

THE CAMBRIAN FOSSILS OF CHENGJIANG, CHINA THE FLOWERING OF EARLY ANIMAL LIFE

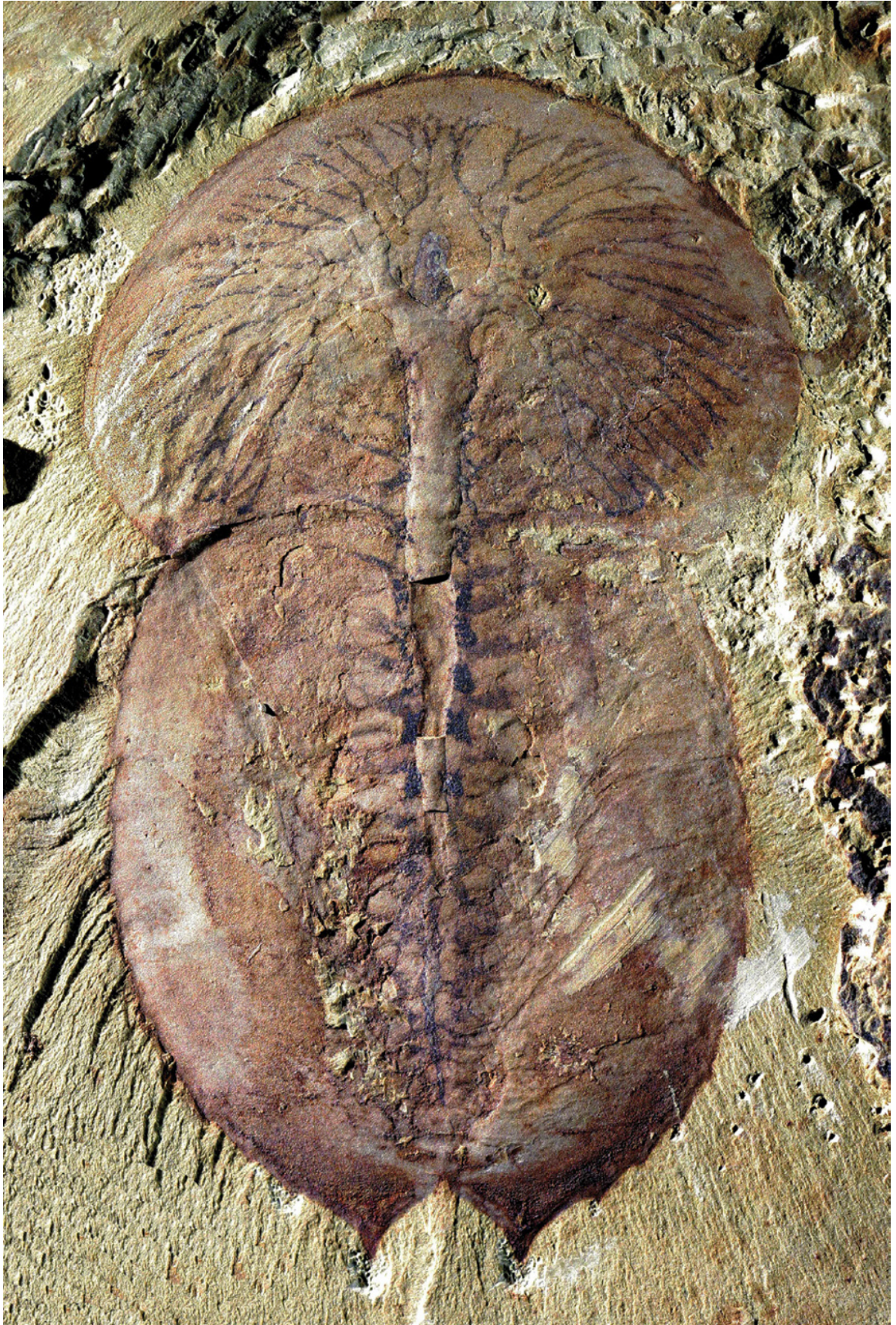
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SECOND EDITION

WILEY Blackwell

The Cambrian Fossils of Chengjiang, China

The Flowering of Early Animal Life



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Second Edition

**Hou Xian-guang, David J. Siveter, Derek J. Siveter,
Richard J. Aldridge, Cong Pei-yun, Sarah E. Gabbott,
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Foreword

