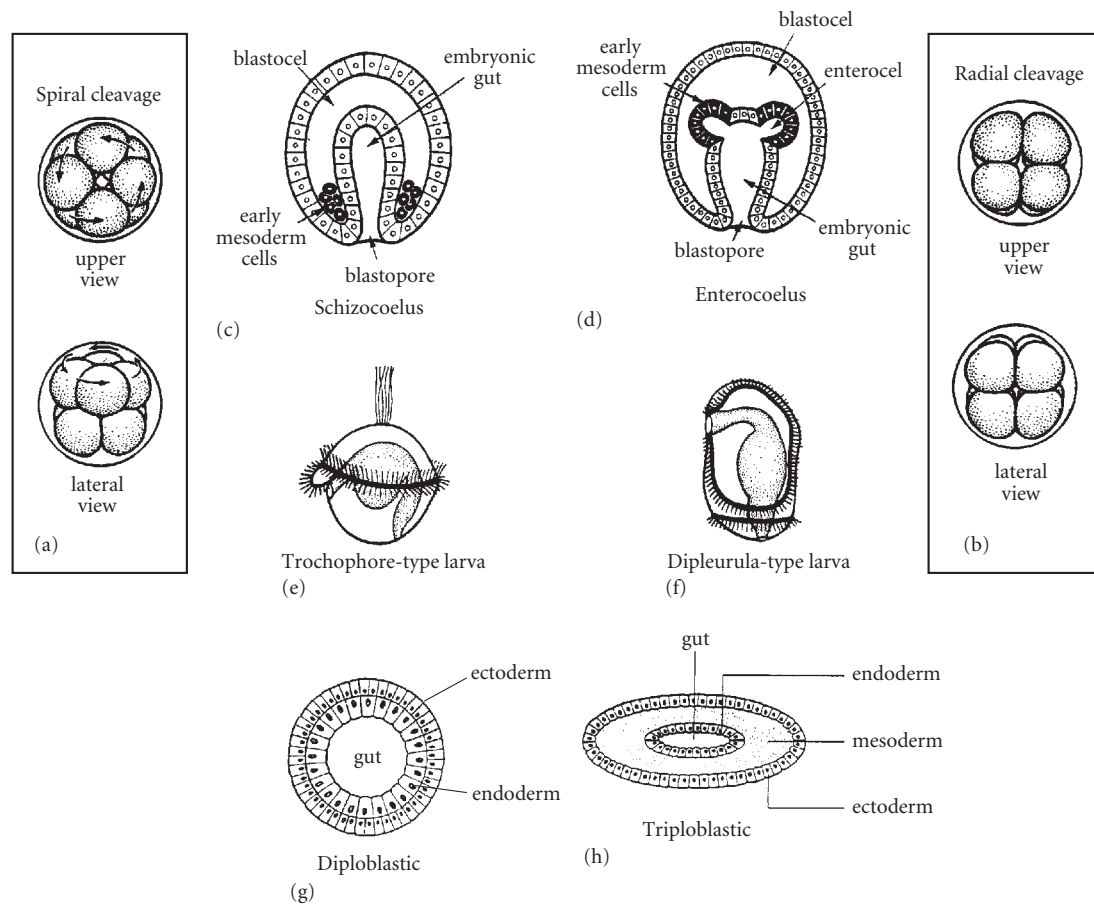


Figure 10.5 Main invertebrate body plans and larvae: upper and lateral views of spiral (a) and radial (b) patterns of cell cleavage; development of the mesoderm in the spiralian (c) and radialians (d); diploblastic (g) and triploblastic (h) body plans and trochophore-type (e) and dipleurula-type (f) larvae.

Table 10.1 Key characteristics of the three main groups of animals.

| Group | Grade | Symmetry | Key character | Larvae |
|-----------|---------------|-------------------------------|-----------------|----------------|
| Porifera | Parazoan | Bilateral and radial symmetry | Collar cells | Blastula larva |
| Cnidaria | Diploblastic | Radial symmetry | Cnidoblasts | Planula larva |
| Bilateria | Triploblastic | Bilateral symmetry | Digestive tract | Various types |

rians. And finally the development of the celom or body cavity characterizes most of the animal groups found as fossils. The celom usually functions as a hydrostatic skeleton and is related to locomotion. But the presence and organization of the celom is not phylogenetically significant; the celom has evolved several times and in some groups, such as the flatworms, there are at least two types of celomic cavities.

The annelid worms and the arthropods have a celom divided along its length into

segments; each segment possesses identical paired organs such as kidneys and gonads together with appendages. The mollusks, on the other hand, have an undivided celom situated mesodermally and irregularly duplicated organs.

The remaining bilaterians, such as the phoronids, brachiopods, bryozoans, echinoderms and hemichordates have a celom that is divided longitudinally into two or three zones each with different functions. Based around this plan, animals with a specialized feeding

and respiratory organ, the **lophophore**, are characterized by sac-like bodies; but this is no guarantee that these so-called “lophophorates”, brachiopods and bryozoans, are in fact closely related. The hemichordates possess a crown of tentacles and some have paired gill slits. The echinoderms have an elaborate water vascular system that drives feeding, locomotion and respiration.

The identification of invertebrate body plans is a useful method of grouping organisms according to their basic architecture. However, similarities between grades of construction unfortunately do not always mean a close taxonomic relationship. Be aware that certain body plans have evolved more than once in different groups. Skeletons too, for example, have evolved a number of times in a variety of forms.

The skeleton is an integral part of the body plan of an animal, providing support, protection and attachment for muscles. Many animals such as the soft-bodied mollusks (slugs) possess a hydraulic skeleton in which the movement of fluid provides support. Rigid skeletons based on mineralized material may be external (**exoskeleton**), in the case of most invertebrates, or internal (**endoskeleton**) structures, in the case of a few mollusks (e.g. belemnites), echinoderms and vertebrates. Growth is accommodated in a number of ways. Most invertebrate skeletons grow by the addition of new material, a process termed **accretion**. Arthropods, however, grow by periodic bursts between intervals of **ecdysis** or molting; echinoderms grow by both accretion to existing material and by the appearance of new calcitic plates.

Classification and relationships

Classifications based on purely morphological data and embryology have met with problems. Difficulties in establishing homologous characters and homoplasy (see p. 129) have contributed to a number of different phylogenies. The locator tree (Fig. 10.6), however, outlines some of the main features of animal evolution. From the base of the metazoan tree, the demosponges and calcisponges are the simplest animals whereas the cnidarians are the most basal eumetazoans. Three robust bilaterian groupings are recognized mainly on molecular data: the ecdysozoans, the spir-

alians and the deuterostomes. The ecdysozoans and the spiralian comprise the **protostomes** (“first mouth”) where the mouth develops directly from the first opening, the blastopore, resulting from cell growth and migration. The **deuterostomes** (“second mouth”), however, have a mouth arising from a secondary opening; the true blastopore often develops as an anus. Not all phyla fit simply into these two major divisions, but using a consensus based on comparative morphology, two main streams emerge: the echinoderm–hemichordate–chordate (deuterostomous) and the mollusk–lophophorate–annelid–arthropod (protostomous) groupings (Box 10.2).

Other studies have laid emphasis on the similarities between the larval stages of organisms to investigate phylogenetic relationships.

Most invertebrates develop first a larval stage that may be either **planktotrophic**, free-living and feeding on plankton, or **lecithotrophic**, essentially benthic and feeding on yolk sacs. There is a range of different larval types. For example the nauplius larva is most typical of crustaceans, the planula characterizes the cnidarians, the trochophore larva occurs in the mollusks and the polychaetes whereas the shelled veliger also characterizes the mollusks. Thus those groups (annelids and mollusks) with trochophores may have shared a common ancestor. Invertebrate larvae are occasionally identified in the fossil record. With the availability of more advanced preparatory and high-tech investigative techniques, studies of fossil larvae may yet become a viable part of paleontology.

FOUR KEY FAUNAS

The three great evolutionary faunas of the Phanerozoic, the Cambrian, Paleozoic and Modern (see p. 538), developed during a timeframe of some 550 myr. Nevertheless, in the 100 myr that include the transition between Precambrian and Phanerozoic life, there were a number of distinctive groups of animals that together paved the way to the spectacular diversity we see today in marine and terrestrial communities. The **Ediacara biota** and **small shelly faunas**, together with those that developed during the **Cambrian explosion** and **Ordovician radiation**, set the scene for life on our planet.



Box 10.2 Molecular classification

Can molecular data help? Kevin Peterson and his colleagues (2004, 2005) have presented a minimum evolution analysis (see p. 129) based on amino acid data derived from housekeeping genes (Fig. 10.6). The cladogram separates the Deuterostomia (echinoderms + hemichordates) from the Protostomia, which includes the Spiralia (mollusks + annelids + nemerteans + platyhelminthes) and the Ecdysozoa (arthropods + priapulids). Both are united within the Triploblastica that, together with the cnidarians, forms the Bilateria; the Eumetazoa comprise the Bilateria + Cnidaria and the metazoan clade is completed with the addition of the calcisponges and demosponges. Thus the last common ancestor of the Metazoa was probably rather like a modern sponge. The tree, however, lacks data from a number of problematic groups such as the Bryozoa and Brachiopoda, both commonly united on the basis of their lophophores. Moreover to date it has proved impossible to resolve polychotomies such as that including the mollusks, annelids and brachiopods (see also Aguinaldo & Lake 1998).

These molecular results are being increasingly accepted by zoologists as analysis of different gene datasets produce the same results. The hunt is now on for morphological characters of some of the major clades discovered by molecular means. A good example is the shedding of the exoskeleton (ecdysis) by the Ecdysozoa, a strong morphological synapomorphy that had once been thought to have evolved convergently in arthropods, nematodes and the others.

