1 Geological Time and the Evolution of Early Life on Earth

Our planet is some 4540 million years old. We have little record of Earth's history for the first half billion years, but rocks have been found in Canada that date back some 4000 million years (Bowring & Williams 1999). There are yet older indications of the early Earth in the conglomerates of the Jack Hills of Australia, where tiny zircon crystals recycled from much older rocks give ages as old as 4400 million years (Wilde *et al*. 2001), and therefore their formation occurring a little after the birth of our planet. These zircons are important, because chemical signals within the crystals suggest the presence of water, a prerequisite for life on Earth, and also the lubricant for plate tectonics, which provides an active mineral and nutrient cycle to sustain life.

Because Earth's history is so enormous from a human perspective, it has been divided up into more manageable packets of time, comprising four eons, the Hadean, the Archean, the Proterozoic, and the Phanerozoic (Fig. 1.1); the Hadean, Archean, and Proterozoic are jointly termed the Precambrian. In practice, the boundaries between these eons represent substantial changes in the Earth system driven by such components as plate tectonics, the interaction of life and the planet, and by the evolution of ever more complex biological entities. The boundary between the extremely ancient Hadean and Archean is set at about 4000 million years, whilst that between the Archean and Proterozoic is drawn at 2500 million years. The beginning of the Phanerozoic (literally meaning 'manifest life') is recognized by evolutionary changes shown by animals about 541 million years ago. The Archean is subdivided into the Eoarchaen (4000–3600 million years), the Paleoarchean (3600–3200 million years ago), the Mesoarchean (3200–2800 million years ago), and the Neoarchean (2800–2500 million years ago) eras. The Proterozoic is subdivided into the Paleoproterozoic (2500–1600 million years), the Mesoproterozoic (1600–1000 million years), and the Neoproterozoic eras (1000–541 million years). The earliest period of the Phanerozoic eon, the Cambrian, coined after the old Latin name for Wales, was a time that almost all of the major animal groups that we know on Earth today made their initial appearances in the fossil record. Some of the most important fossil evidence for these originations has come from the Chengjiang biota of southern China.

However, the record of life on Earth goes back much further in time than the Cambrian Period, perhaps nearly as far as the record of the rocks. The early, Hadean Earth was subject to heavy bombardment by asteroids, many of which were so large that they would have vaporized early surface waters and oceans. This heavy bombardment ceased some 3900 million years ago, and from this period of the early Archean onwards there have been permanent oceans at the surface of planet Earth. Not long after – from a geological perspective – there is evidence for life. Microfossils of sulfur-metabolizing bacteria are reported from Paleoarchean rocks as old as 3400 million years in Australia (Wacey *et al*. 2011), and there is circumstantial evidence from geochemical studies that carbon isotopes were being fractionated by organic processes as long ago as 3860 million years in the Eoarchean (Mojzsis *et al*. 1996). However, there is a need to treat some of the reports of evidence for very early life with caution, and the further back in time the record is extended the more controversial the claims become (see, e.g., Grosch & McLouglin 2014).

The sparse organic remains of the Archean are microscopic and sometimes filamentous. But there is also macroscopic evidence for early life, represented by microbial mat structures (Noffke *et al*. 2006) and stromatolites (Fig. 1.2). Modern stromatolitic structures are built up through successive layers of sediment being trapped by microbial mats. The resulting stromatolite forms are commonly dome-like or columnar, and these characteristic shapes can be recognized in Paleoarchean sedimentary deposits up to 3500 million years old. Once again, the very oldest