The base of the Cambrian Period is one of the great watersheds in the history of life. In the earlier half of the nineteenth century, Charles Darwin had already recognized the startling change that happens in the fossil record at this horizon, when the fossil remains of metazoans appear in abundance for the first time in many localities around the world. The dawn of the Cambrian marks the appearance of mineralized shells, which apparently originated independently in several animal groups shortly after the beginning of the period. A century or more of careful collecting has only reinforced the distinctiveness of this seminal phase in the story of marine life. Initially, paleontologists concentrated on documenting the sequence of shelly fossils through the interval, in order to establish a basis for the correlation of marine strata. Trilobites – now supplemented by microfossils, like acritarchs – have proved to be of particular importance in stratigraphy for all but the lowest part of the Cambrian, and for a while our picture of early life was colored by the kind of shelly fossils that could be recovered from collecting through the average platform sedimentary rock sequence. However, there was another world that the usual fossil record did not reveal, a world of soft-bodied, or at least unmineralized, animals that lived alongside the familiar snails and trilobites, but which usually left no trace in the fossil record.

C.D. Walcott's discovery of the middle Cambrian Burgess Shale in 1909 cast a new light upon this richer fauna. Thirty years of intensive study by several specialists at the end of the last century have made this fossil fauna one of the best known in the geological column. As well as fossils of a variety of animals that could be readily assigned to known animal phyla, the fauna included a number of oddballs that have stimulated much debate: were they missing links on the stem groups of known animals, or completely new designs that left no progeny? Thanks to S.J. Gould's 1989 book *Wonderful Life*, the Burgess curiosities became well known to general readers from Manchester to Medicine Hat. But what once seemed like a unique window on to the marine world of the Cambrian has since been supplemented by other discoveries no less remarkable. Professor

Hou's discovery of the Chengjiang biota in Yunnan Province, China, in 1984 proved to be a revelation equal to, or even exceeding, that provided by the fauna of the Burgess Shale. In the first place it was even older, taking us still closer to what has been described as the "Big Bang" at the dawn of complex animal life. Second, its preservation was, if anything, more exquisite. Third, an even greater variety of organisms was preserved – some, evidently, related to Burgess Shale forms, but others with peculiarities all of their own. The awestruck observer was granted a privileged view of a sea floor thronging with life, only (geologically speaking) a short time after the earliest shelly fossils appeared in underlying strata. The fauna included what have been claimed as the earliest vertebrates (*sensu lato*) and thus has more than a passing claim to interest in our own anthropocentric species. There are arthropods beyond imagining, "worms" of several phyla, large predators, and lumbering lobopodians; while the trilobites, so long regarded as the archetypal Cambrian organism, are just one among many successful groups of animals. Once you have seen the Chengjiang fauna you will be forced to shed your preconceptions about ecological simplicity in early Phanerozoic times. This was a richly varied biota.

The present book is a state of the art update following upon the first detailed, popular account of the Chengjiang fauna published by Professor Hou and his colleagues in 2004. It is astonishing how these Cambrian strata continue to yield new and unexpected finds, and a new edition of this work provides a much richer account of many more animals. More than 30 species have been added in this edition. Over the last decade, the biology of the fauna as a whole has become better understood, as well as the geological circumstances under which it is preserved. This allows for an up-to-date overview of the current science in an extended introduction to a more comprehensive field guide to the fossil species, which are arranged according to the latest ideas of their evolutionary relationships. A few paleontologists who were not on the original team have added their special areas of expertise to the description of key specimens; two of the original authors have sadly died in

the intervening years. It is more evident than ever that there were extraordinarily varied Cambrian relatives of some groups of animals that are comparatively insignificant among the living fauna. Lobopodians are rarely encountered by the average naturalist today, but in the Cambrian seas they flourished in almost bewildering variety, including heavily armored forms on one hand, and creatures of ephemeral delicacy on the other. It continues to astonish that animals as fragile as comb jellies – which are destroyed today by the merest glance of an oar – can be preserved in such exquisite detail. Since the first edition of the Chengjiang fossils was published, the early story of our own phylum – Chordata – has become populated with quite an extensive cast of characters. It seems that evolution had already accomplished many important steps that were seminal to the living phyla of animals, as proved by the array of stem species that populated the Cambrian seas.