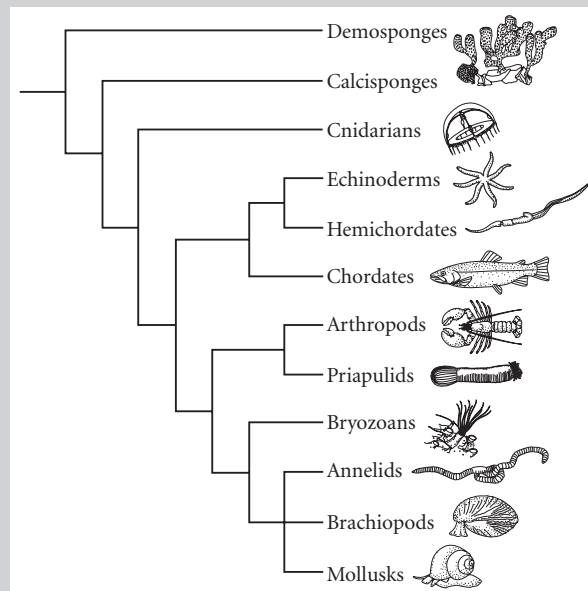


Figure 10.6 Phylogenetic relationships among the main invertebrate groups. (Phylogeny courtesy of Kevin Peterson.)

Ediacara biota

Since the first impressions of soft-bodied organisms were identified in the Upper Proterozoic rocks of Namibia and in the Pound Quartzite in the Ediacara Hills, north of Ade-

laide in southern Australia in the late 1940s, this remarkable assemblage has now been documented from 30 localities on five continents (Fig. 10.7). More than 100 species of these unique organisms have been described on the basis of molds usually preserved in

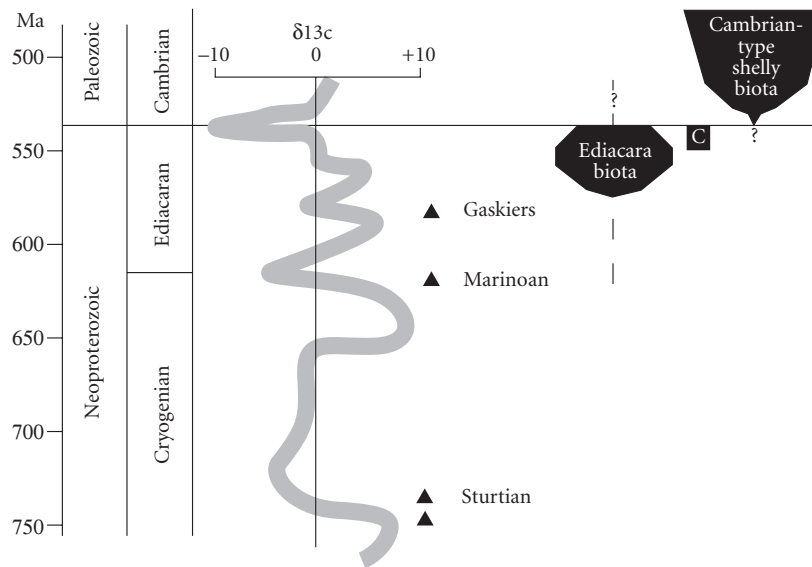


Figure 10.7 Stratigraphic distribution of the Ediacara biota. Solid triangles, glaciations; C, calcified metazoans; T, position of the Twitya disks. (Based on Narbonne 2005.)

shallow-water siliciclastic sediments, consisting of clasts of silicic-rich rocks, or volcanic ash, more rarely carbonates or even turbidites. The sediments were deposited during specific events, such as a storm, and are usually termed event beds. Deep-water biotas are also known such as those from Mistaken Point in Newfoundland. The style of preservation plays an important role in understanding these organisms (Narbonne 2005). The widespread development of algal mats, prior to the Cambrian substrate revolution (see p. 330), suggests that these too aided preservation, sometimes providing “death masks”, of these non-skeletal organisms.

Although morphologically diverse, the Ediacaran organisms have many features in common. All were soft-bodied, with high surface to volume ratios and marked radial or bilateral symmetries. These thin, ribbon-shaped animals may have operated by direct diffusion processes where oxygen entered through the skin surface, so gills and other more complex internal organs were perhaps not required. Most Ediacaran organisms have been studied from environments within the photic zone; many collected from deeper-water deposits are probably washed in. Provincialism among these Upper Proterozoic biotas was weak with many taxa having a nearly worldwide distribution. It is possible that the flesh of the Ediacaran organisms lit-

tered areas of the Late Precambrian seafloor; predators and scavengers had yet to evolve in sufficient numbers to remove it.

Morphology and classification

Traditionally the Ediacaran taxa, a collection of disks, fronds and segmented bodies, have been assigned to a variety of Phanerozoic invertebrate groups on the basis of apparent morphological similarities. In many cases considerable speculation is necessary and many assumptions are required to classify these impressions. Most of the species have been assigned to coelenterate groups, although some taxa have been identified as, for example, arthropods or annelids. Michael Fedonkin (1990), however, suggested a form classification based on the morphology and structure of these fossils. Key areas of his classification are summarized in Box 10.3 and typical examples illustrated in Figure 10.8. The bilateral forms were probably derived from an initial radial body plan. The concept and classification of the Ediacara biota is in a state of flux and Fedonkin’s classification is one of a number of attempts to rationalize the group, assuming the majority are in fact animals. Some have argued, nevertheless, that the Ediacarans are organisms unrelated to modern metazoans (Box 10.4), or are even Fungi.



Box 10.3 The Ediacaran animals: a form classification

RADIATA (RADIAL ANIMALS)

Three main classes are defined. Most colonial organisms in the fauna, for example *Charnia*, *Charniodiscus* and *Rangia*, are assigned to coelenterates and were part of the sessile benthos. The affinities of these animals have been debated in detail, but their close similarity to the sea-pens suggests an assignment to the pennatulaceans.

Class CYCLOZOA

- These animals have a concentric body plan with a large disk-shaped stomach and the class includes mostly sessile forms such as *Cyclomedusa* and *Ediacaria*. About 15 species of jellyfish-like animals have been described and in some, for example, *Eoporpita* tentacles are preserved

Class INORDOZOA

- Medusa-like animals with more complex internal structures, for example *Hielmalora*

Class TRILOBOZOA

- Characterized by a unique three-rayed pattern of symmetry. *Tribrachidium* and *Albumares* are typical members of the group

BILATERIA (BILATERAL ANIMALS)

This division contains both smooth and segmented forms.

Smooth forms

- These morphotypes are rare. They include *Vladimissa* and *Platypholina*, which may be turbellarians, a type of platyhelminthes worm

Segmented forms

- Much of the Ediacara fauna is dominated by segmented taxa inviting comparisons with the annelids and arthropods. *Dickinsonia*, for example, may represent an early divergence from the radial forms whereas *Spriggina*, although superficially similar to some annelids and arthropods, possesses a unique morphology

Ecology

There is little doubt that the Ediacara biotas dominated the latest Precambrian marine ecosystem, occupying a range of ecological niches and pursuing varied life strategies probably within the photic zone (Fig. 10.10). There is no evidence to suggest that any of the Ediacaran organisms were either infaunal or pelagic, thus in contrast to the subsequent Cambrian Period, life was restricted to the seabed. It is also possible that these flattened organisms hosted photosymbiotic algae, maintaining an autotrophic existence in the tranquil “garden of Ediacara” as envisaged by

Mark McMenamin (1986), although this model has its opponents. McMenamin considered that the ecosystem was dominated by medusoid pelagic animals, and that attached, sessile benthos and infaunal animals were sparse; the medusoids have been reinterpreted as bacterial colonies or even holdfasts. Food chains were thus probably short and the trophic structure was apparently dominated by suspension and deposit feeders.

Biogeography

Although provincialism was weak among the Ediacara biotas, three clusters have been rec-

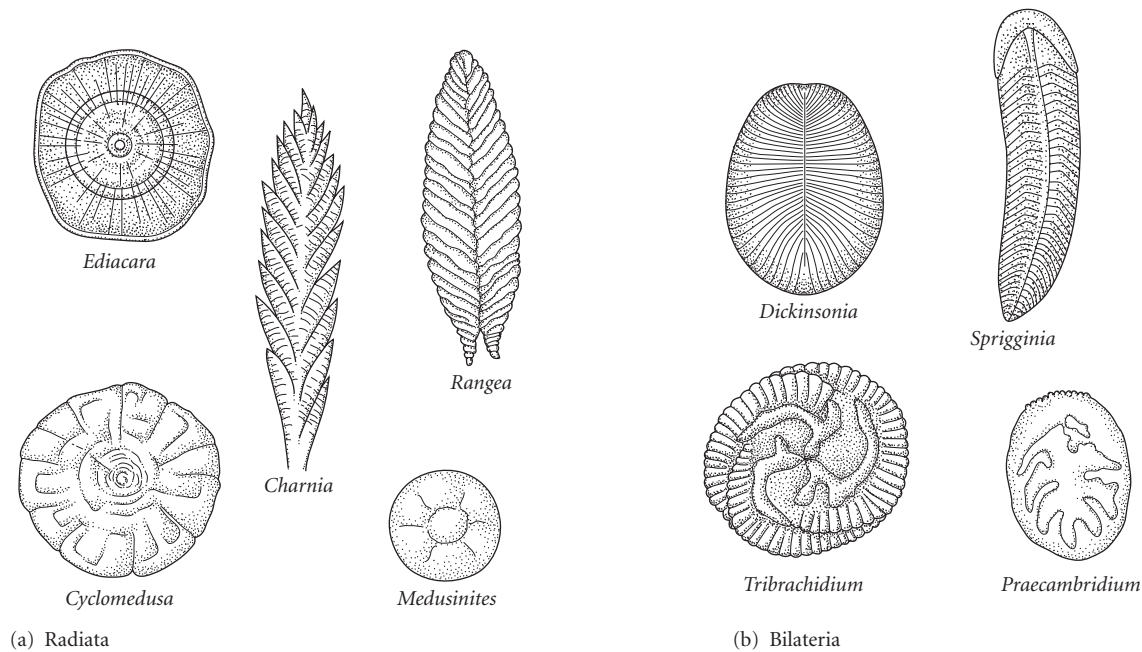


Figure 10.8 Some typical Ediacara fossils: (a) the Radiata, which have been associated with the cnidarians, and (b) the Bilateria, which may be related to the annelids and arthropods. *Ediacaria* ($\times 0.3$), *Charnia* ($\times 0.3$), *Rangea* ($\times 0.3$), *Cyclomedusa* ($\times 0.3$), *Medusinites* ($\times 0.3$), *Dickinsonia* ($\times 0.6$), *Spriggina* ($\times 1.25$), *Tribrachidium* ($\times 0.9$) and *Praecambridium* ($\times 0.6$). (Redrawn from various sources by Anne Hastrup Ross.)