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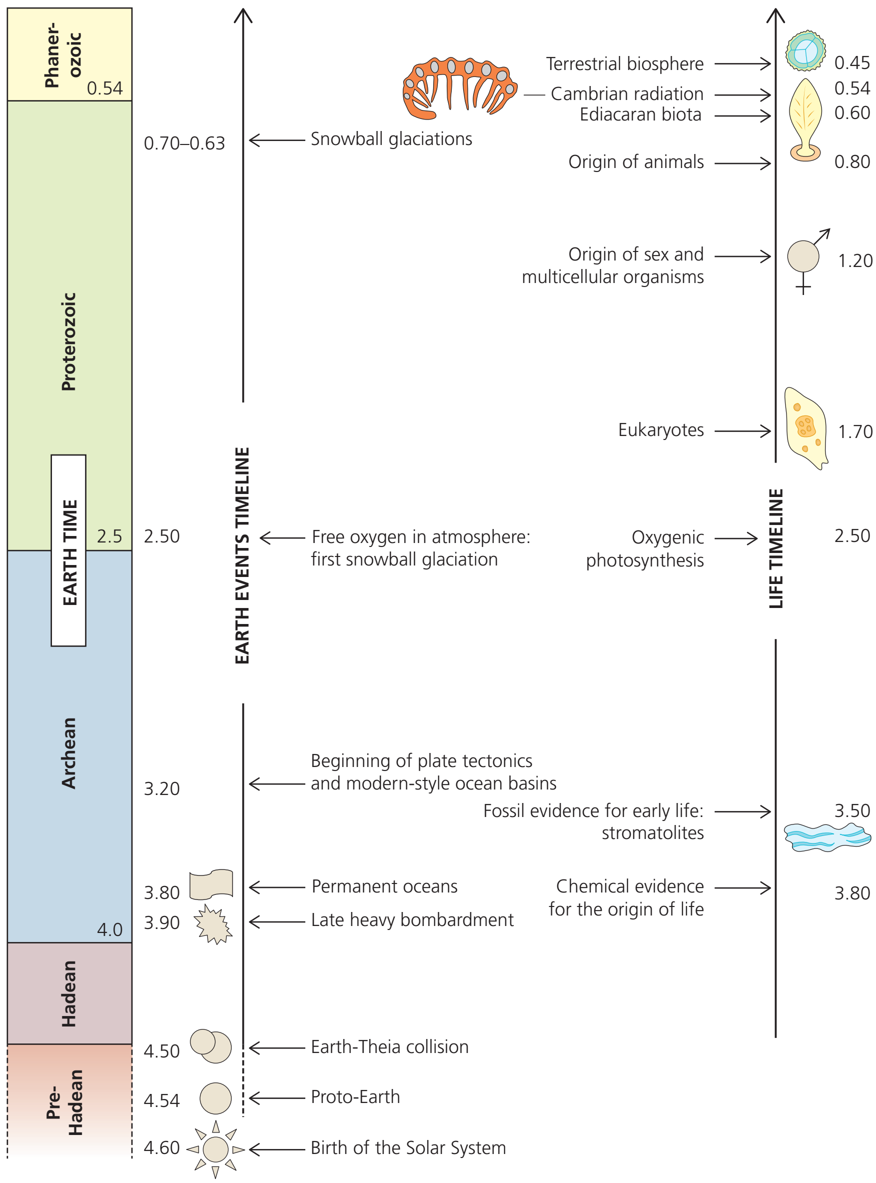

Figure 1.1 Some major events in the history of the Earth and early life.

stromatolites are somewhat controversial, and it is possible that they could have been constructed by abiogenic processes rather than by living organisms (Grotzinger & Rothman 1996).

The microorganisms identified living in modern stromatolitic communities represent a wide range of types of life, including filamentous and coccoid cyanobacteria, microalgae, bacteria, and diatoms (Bauld *et al.* 1992). If we accept the combined evidence from microfossils, microbial mats, stromatolites and carbon isotopes, then it appears that life may have begun on Earth some 3500 million years ago, or possibly somewhat earlier, and that these life forms included microorganisms that could generate their own energy by chemo- or photosynthetic processes. Whether these earliest microorganisms used oxygenic photosynthesis – utilizing carbon dioxide and water to make energy and thereby releasing free oxygen – is controversial, and there is little evidence of a build-up of oxygen in the Earth's atmosphere until much later. But by the boundary between the Archean and Proterozoic eons, 2500 million years ago, cyanobacterial microorganisms using oxygenic photosynthesis had certainly evolved. These are responsible for one of the key events in the evolution of the Earth's biosphere, the Great Oxygenation Event between 2400 and 2100 million years ago. This event led to atmospheric levels of oxygen rising to about 1% of the current level, and it is evidenced by the disappearance of reduced detrital minerals such as uraninite (uranium ore) from sedimentary deposits younger than this age worldwide (Pufahl & Hiatt 2012). The oxygenation of Earth's atmosphere and hydrosphere was to have profound implications for the path of life. It provided new mechanisms of energy supply, and also pushed to the