But this book provides much more than a picture gallery, exquisite though the photographs are. It is a catalog of origins. While advances in molecular science have firmed up our knowledge of the relationships between animal groups, none of this hard science is able to provide a vision of what life was like more than 500 million years ago. Only paleontology can show what steps were taken on the inconceivably long journey through geological time. We could not have predicted *Fuxianhuia* from the modern fauna, let alone the great appendage arthropods or anomalocarids. The Chengjiang fauna opens a window on to the generation of novelty of design. The organisms that populated the distant past were not mere stepping stones on the way to the present day, but rather a rich variety of idiosyncratic

animals each with their own way of earning a living in an early marine world. The Chengjiang fauna even supplies evidence of their behavior in swarming, feeding, or reproduction. The sophistication of design and behavior so often displayed raises questions about timing. Is it really conceivable that such variety could have arisen within just a few million years? And if so, what genetic mechanisms could have released such creativity in so short a time? Or was there an earlier, Ediacaran evolutionary fuse that ignited the subsequent explosion, for which the field evidence still largely eludes us? As so often, new discoveries serve to generate new questions.

Some readers may prefer to let their imaginations lead the way: the fossils allow a vision of a Cambrian sea swarming with not-quite-shrimps and trilobites, where giant predators of extinct kinds preyed upon elegant, slender animals that probably included our own, most distant ancestors. Vision was already important for both the hunter and the hunted. Worms of sundry kinds disturbed the soft sediment, while filter feeders like sponges extracted nutrients from a rich sea. There was already the glimmer of the marine ecology we recognize today, for all that many of the animals living in the Cambrian strike such a strange note. If evolution still had far to travel, it was through a familiar seascape. Exceptionally preserved fossil faunas like those of Chengjiang provide more than just an inventory of ancient life. They allow us to animate the past. They tell us from whence we came.

Richard Fortey FRS, FRSL, FLS
Henley-on-Thames, January 2017

Preface

The Chengjiang exceptionally preserved biota is a vital key in helping to unravel the evolution of early life during a period of time when multicellular organisms were first becoming common in the fossil record. The unearthing in Yunnan Province in 1984 of the abundant and exquisite fossils of the Chengjiang Lagerstätte, in rocks of early Cambrian age, represents one of the most significant paleontological discoveries of the twentieth century. The fossils preserve fine details of the hard parts and soft tissues of animals approximately 520 million years old. Set against the buff-colored host rock, the celebrated Chengjiang fossils are wondrous objects in their own right as well as representing a trove of paleobiological, evolutionary, and paleoecological information.

Through media coverage and countless publications in journals and in volumes resulting from scientific meetings, the Chengjiang biota is known world-wide to practitioners and students of geology, biology, and evolution. Much of the primary documentation is in Chinese. This book represents the only work in English that presents a comprehensive overview of the biota. It has resulted from long established links between Professor Hou Xian-guang, the discoverer of the Chengjiang Lagerstätte, and his colleagues at Yunnan University and those at the universities of Leicester and Oxford, and the Natural History Museum, London. About 250 species have been recorded from the biota, the vast majority of which have been established on material from the Lagerstätte itself. Details on the authorship of each species of the biota and the date when it was established are given in the list at end of this book, together with synonyms and possible synonyms for those taxa that we are able to evaluate based on published information. It was not intended that every known species from the Chengjiang biota should be treated herein. We have simply provided a large selection, with major groups and their species ordered phylogenetically from less to more derived forms (see Chapter 29 for an overview). The systematic position of many Chengjiang species is controversial and has in some cases attracted widely different opinions. It is hoped that with the publication of this book the sheer beauty, diversity, and scientific importance of these fossils from southwestern

China will become even more widely known and appreciated by scientists and the public at large.

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The majority of the photographs in this book were captured by Derek Siveter using a Canon 5D DSLR camera attached to Nikon Multiphot macrophotographic equipment, using Macro-Nikkor lenses and incident fiberoptic lighting; some images were taken using a Nikon D3X camera and an AF-S VR105 mm macro lens. Some images were captured using polarized light. The general methodology builds on that outlined in Siveter (1990), as used with the Leitz Aristophot equipment. The digital images were adjusted using Adobe Photoshop (Creative Suite 6) software.

For those e-readers who want to calibrate the size of an image at a magnification other than that given in the book, the width of the coloured rectangle line bounding the image is 171 mm.