ognized based on multivariate biogeographic analysis (see p. 45) by Ben Waggoner (2003): (i) the Avalon assemblage is from deep-water, volcanoclastic settings in eastern Newfoundland; (ii) the White Sea assemblage represents the classic Vendian section in the White Sea, Russia; and (iii) the Nama assemblage is a shallow-water association from Namibia, West Africa. Unfortunately the distribution of these assemblages does not match any paleogeographic models for the period and the clusters may rather represent a mixture of environmental and temporal factors (Grazhdankin 2004).

Extinction of the Ediacarans

The Ediacara biota, as a whole, became extinct about 550 Ma. Nevertheless, in terms of longevity, the ecosystem was very successful and a few seem to have survived into the Cambrian. The rise of predators and scavengers together with an increase in atmospheric oxygen may have at last prevented the routine preservation of soft parts and soft-bodied

organisms. More importantly, the Ediacara body plan offered little defense against active predation. There is abundant evidence for Cambrian predators: damaged prey, actual predatory organisms and the appearance of defense structures, such as trilobite spines and multielement skeletons. All suggest the existence of a predatory life strategy that was probably established prior to the beginning of the Cambrian Period. The Proterozoic–Cambrian transition clearly marked one of the largest faunal turnovers in the geological record, with a significant move from soft-bodied, possibly photoautotrophic, animals to heterotrophs relying on a variety of nutrient-gathering strategies. It is, however, still uncertain whether a true extinction, or the slamming shut of a taphonomic window, accounted for the disappearance of the Ediacara biota from the fossil record.

Cloudina assemblages

Although the Ediacara biotas were overwhelmingly dominated by soft-bodied organisms,



Box 10.4 Vendobionts or the first true metazoans

The apparently unique morphology and mode of preservation of the Ediacara biota has led to much debate about the identity and origins of the assemblage. Adolf Seilacher (1989) argued that these organisms were quite different from anything alive today in terms of their constructional and functional morphology (Fig. 10.9). Apart from a distinctive mode of preservation, the organisms all share a body form like a quilted air mattress: they are rigid, hollow, balloon-like structures with sometimes additional struts and supports together with a significant flexibility. Seilacher termed the Ediacaran organisms **vendobionts**, meaning organisms from the Vendian, and he speculated about their unique biology. Reproduction may have been by spores or gametes. The skin must have been flexible, although it could crease and fracture, and it must have acted as an interface for diffusion processes. This stimulating and original view of the Ediacarans, however, remains controversial. Several members of the Vendobionta have been interpreted as regular metazoans, suggesting a less original explanation for the Ediacara group.

Leo Buss and Adolf Seilacher (1994) suggested a compromise. Their phylum Vendobionta includes cnidarian-like organisms lacking cnidae, the stinging apparatus typical of the cnidarians. Vendobionts thus comprise a monophyletic sister group to the Eumetazoa (ctenophorans + bilaterians). This interpretation requires the true cnidarians to acquire cnidae as an apomorphy for the phylum.

The vendobiont interpretation has opened the doors for a number of other interpretations and the understanding of Ediacaran paleobiology is as open as ever: some authors have suggested the Ediacarans are giant protists, lichens, prokaryotic colonies or fungus-like organisms. However most agree that the Ediacara assemblage includes some crown- and stem-group sponges and cnidarians, a conclusion proposed by Sprigg in the late 1940s. This is supported by biomarker and molecular clock data.

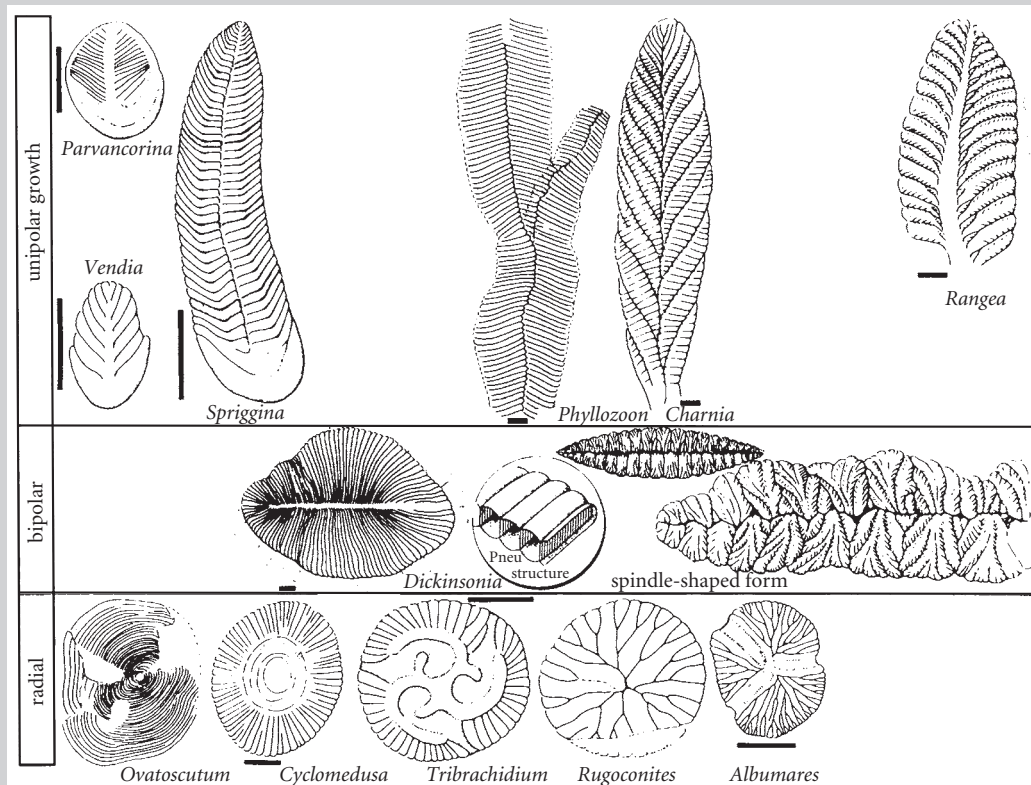


Figure 10.9 Vendozoan constructional morphology, recognizing unipolar, bipolar and radial growth modes within the Ediacara-type biota. Scale bars, 10 mm. (From Seilacher 1989.)

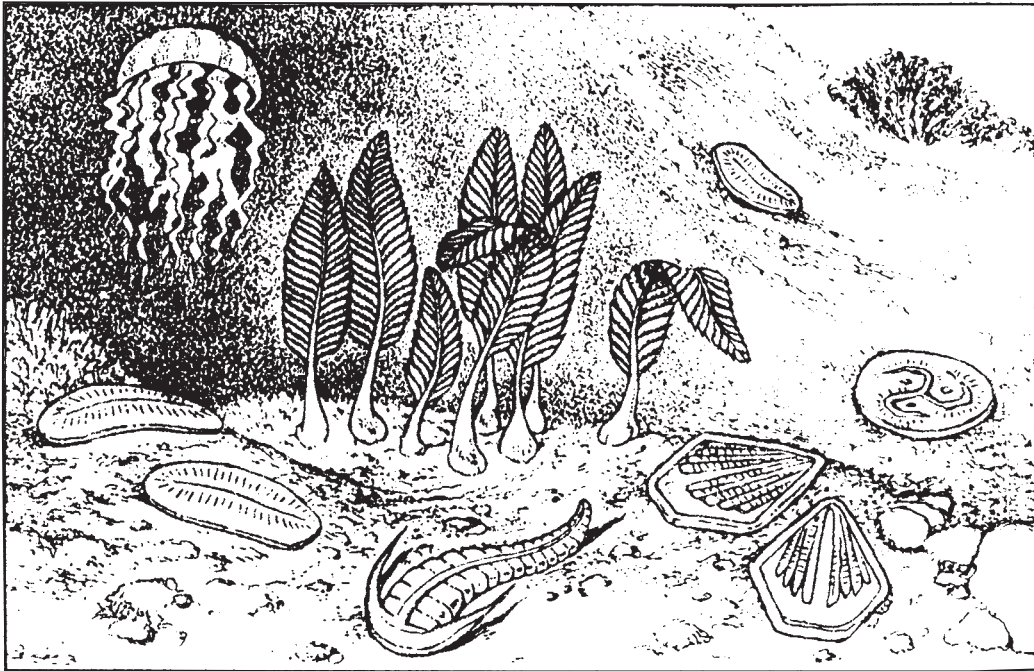


Figure 10.10 An Ediacara community including a fixed and mobile tiered benthos.

minute conical shells were also present in some Ediacaran successions, including localities in Brazil, China, Oman and Spain. *Cloudina* was possibly a cnidarian-type organism with a unique shell structure having new layers forming within older layers. Moreover it was probably related to a suite of similar shells such as *Sinotubulites*, *Nevadatubulus* and *Wyattia* that also occurred close to the Precambrian–Cambrian boundary. In addition to complex multicellularity, modularity, locomotion and predation, biomineralization was already far advanced in the Late Proterozoic, providing a link with what was to follow in the Nemakit-Daldynian assemblages of the earliest Cambrian. Some of the shells of *Cloudina* are bored, suggesting the presence of predators (Fig. 10.11), although it is not certain the animals were still living when bored.