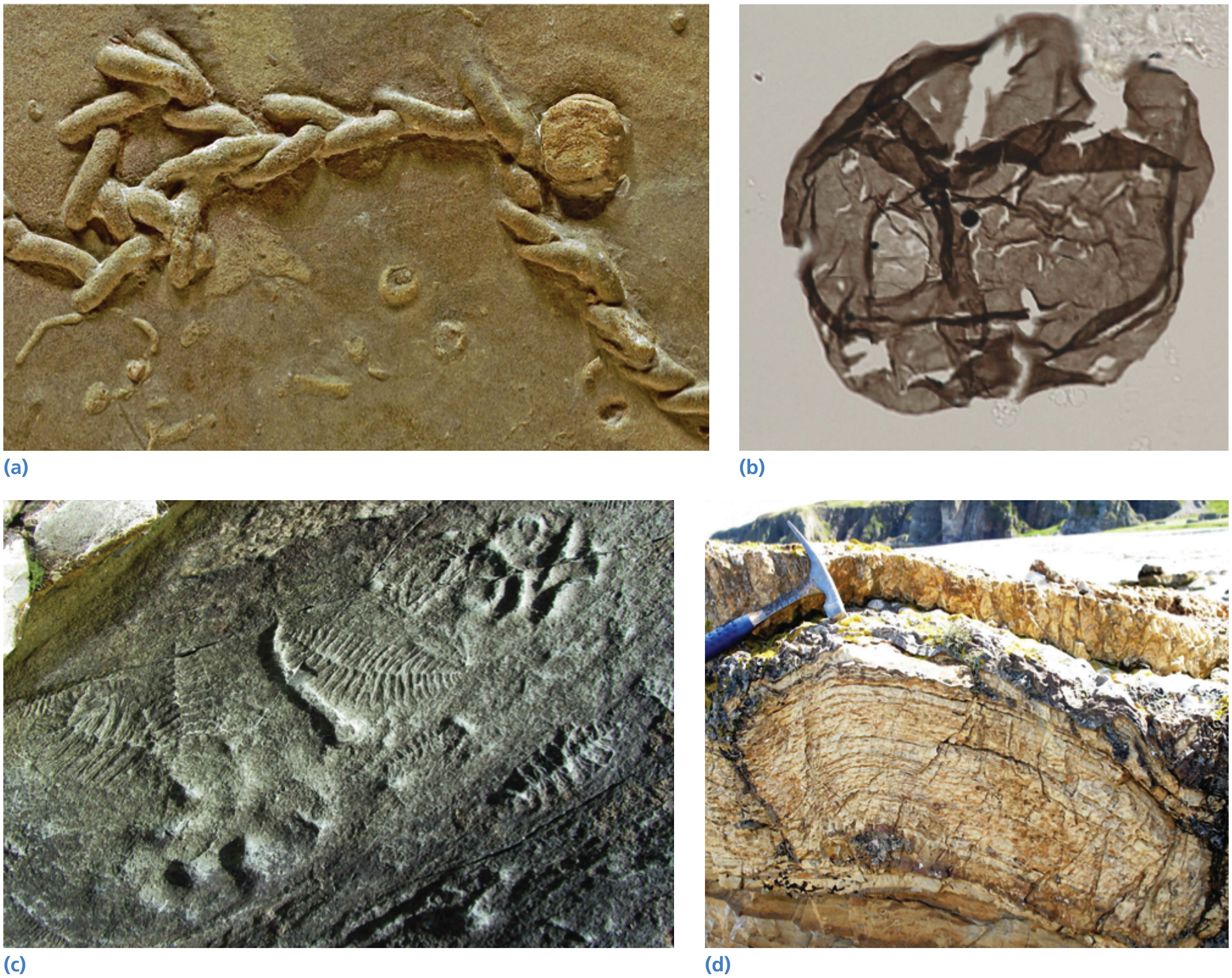

Figure 1.2 Representative fossils of the early history of life on Earth. **(a)** The trace fossil *Treptichnus*, burrows from early Cambrian strata in Sweden, signaling the movement of bilaterian animals through the seabed, ×1.5. **(b)** An Ediacaran acritarch, a probable resting cyst of a unicellular eukaryotic phytoplanktonic organism, ×1000; these were important primary producers in the Proterozoic and early Phanerozoic oceans. **(c)** Ediacaran organisms on a late Proterozoic marine bedding plane surface characteristic of Earth's first widespread complex multicellular ecosystems; Mistaken Point, Mistaken Point Ecological Reserve, Newfoundland. The specimen upper center is about 20 cm long. **(d)** Late Proterozoic stromatolites, microbial mat structures; Bonahaven Formation, Islay, Scotland, see Estwing hammer for scale.

margins of existence in Earth's earliest biosphere those organisms of the Archean that were adapted for an anoxic world and for which free oxygen was toxic.

There is a much richer and less controversial record of life in rock strata of Paleoproterozoic and Mesoproterozoic age. Microbial mats and stromatolites constructed by cyanobacteria are quite abundant, and it is likely that cyanobacteria had become diversified by the mid-Paleoproterozoic (Knoll 1996). There are also fossil data showing that one of the most significant steps in evolutionary history had taken place by this time – the appearance of complex, eukaryotic cells (Fig. 1.2). Eukaryotes are distinguished from the more ancient prokaryotes by their larger size, and by their much more complicated organization, with a membrane-bound nucleus containing DNA organized on chromosomes, and a variety of organelles within the cytoplasm. There are tell-tale signatures in fossils that identify eukaryotes in Paleoproterozoic rocks. Prokaryotic cells such as bacteria can be large. They can have processes that project out from the cell, and they can have cell structures that preserve as fossils. However, no single prokaryotic cell possesses all of these characters, and neither do they possess a nucleus or the complex surface architecture of eukaryotes. Based on these pragmatic criteria, the first appearance of eukaryotes is seen in fossils from rocks in China and Australia about 1700 million years ago (Knoll *et al*. 2006).