We thank the following for images: Jean-Bernard Caron (Royal Ontario Museum; Burgess Shale fossil); Chen Junyuan (Early Life Research Center, Chengjiang; *Shankouclava*, *Iotuba*, *Maotianchaeta* and *Eophoronis*); Ian Fairchild (Birmingham University; stromatolites from the Bonahaven Formation); Diego García-Bellido (University of Adelaide; Emu Bay Shale arthropod eye); David Harper (University of Durham; Sirius Passet arthropod); Tom Harvey (Leicester University; Cambrian acritarch and [with Nick Butterfield, Cambridge University], small carbonaceous fossil); Luo Hui-lin

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Gareth Monger (Chelicerata), Scott Hartman (Chaetognatha, Yunnanozoa), Nobu Tamura (Vetulicolia), and Yan Wong (Vertebrata).

Most of the Chengjiang material figured in this book is housed at the Yunnan Key Laboratory for Palaeobiology (YKLP), formerly the Research Center for the Chengjiang Biota (RCCBYU), Yunnan University, Kunming. Other figured material is in the Nanjing Institute of Geology and Palaeontology (NIGPAS), Academia Sinica; the Yunnan Institute of Geological Sciences (YIGS), Kunming; Chengjiang Fossil Museum (CFM; formerly Chengjiang County Museum), Chengjiang; Early Life Evolution Laboratory, School of Earth Sciences and Resources, China University of Geosciences (ELEL), Beijing; and the Early Life Research Center (ELRCC), Chengjiang.

Spellings used in this book in general follow American usage. In fossil names and in the names of institutes, use of the prefix 'Palaeo', or 'Paleo', follows the officially erected fossil name, or the official name of the institute.

Part One

Geological and Evolutionary Setting of the Biota

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 Eoarchean (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 & McLoughlin 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