Small shelly fauna

A distinctive assemblage of small shelly fossils has now been documented in considerable detail from the Precambrian–Cambrian transition; the assemblage is most extravagantly developed in the lower part of the Cambrian defined on the Siberian platform, traditionally called the Tommotian, which gives its name

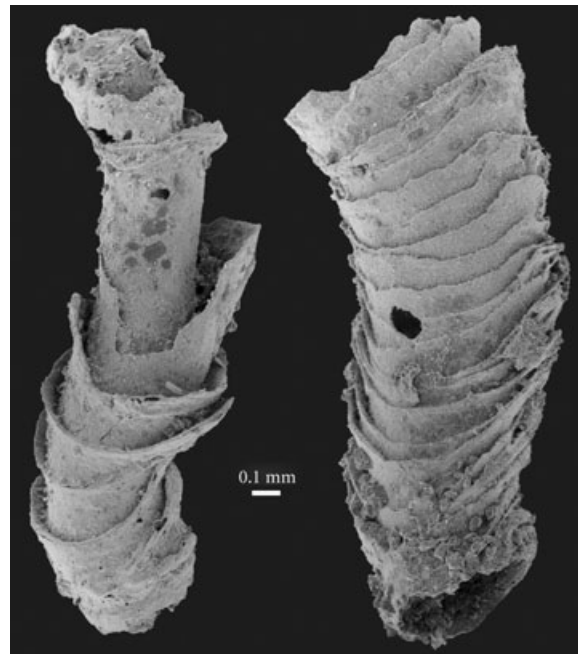


Figure 10.11 The calcareous tube *Cloudina* displaying indications of predation. (Courtesy of Stefan Bengtson.)

to the fauna. A great deal is now known about the stratigraphic distribution and paleobiogeography of these organisms through current

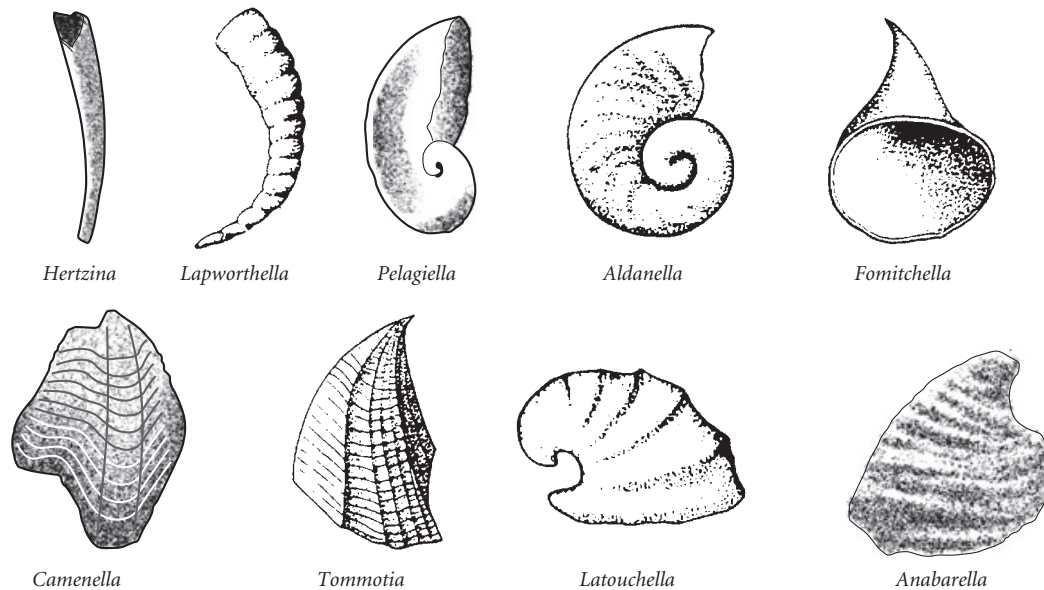


Figure 10.12 Elements of the Tommotian-type or small shelly fauna. Magnification approximately $\times 20$ for all, except *Fomitchella* which is about $\times 40$. (Based on various sources.)

interest in the definition of the base of the Cambrian System. Nevertheless, the biological affinities of many members of the Tommotian fauna have yet to be established. The assemblage, although dominated by minute species, together with small sclerites of larger species, represents the first major appearance of hard skeletal material in the fossil record, some 10 myr before the first trilobites evolved (see p. 363).

This type of fauna is not restricted to the Tommotian Stage; small shelly fossils are also common in the overlying Atdabanian Stage (see below) and similar assemblages of mainly phosphatic minute shells have been reported from younger condensed sequences in the Paleozoic. The shell substance of the carbonate skeletons within the fauna seems to have been controlled by the ambient seawater chemistry; Nemakit-Daldynian assemblages were mainly aragonite, whereas younger shells were mainly calcitic (Porter 2007). Tommotian-type faunas probably finally disappeared with the escalation of predation during the Mesozoic.

Some scientists such as Stephen Jay Gould suggested the less time-specific term, small shelly fossils to describe these assemblages. The fauna is now known to include a variety of groups united by their minute size and sudden appearance near the base of Cam-

brian. The small shelly fauna probably dominated the earliest Cambrian ecosystems when many metazoan phyla developed their own distinctive characteristics, initially at a very small scale. Nevertheless, some of this small size may be a preservational artifact, since phosphatization only works at a millimeter scale.

Composition and morphology

Many of the Tommotian skeletons (Fig. 10.12) were retrieved from residues after the acid etching of limestones; thus there is a bias towards acid-resistant skeletal material in any census of the group as a whole. Moreover, there is currently discussion concerning whether the acid-resistant skeletons of the Tommotian-type animals were primary constructions or secondary replacement fabrics. Or perhaps these shells survived in the sediments because of particular chemical conditions in the oceans at the time that allowed phosphatic fossils to survive (Porter 2004). The Tommotian animals had skeletons composed of a variety of materials. For example, *Cloudina* and the anabaritids were tube-builders that secreted carbonate material, whereas *Mobergella* and *Lapworthella* consisted of sclerites comprising organisms that secreted phosphatic material; *Sabellidites* is an organic-

walled tube possibly of an unsegmented worm.

Many of the Tommotian animals are **form taxa** (that is, named simply by their shapes) because the biological relationships of most cannot be established and often there are few clues regarding the function and significance of each skeletal part. Most are short-lived and have no obvious modern analogs. Two groups are common – the hyolithelminthids have phosphatic tubes, open at both ends, whereas the tommotiids are usually phosphatic, cone-shaped shells that seem to belong in bilaterally symmetric sets.

Discoveries of near-complete examples of *Microdictyon*-like animals from the Lower Cambrian of China have helped clarify the status and function of some elements of the Tommotian fauna. These worms have round to oval plates arranged in pairs along the length of the body, which may have provided a base for muscle attachment associated with locomotion. As noted previously, many of the small shelly fossils are probably the sclerites of larger multiplated worm and worm-like animals (Box 10.5).

The Meishucunian biota

The Meishucunian Stage of South China has yielded some of the most diverse Tommotian-type assemblages in strata of Atdabanian age (see Appendix 1). Qian Yi and Stefan Bengtson (1989) have described nearly 40 genera that belong to three largely discrete, successive assemblages through the stage. First, the *Anabarites*–*Protohertzina*–*Arthrochites* assemblage is dominated by tube-dwelling organisms such as *Anabarites*; the *Siphonogchites*–*Paragloborilus* assemblage contains mobile mollusk-like and multiplated organisms together with some tube-dwellers and possible predators; whereas the *Lapworthella*–*Tannuolina*–*Sinosachites* association has mainly widespread multiplated animals.

Many of these fossils are known from Lower Cambrian horizons elsewhere in the world, highlighting the global distribution of many elements of the fauna. However, the three “community” types are rather mysterious, and probably represent different ecosystems, but it is hard to speculate further.

Distribution and ecology

Although it is still unclear whether many of the Tommotian skeletons are single shells or single sclerites and the autecology of most groups is unknown, the assemblage was certainly the first example in evolution of a skeletalized benthos. Very few of the Tommotian skeletal parts exceed 1 cm; nevertheless many shells were the armored parts of larger worm-like animals. And both mobile and fixed forms occurred together with archaeocyathans and non-articulate brachiopods. The microbenthos of the Tommotian was succeeded by a more typical Cambrian fauna, dominated by trilobites, non-articulate brachiopods, monoplacophoran mollusks and primitive echinoderms together with the archaeocyathans during the Atdabanian Stage (Fig. 10.14).