Later still, during the Mesoproterozoic, came the origination of sex, with its ability to exchange genetic information and thereby increase the genetic variability of life, and the development of multicellular structures, with their ability for some cells to become specialized for different functions. Amongst the earliest multicellular and sexually reproducing organisms is the putative red alga

Bangiomorpha, which lived in shallow seas some 1200 million years ago. It possessed specialized cells to make a holdfast for attaching to the seabed, and from its holdfast arose filaments composed of multiple cells, the arrangement of these cells being comparable to the modern red alga *Bangia* (Butterfield 2000).

The first metazoans (animals) arose during the Neoproterozoic. Typical metazoans build multicellular structures with cells combining into organs and specializing in different functions, such as guts, hearts, livers, or brains. However, probably the most primitive of metazoan organisms are the sponges, which build three-dimensional structures that control the flow of water through the body, but lack tissues differentiated to form specific organs. Fossil and biochemical evidence supports the presence of sponges or their ancestors originating at between 635 and 713 million years old (Love *et al*. 2009; Love & Summons 2015), perhaps originating at the time of the snowball glaciations (though others consider that the oldest compelling evidence for crown-group sponges is early Cambrian in age; e.g., Antcliffe 2015). Sponges represent an important stage in the evolution of ocean ecosystems because they act as natural vacuum cleaners, sweeping up organic debris and thus reducing turbidity in the water column. They also concentrate organic material and therefore provide an important food supply for other organisms (de Goeij *et al*. 2013).

Several tens of million years after the first putative evidence for sponges, the rock record reveals fossils of an enigmatic group of organisms known as the Ediacara fossils, so-called because they were first discovered in the Ediacara Hills of South Australia; they are now known from more than 30 localities worldwide. Though the earliest ediacarans are dated to approximately 575 million years old, the main assemblages are found in rocks spanning an interval from about 565 to 542 million years ago (Droser *et al*. 2006). Many workers have related the variety of soft-bodied forms found in these Neoproterozoic strata to well-known animal phyla, including cnidarians, annelids, mollusks, arthropods, and echinoderms, but such assertions of relationship are highly debated. Ediacarans (Fig. 1.2) include the putative mollusk *Kimberella*, which may have grazed on microbial mats on the seabed, the elongate *Spriggina* and the frondose *Charniodiscus*. Seilacher (1992) controversially proposed that the ediacarans belonged to a distinct and independent clade, the Vendobionta, with a construction like an air mattress and totally different from that of subsequent animals. One author has also suggested that ediacarans are not marine, but represent organisms living in terrestrial soils (Retallack 2013). Whatever their relationships, most of the Ediacaran organisms disappeared by the beginning of the Cambrian, with just a few examples in Cambrian strata suggesting that these forms persisted for a while alongside their more familiar successors.

Other evidence of animal life in the Neoproterozoic and early Cambrian comes from trace fossils (Fig. 1.2), including those in strata coeval with the Ediacaran biota (Jensen 2003). Mostly, these traces are simple tracks and horizontal burrows, with some meandering grazing structures, but there appears to have been insufficient activity to cause complete reworking (bioturbation) of sediment within the seabed. The organisms responsible for these traces are not normally preserved as fossils (at least not so that the link between the two can be demonstrated), but the trails are generally attributed to the activities of mobile "worms" with hydrostatic skeletons. Such an anatomy would indicate a triploblastic (three layers) grade of tissue organization characteristic of animals with a bilateral body plan.

Ediacaran organisms may have essentially scratched the surface of the Neoproterozoic seabed and were probably unable to utilize the supply of organic material or nutrients buried beneath the surface, or to use this sediment as a domicile or habitat. Rocks about 541 million years ago record a fundamental change in animal diversity and behavior signaled by the *Treptichnus pedum* trace fossil assemblage, which marks the base of the Phanerozoic Eon, and reveals evidence for widespread bilaterally symmetrical animals – those with a definite head and tail end, a body plan that is a prerequisite for making a directional burrow (Vannier *et al.* 2010). This fundamental change in the structure and complexity of marine ecosystems is dramatically captured by the approximately 520 million-year-old Cambrian fossils of the Chengjiang biota, and reflects an ecosystem we can recognize, in many respects, as essentially modern.