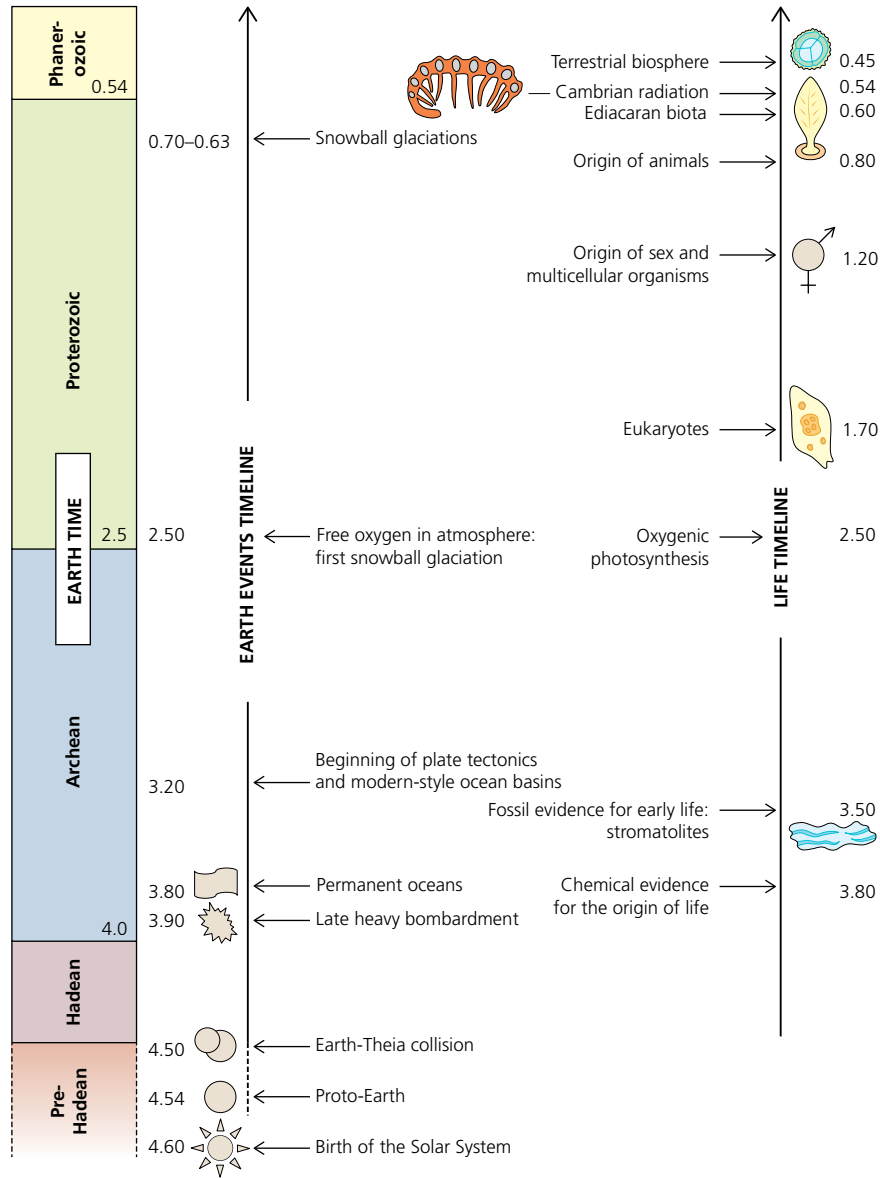


Figure 1.1 Some major events in the history of the Earth and early life.