Cambrian explosion

The Cambrian explosion suddenly generated many entirely new and spectacular body plans (Box 10.6) and coincides with the appearance of the Bilateria over a relatively short period of time (Conway Morris 1998, 2006). This rapid diversification of life formed the basis for Stephen Jay Gould’s bestseller, *Wonderful Life* (1989), which took its title from the Frank Capra 1946 film *It’s a Wonderful Life*. The rapid appearance of such a wide range of apparently different animals has suggested two possible explanations. The “standard” view is that the diversification of bilaterians happened just as fast as the fossils suggest, and that some reasons must be sought to explain why many different animal groups apparently acquired mineralized skeletons at the same time. An alternative view arose after initial molecular studies had suggested that animals diverged some 800 myr before the beginning of the Cambrian (e.g. Wray et al. 1996). If these molecular views were correct, then the absence of fossils of modern animal phyla through the Proterozoic would have to be explained by an interval of cryptic evolution of probable micro- and meiotic organisms, living between grains of sand, operating beneath the limits of detection prior to the explosion (Cooper & Fortey 1998). Greater refinement of Cambrian stratigraphy, the taxonomy and phylogeny of key Cambrian taxa and their relative appearance in the fossil



Box 10.5 Coelosclerites, mineralization and early animal evolution

The coeloscleritophorans are an odd group of animals based on the unique structure of their sclerites that appeared first in the Tommotian (Fig. 10.13). The sclerites are made of thin mineralized walls surrounding a cavity with a small basal opening. Once formed, the sclerites did not grow and were secreted by the mineralization of organic material occupying the cavity. The sclerites have longitudinal fibers and overlapping platelets within the mineralized wall. These animals may be extremely important in understanding the origin of biomineralization and the fuse for the Cambrian explosion, as argued by Stefan Bengtson (2005). Coelosclerites may be structures that are not known in any living animal but that were shared by both the bilaterians and non-bilaterians and probably characterized both ecdysozoans and spiralian. Coelosclerites may then have been lost, possibly by progenesis (see p. 145) from the larval to juvenile stages. If these features were developed in larger bilaterians then it is possible that within the Ediacara fauna giant forms – tens of centimeters in length – lurked, adorned by spiny and scaly sclerites. This is a controversial but nonetheless stimulating view that adds even more variety to our interpretations of early metazoan evolution.



Figure 10.13 Coelosclerites. Chancelloriids: 1 and 2, *Chancelloria*; 3, *Archiasterella*; 4, *Eremactis*. Sachtid: 5, *Hippopharangites*. Siphonoguchitids: 6, *Drepanochites*; 7, *Siphogonuchites*; 8, *Maikhanella*. Scale bars, 100 μm . (Courtesy of Stefan Bengtson.)

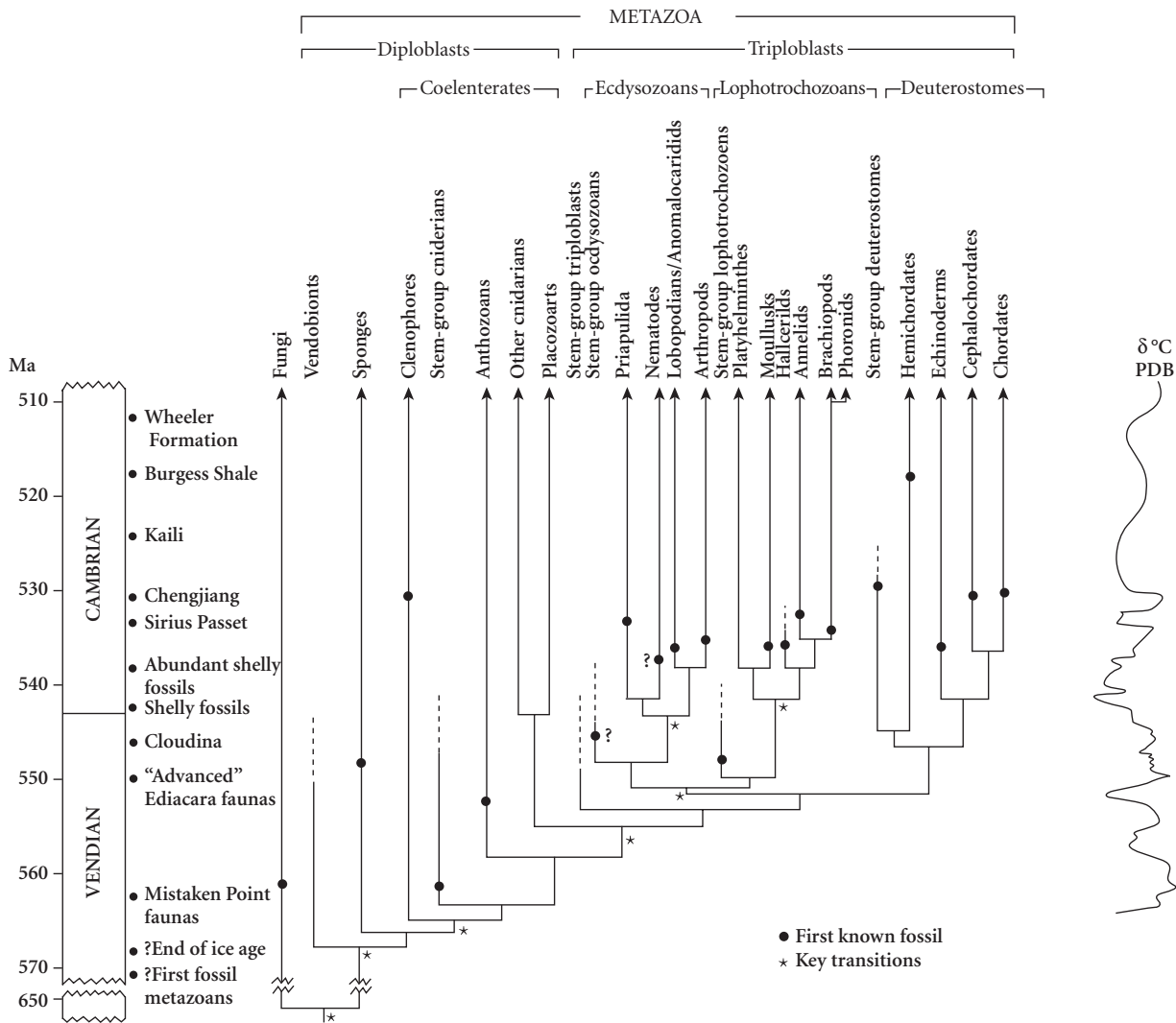


Figure 10.14 Stratigraphic distribution of Late Precambrian and Early Paleozoic metazoan taxa, some key morphological transitions and the carbon isotope record ($\delta^{13}\text{C}$). PDB, Vienna Pee Dee belemnite, the standard material for relative carbon isotope measurements. (Based on various sources.)

record, together with a revised molecular clock (see p. 133), have suggested an alternative hypothesis. The current Lower to Middle Cambrian fossil record displays the sequential and orderly appearance of successively more complex metazoans (Budd 2003), albeit rather rapidly (Fig. 10.16), and the timing is closely matched by revised molecular time scales (see p. 235; Peterson et al. 2004). Nevertheless there is some suggestion from the biogeographic patterns of trilobites that the divergence of many metazoan lineages may have already begun 30–70 myr earlier (Meert & Lieberman 2004) and speciation rates during the explosion were not in fact so incredible compared with those of other diversifications

preserved in the fossil record (Lieberman 2001).

Much of our knowledge of the Cambrian explosion is derived from three spectacular, intensively-studied Lagerstätte assemblages: Burgess (Canada), Chengjiang (China) and Sirius Passet (Greenland). The diversities of the Cambrian “background” faunas are generally much lower and arguably contain less morphologically different organisms. Reconstructions of these seafloors are possible (Fig. 10.17). But whereas the Cambrian explosion provided higher taxa, in some diversity, the Ordovician radiation generated the sheer biomass, biodiversity and biocomplexity that would fill the world’s oceans.



Box 10.6 Roughness landscapes

There have been a number of explanations for the rapid explosion of life during the Early and Mid Cambrian involving all sorts of developmental (genetic), ecological and environmental factors. Why, too, was this event restricted to the Cambrian? Was there some kind of developmental limitation, an ecological saturation, or were there simply no further ecological opportunities left to exploit? One interesting model that may help explain the ecological dimension of the event involves the use of fitness landscapes. The concept is taken from genetics but can be adapted to morphological information (Marshall 2006). Biotas can be plotted against two axes, each representing morphological rules that can generate shapes. The Ediacaran fauna has only three recognizable bilaterians, so the landscape is relatively smooth with only three peaks. On the other hand the Cambrian explosion generated at least 20 bilaterian body plans and a very rough landscape rather like the Alps or the Rockies (Fig. 10.15). What roughened the landscape, or why were there more bilaterians in the Cambrian fauna? Much of the bilaterian genetic tool kit was already in place in the Late Proterozoic and the environment was clearly conducive to their existence. The “principle of frustration” (Marshall 2006), however, suggests that different needs will often have conflicting solutions, ensuring that the best morphological design is rarely the most optimal one. Is it possible that, with the rapid development of biotic interactions such as predation, many morphological solutions were developed, some less than optimal but nevertheless driving a roughening of the fitness landscape. Thus “frustration”, the multiplication of attempted solutions to new opportunities, led to the roughening of the Cambrian landscape and may have been an important factor in the Cambrian explosion.