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

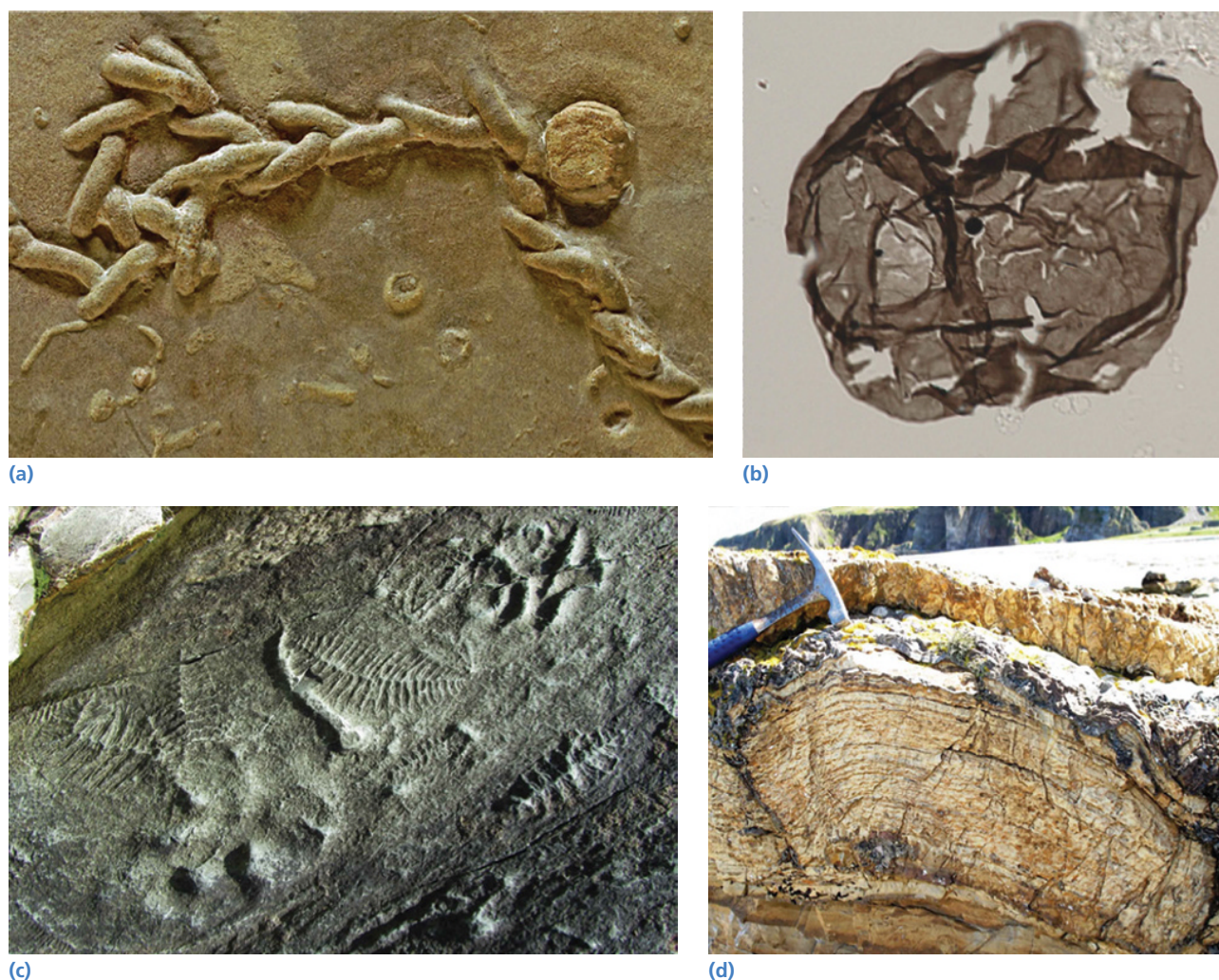


Figure 1.2 Representative fossils of the early history of life on Earth. **(a)** The trace fossil *Treptichnus*, burrows from early Cambrian strata in Sweden, signaling the movement of bilaterian animals through the seabed, $\times 1.5$. **(b)** An Ediacaran acritarch, a probable resting cyst of a unicellular eukaryotic phytoplanktonic organism, $\times 1000$; 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.

2 The Evolutionary Significance of the Chengjiang Biota

It is hard to overstate the evolutionary significance of the Chengjiang biota. Perhaps the most obvious impact it has had on our understanding of the history of life is in providing direct evidence for the anatomical complexity of organisms and ecosystems 520 million years ago, but many other things follow from this, and historically, the chief interest in Cambrian sites of exceptional preservation, such as the Chengjiang, has derived from the long-standing controversy concerning the Cambrian explosion of life (Figs 2.1 and 2.2).

It has long been known that the fossil record of life exhibits a profound transition in the Cambrian (Fig. 2.2). For billions of years the record of life on Earth consists almost exclusively of simple organic-walled fossils, most of which are microscopic, together with widespread evidence of microbial communities preserved primarily as stromatolites. Then, in the Ediacaran Period, more complex organisms appear for the first time, including fossils that are plausibly interpreted as the remains of animals (Xiao & Laflamme 2009). However, only very few Ediacaran forms can be allied to living phyla, and in the absence of conclusive anatomical evidence many Ediacaran organisms generate more than their share of controversy. By the time of the Cambrian Period things look very different: the fossil record is full of well-known shelly organisms such as trilobites and brachiopods, and the Chengjiang biota preserves the first fossils of many of the phyla that have characterized marine ecosystems ever since. This is the Cambrian explosion.

The big question concerning the Cambrian explosion, a question that famously troubled Darwin, is simple: is it real? Does the pattern shown by the fossil record reflect a period of dramatic change in the abundance, diversity, and complexity of life on Earth – a period of time unlike any other before or since, when new types of organism suddenly appeared in the space of a few tens of millions of years? Or, does this pattern reflect change in the nature of the fossil record, with a long pre-Cambrian history of

gradual evolutionary appearance of the different kinds of organisms? A history of which we have no direct fossil evidence because the remains of the organisms were never fossilized. Failure to fossilize may reflect the small size of organisms or their lack of decay-resistant body parts, or the absence of the right conditions for fossilization; whatever the reason, it must also explain the lack of trace fossil evidence of their activity. In this context, the Chengjiang biota, early Cambrian in age, but with abundant evidence of complex organisms, most of which can be accommodated among the familiar branches of the tree of life, has added fuel to the fire.

The last few decades have seen the issue of the Cambrian explosion debated with renewed vigour (e.g., Conway Morris 2003; Budd 2008a; Erwin & Valentine 2013) because new types of evidence suggested protracted and cryptic Precambrian origins for many groups of organisms (Wray *et al.* 1996). This is the so-called long evolutionary fuse to the explosion (Cooper & Fortey 1998), evidence for which came primarily from attempts to use accumulated differences in molecular composition between extant animals to determine how long ago they shared their last common ancestor. This approach, known as molecular clock analysis, looks at complex molecules – proteins, such as haemoglobin, or DNA – and compares the number of differences between taxa. If the rate at which these differences accumulate, by substitution of amino acids, is known (see below), then the amount of time since two taxa diverged can be calculated, thus dating the time of origin of clades (clades are the branches on the tree of life, comprising all the species that share a particular common ancestor; mammals, for example, are a clade because mammal species are more closely related to other mammal species than they are to species of other groups of animals, and all mammals thus share a common ancestor that those other animals do not). For a number of years, proponents of the molecular clock approach to dating the origins of clades produced dates for