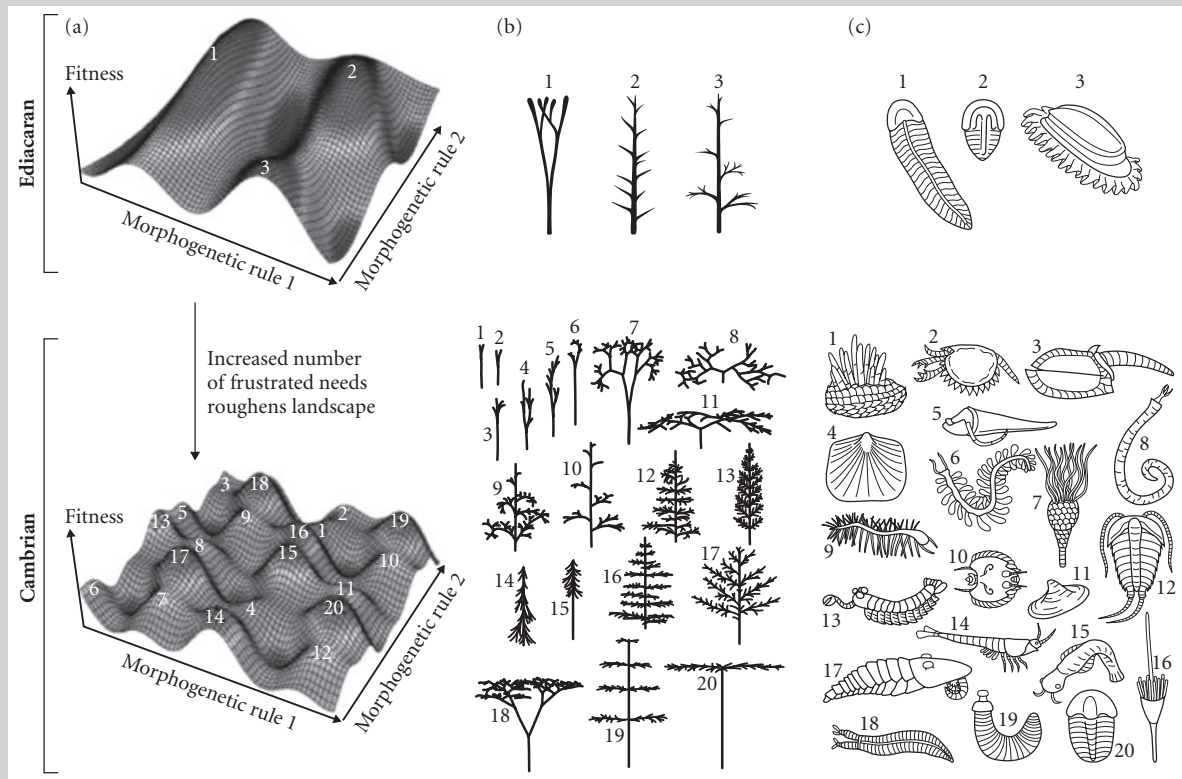


Figure 10.15 Comparison of Ediacaran and Cambrian landscapes: (a) fitness landscapes; (b) locally optimal morphologies (Nicklas' plants); and (c) locally optimal morphologies (bilaterian animals). (Based on Marshall 2006.)

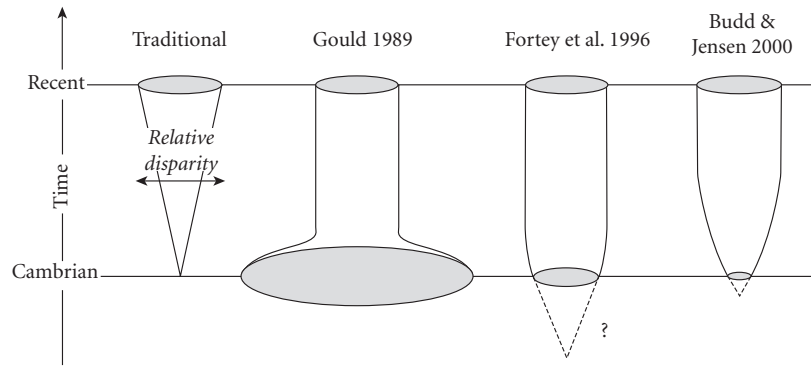


Figure 10.16 Modes of the Cambrian explosion. (Based on Budd & Jensen 2000.)

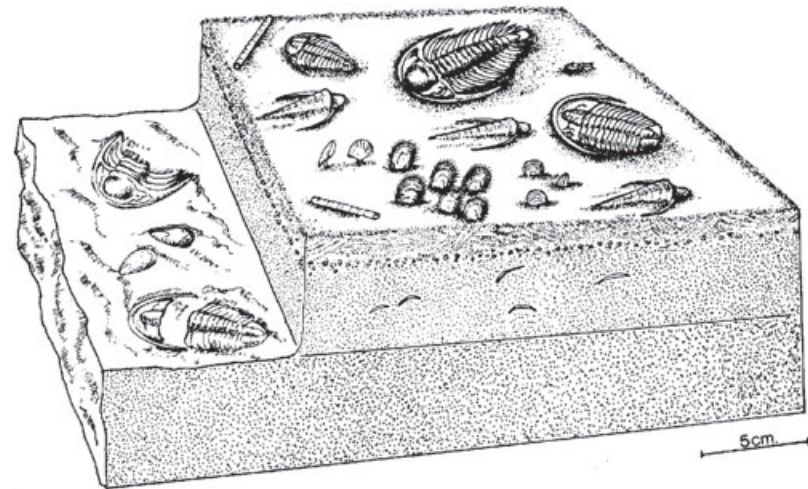
Ordovician radiation

During an interval of some 25 myr, during the Mid to Late Ordovician, the biological component of the planet's seafloors was irreversibly changed. A massive hike in biodiversity was matched by an increase in the complexity of marine life (Harper 2006). The event witnessed a three- to four-fold increase in, for example, the number of families, leveling off at about 500; these clades would dominate marine life for the next 250 myr. Nevertheless the majority of "Paleozoic" taxa were derived from Cambrian stocks. With the exception of the bryozoans (see p. 313), no new phyla emerged during the radiation, although more crown groups emerged from the stem groups generated during the Cambrian explosion.

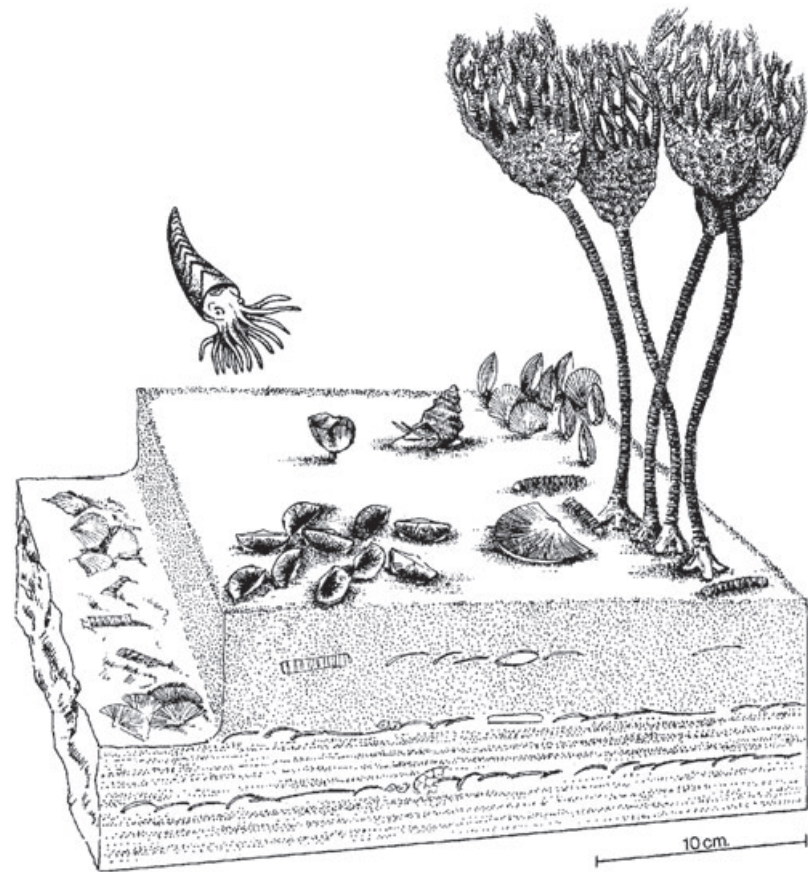
The great Ordovician radiation is one of the two most significant evolutionary events in the history of Paleozoic life. In many ways the Ordovician Period was unique, enjoying unusually high sea levels, extensive, large epicontinental seas, with virtually flat seabeds, and restricted land areas, many probably represented only by archipelagos. Magmatic and tectonic activity was intense with rapid plate movements and widespread volcanic activity. Island arcs and mountain belts provided sources for clastic sediment in competition with the carbonate belts associated with most of the continents. Biogeographic differentiation was extreme, affecting plankton, nekton and benthos, and climatic zonation existed, particularly in the southern hemisphere.

Finally, during the Mid Ordovician, the Earth was bombarded with asteroids that appear in some way also to be linked to the biodiversification (Schmitz et al. 2008). Taken together, these conditions were ideal for all kinds of speciation processes and the evolution of ecological niches. Most significant was the diversification of skeletal organisms, including the brachiopods, bryozoans, cephalopods, conodonts, corals, crinoids, graptolites, ostracodes, stromatoporoids and trilobites that we will read about later.

Whereas the Cambrian explosion involved the rapid evolution of skeletalization and a range of new body plans, together with the extinction of the soft-bodied Ediacara biota and the appearance of the Bilateria, the Ordovician diversification generated few new higher taxa, for example phyla, but witnessed a staggering increase in biodiversity at the family, genus and species levels. This taxonomic radiation, which included members of the so-called "Cambrian", "Paleozoic" and "Modern" evolutionary biotas (see p. 538), set the agenda for much of subsequent marine life on the planet against a background of sustained greenhouse climates. Although many outline analyses have been made, there are relatively few studies of the ecological and environmental aspects of the Ordovician diversification (Bottjer et al. 2001). Moreover the causes of the event, and its relationship to both biological and environmental factors, are far from clear. Evolution of the plankton, however, may have been a primary factor (Box 10.7).