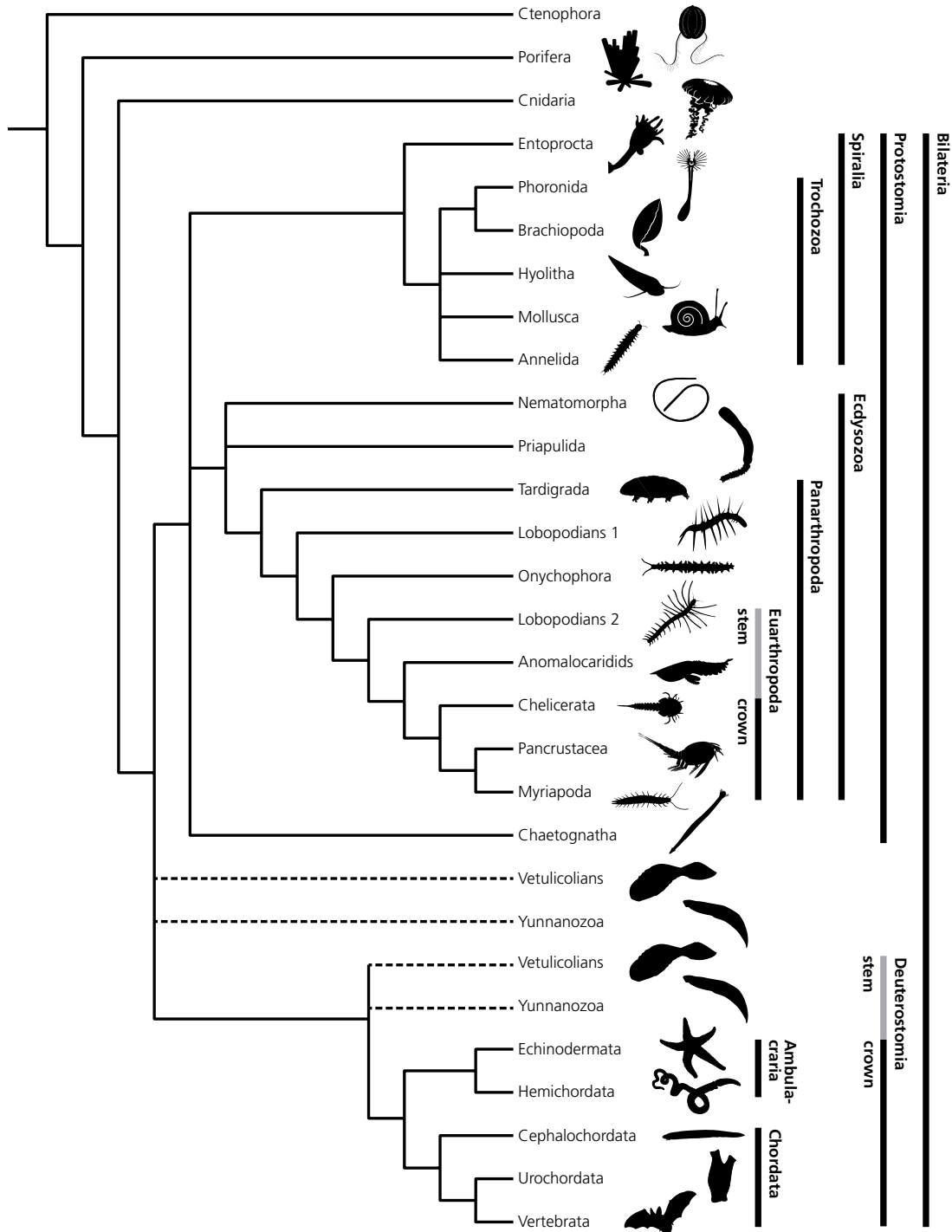


Figure 2.1 Phylogenetic relationships and classification of the major clades of animals. For clarity, a few phyla are excluded; these are mostly those that are unknown from fossils or have no bearing on discussions of the affinities of Chengjiang fossils. (See Preface for silhouette image credits.)

the origins of extant phyla that far exceeded anything then known in the fossil record, suggesting the Cambrian explosion was nothing more than an explosive increase in fossilization, not a major change in the diversity of life (Cooper & Fortey 1998). However, improvements in methods and better calibration, using fossils, of the rate at which the molecular clock ticks have significantly reduced the discordance

between clock-based dates of the origins of phyla and their first fossil record. This has led to the conclusion that although the fossil record is far from perfect, and the precise timing can never be known from the fossil record alone (nor from comparison of molecules alone, for that matter), the Cambrian explosion is a real evolutionary event, reflecting irreversible changes in the complexity and abundance