(a)



(b)

Figure 10.17 The Cambrian (a) and Ordovician (b) seafloors. (Based on McKerrow 1978.)



Box 10.7 Larvae and the Ordovician radiation

Many factors, mainly ecological and environmental, have been invoked to explain the great Ordovician biodiversification or Ordovician radiation. Did the diversification have its origins in the plankton? Most early bilaterians probably had benthic lecithotrophic larvae (see p. 241). But the Cambrian oceans, relatively free of pelagic predators, offered great possibilities. Exploitation of the water column by larvae occurred a number of times independently, turning the clear waters of the Early Cambrian into a soup of planktonic organisms in the Ordovician. The fossil record and molecular clock data suggest that at least six different feeding larvae developed from non-feeding types between the Late Cambrian and Late Silurian (Peterson 2005). In addition to planktotrophic larvae, the oceans were rapidly colonized by diverse biotas of other microorganisms such as the acritarchs (see p. 216). The dramatic diversification of the suspension-feeding benthos coincides with the evolution of planktotrophy in a number of different lineages (Fig. 10.18). These factors had an undoubted effect on the diversification of Early Paleozoic life, which reached a plateau of diversity during the Ordovician.

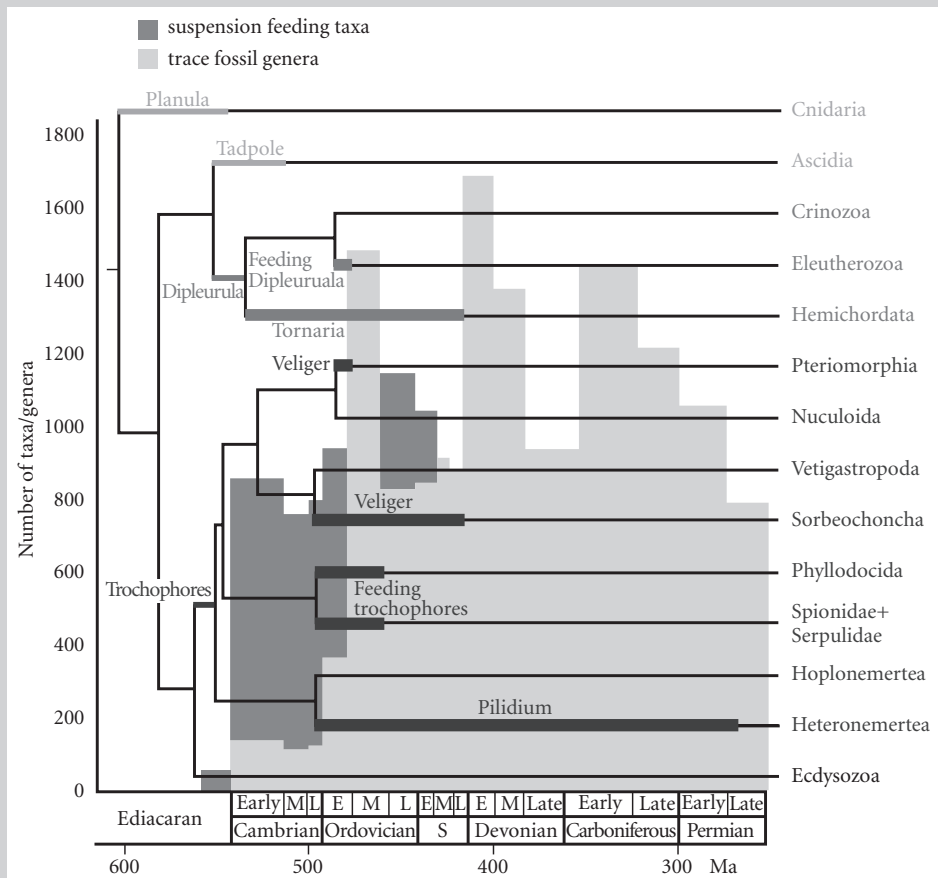


Figure 10.18 Origin of larval types and the Ordovician radiation as deduced from the fossil record and molecular clock data. The numbers of genera of key suspension-feeding taxa are indicated on the histogram in light tint, and, in dark tint, the numbers of genera of trace fossils. (Based on Peterson 2005.)

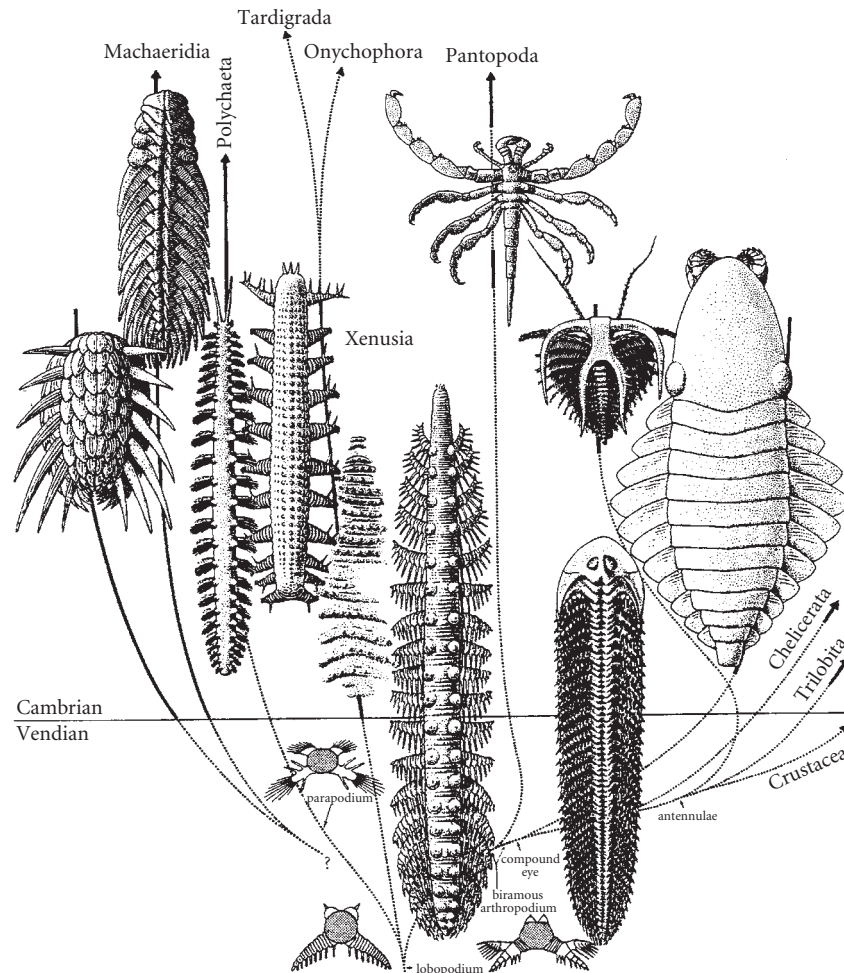


Figure 10.19 Significance of the diverse worm-like animals at the Precambrian–Cambrian boundary and the postulated origins of some major clades. (Based on Dzik, J. & Krumbiegel, G. 1989. *Lethaia* 22.)

SOFT-BODIED INVERTEBRATES

Of the 25 or so commonly recognized animal phyla, fewer than nine (35%) have an adequate fossil record. Many are small phyla represented by relatively few species. However, there are a number of larger phyla whose poor fossil record reflects the lack of a preservable skeleton, although a number of these soft-bodied forms are preserved in fossil Lagerstätten. Most are worms or worm-like organisms (Fig. 10.19). But in spite of unspectacular fossil records, there is considerable interest in these poorly represented invertebrates. The origins of many higher taxa must be sought within the plexus of worm-like organisms. Moreover, the evidence from the

Burgess Shale and other such exceptionally preserved faunas suggests that many of these soft-bodied groups dominated certain marine paleocommunities in terms of both numbers and biomass and additionally contributed to associated trace fossil assemblages.

The platyhelminths or the flatworms are bilateral animals with organs composed of tissues arranged into systems. Most are parasites, but the turbellarians are free-living carnivores and scavengers. The Ediacaran animals *Dickinsonia* and *Palaeoplato* have been assigned to the turbellarian flatworms by some authors; similarly *Platydendron* from the Middle Cambrian Burgess Shale has been ascribed to the platyhelminthes.

The ribbon worms, or nemertines, are characterized by a long anterior sensory proboscis. The majority are marine, although some inhabit soil and freshwater. Although the bizarre *Amiskwia* from the Middle Cambrian Burgess Shale was assigned to this group, recent opinion suggests it is merely convergent on the nemertine body shape. Some of the Tommotian animals may also be nemertine worms. The nematodes or roundworms are generally smooth and sac-like.

The priapulid worms are exclusively marine, short and broad with **probosces** (“noses”; singular, proboscis) covered in spines and warts. The Middle Cambrian Burgess Shale contains seven genera assigned to at least five families. The Burgess forms are all characterized by priapulid probosces, and most have little in common with modern forms. Nevertheless the most abundant taxon, *Ottoia*, is very similar to the living genus *Halicyptus*. Elsewhere in the fossil record the Upper Carboniferous Mazon Creek fauna has yielded *Priapulites*, which has a distinctly modern aspect.

The annelid worms, such as the common earthworm and lugworm, have ring-like external segments that coincide with internal partitions housing pairs of digestive and reproductive organs; the nervous system is well developed and the head has distinctive eyes. The annelid body is ornamented by bristles that aid locomotion and provide stability. Most are predators or scavengers living in burrows. The polychaetes or paddle worms have the most complete fossil record; the record is enhanced by the relatively common preservation of elements of the phosphatic jaw apparatus known as **scolecodonts** (see p. 359). Although some Ediacaran animals, such as *Spriggina*, have been associated with the polychaetes, the first undoubted paddle worms are not known until the Cambrian. A diverse polychaete fauna has been described from the Burgess Shale; it even contains *Canada spinosa*, similar to some living polychaetes.

Review questions

1 Traditional methods of reconstructing the phylogeny of the early metazoans based on morphology have encountered problems. Is the concept of body plans still useful and if so, for what?

- 2 Interpretations of Ediacaran biotas are as far from a consensus as ever. Why are the Ediacara organisms so difficult to classify and understand?
- 3 The identification of embryos and trace fossils are both important evidence of animal life. How can both be used to indicate the presence of metazoan life?
- 4 Was the Cambrian explosion one of animals or fossils? How large was the role of taphonomy in the manifestation of the Cambrian explosion?
- 5 Within an interval of 100 million years the planet’s seafloors were changed for ever. Briefly compare and contrast the changing seascapes through the Ediacaran, Cambrian and Ordovician periods.

Further reading

- Briggs, D.E.G. & Fortey, R.A. 2005. Wonderful strife: systematics, stem groups, and the phylogenetic signal of the Cambrian radiation. *Paleobiology* 31 (Suppl.), 94–112.
- Brusca, R.C. & Brusca, G.J. 2002. *Invertebrates*, 2nd edn. Sinauer Associates, Sunderland, MA.
- Conway Morris, S. 2006. Darwin’s dilemma: the realities of the Cambrian explosion. *Philosophical Transactions of the Royal Society B* 361, 1069–83.
- Gould, S.J. 1989. *Wonderful Life. The Burgess Shale and the Nature of History*. W.W. Norton & Co., New York.
- Nielsen, C. 2003. *Animal Evolution. Interrelationships of the Living Phyla*, 2nd edn. Oxford University Press, Oxford, UK.
- Valentine, J.W. 2004. *On the Origin of Phyla*. University of Chicago Press, Chicago.

References

- Aguinaldo, A.M.A. & Lake, J.A. 1998. Evolution of multicellular animals. *American Zoologist* 38, 878–87.
- Bengtson, S. 2005. Mineralized skeletons and early animal evolution. In Briggs, D.E.G. (ed.) *Evolving Form and Function*. New Haven Peabody Museum of Natural History, Yale University, New Haven, CT, pp. 101–17.
- Bottjer, D.J., Droser, M.L., Sheehan, P.M. & McGhee, G.R. 2001. The ecological architecture of major events in the Phanerozoic history of marine life. In Allmon, W.D. & Bottjer, D.J. (eds) *Evolutionary Paleocology*. Columbia University Press, New York, pp. 35–61.
- Brasier, M.D. & McIlroy, D. 1998. *Neonereites uniserialis* from c. 600 Ma year old rocks in western

- Scotland and the emergence of animals. *Journal of the Geological Society, London* **155**, 5–12.
- Budd, G.E. 2003. The Cambrian fossil record and the origin of the phyla. *Integrative Comparative Biology* **43**, 157–65.
- Budd, G.E. 2008. The earliest fossil record of the animals and its significance. *Philosophical Transactions of the Royal Society B* **363**, 1425–34.
- Budd, G.E. & Jensen, S. 2000. A critical reappraisal of the fossil record of bilaterian phyla. *Biological Reviews* **75**, 253–95.
- Buss, L.W. & Seilacher, A. 1994. The phylum Vendobionta: a sister group of the Eumetazoa? *Paleobiology* **20**, 1–4.
- Canfield, D.E., Poulton, S.W. & Narbonne, G.M. 2007. Late-Neoproterozoic deep-ocean oxygenation and the rise of animal life. *Science* **315**, 92–5.
- Conway Morris, S. 1998. The evolution of diversity in ancient ecosystems: a review. *Philosophical Transactions of the Royal Society B* **353**, 327–45.
- Conway Morris, S. 2006. Darwin's dilemma: the realities of the Cambrian explosion. *Philosophical Transactions of the Royal Society B* **361**, 1069–83.
- Cooper, A. & Fortey, R.A. 1998. Evolutionary explosions and the phylogenetic fuse. *Trends in Ecology and Evolution* **13**, 151–6.
- Donogue, P.C.J. 2007. Embryonic identity crisis. *Nature* **445**, 155–6.
- Donoghue, P.C.J., Bengtson, S., Dong Xi-ping et al. 2006. Synchrotron X-ray tomographic microscopy of fossil embryos. *Nature* **442**, 680–3.
- Droser, M.L., Jensen, S. & Gehling, J.G. 2002. Trace fossils and substrates of the terminal Proterozoic-Cambrian transition: implications for the record of early bilaterians and sediment. *Proceedings of the National Academy of Sciences, USA* **99**, 12572–6.
- Fedonkin, M.A. 1990. Precambrian metazoans. In Briggs, D.E.G. & Crowther, P.R. (eds) *Palaeobiology, A Synthesis*. Palaeontological Association and Blackwell Scientific Publications, Oxford, UK, pp. 17–24.
- Fortey, R.A., Briggs, D.E.G. & Wills, M.A. 1996. The Cambrian evolutionary “explosion”: decoupling cladogenesis from morphological disparity. *Biological Journal of the Linnean Society* **57**, 13–33.
- Gould, S.J. 1989. *Wonderful Life. The Burgess Shale and the Nature of History*. W.W. Norton & Co., New York.
- Grazhdankin, D. 2004. Patterns of distribution in the Ediacaran biotas: facies versus biogeography and evolution. *Paleobiology* **30**, 203–21.
- Hagadorn, J.W., Xiao Shuhai, Donoghue, P.C.J. et al. 2006. Cellular and subcellular structure of Neoproterozoic animal embryos. *Science* **314**, 291–4.
- Harper, D.A.T. 2006. The Ordovician biodiversification: setting an agenda for marine life. *Palaeogeography, Palaeoclimatology, Palaeoecology* **232**, 148–66.
- Jensen, S. 2003. The Proterozoic and earliest Cambrian trace fossil record: patterns, problems and perspectives. *Integrative Comparative Biology* **43**, 219–28.
- Lieberman, B.S. 2001. A probabilistic analysis of rates of speciation during the Cambrian radiation. *Proceedings of the Royal Society, Biological Sciences* **268**, 1707–14.
- Marshall, C.R. 2006. Explaining the Cambrian “Explosion” of animals. *Annual Reviews of Earth and Planetary Science* **33**, 355–84.
- McKerrow, W.S. 1978. *Ecology of Fossils*. Duckworth Company Ltd., London.
- McMenamin, M.A.S. 1986. The garden of Ediacara. *Palaeo* **1**, 178–82.
- Meert, J.G. & Lieberman, B.S. 2004. A palaeomagnetic and palaeobiogeographic perspective on latest Neoproterozoic and Cambrian tectonic events. *Journal of the Geological Society, London* **161**, 1–11.
- Narbonne, G.M. 2005. The Ediacara biota: Neoproterozoic origin of animals and their ecosystems. *Annual Reviews of Earth and Planetary Science* **33**, 421–42.
- Nielsen, C. 2008. Six major steps in animal evolution: are we derived sponge larvae? *Evolution and Development* **10**, 241–57.
- Peterson, K.J. 2005. Macroevolutionary interplay between planktic larvae and benthic predators. *Geology* **33**, 929–32.
- Peterson, K.J., Cotton, J.A., Gehling, J.G. & Pisani, D. 2008. The Ediacaran emergence of bilaterians: congruence between genetic and the geological fossil records. *Philosophical Transactions of the Royal Society B* **363**, 1435–43.
- Peterson, K.J., Lyons, J.B., Nowak, K.S., Takacs, C.M., Wargo, M.J. & McPeck, M. 2004. Estimating meta-zoan divergence times with a molecular clock. *Proceedings of the National Academy of Sciences, USA* **101**, 6536–41.
- Peterson, K.J., McPeck, M.A. & Evans, D.A.D. 2005. Tempo and mode of early animal evolution: inferences from rocks, Hox, and molecular clocks. *Paleobiology* **31** (Suppl.), 36–55.
- Porter, S.M. 2004. Closing the phosphatization window: testing for the influence of taphonomic megabias on the patterns of small shelly fauna decline. *Palaios* **19**, 178–83.
- Porter, S.M. 2007. Seawater chemistry and early carbonate biomineralization. *Science* **316**, 1302.
- Qian Yi & Benton, S. 1989. Palaeontology and biostratigraphy of the Early Cambrian Meishucunian Stage in Yunnan Province, South China. *Fossils and Strata* **24**, 1–156.
- Rasmussen, B., Bengtson, S., Fletcher, I.R. & McNaughton, N.J. 2002. Discoidal impressions and trace-like fossils more than 1200 million years ago. *Science* **296**, 1112–15.
- Schmitz, B., Harper, D.A.T., Peucker-Ehrenbrink, B. et al. 2008. Asteroid breakup linked to the Great

- Ordovician Biodiversification Event. *Nature Geoscience* **1**, 49–53.
- Seilacher, A. 1989. Vendozoa: organismic construction in the Proterozoic biosphere. *Lethaia* **22**, 229–39.
- Seilacher, A., Bose, P.K. & Pflüger, F. 1998. Triploblastic animals more than 1 billion years ago: trace fossil evidence from India. *Science* **282**, 80–3.
- Valentine, J.W. 2004. *On the Origin of Phyla*. University of Chicago Press, Chicago.
- Waggoner, B. 2003. The Ediacara biotas in space and time. *Integrative Comparative Biology* **43**, 104–13.
- Wray, G.A., Levinton, J.S. & Shapiro, L.M. 1996. Molecular evidence for deep pre-Cambrian divergences amongst metazoan phyla. *Science* **214**, 568–73.