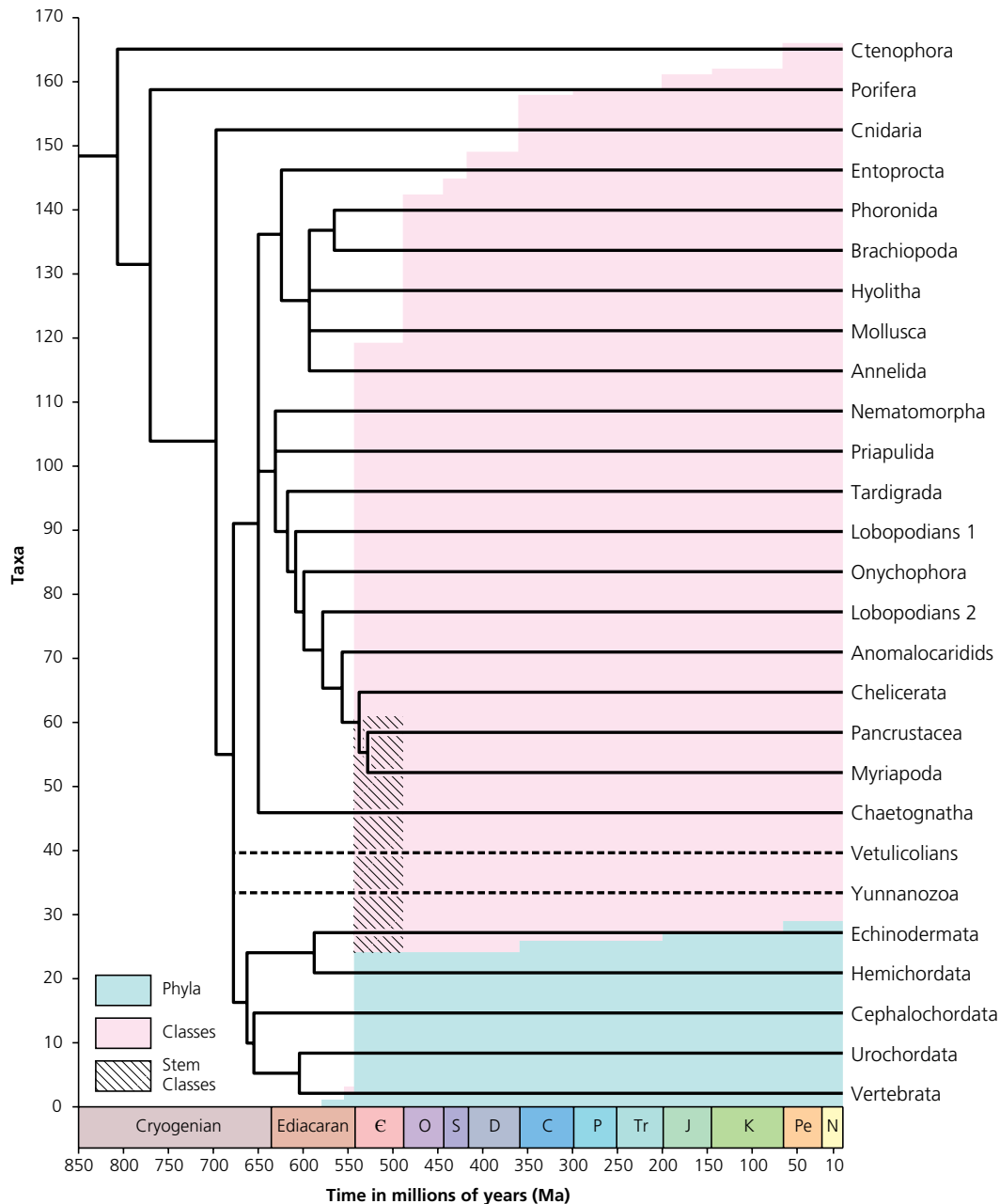


Figure 2.2 Time of origin of the major animal clades. The date of the branching points in the cladogram (hypothesis of relationships as in Fig. 2.1) is based on molecular clock analysis. The colored blocks show the establishment of anatomically distinct, higher level taxa (phyla and classes) as revealed by the fossil record – the Cambrian explosion of animal life (modified from Erwin *et al.* 2011).

of animals that took place over a period of a few tens of millions of years in the Ediacaran and earliest Cambrian (Peterson *et al.* 2005; Erwin *et al.* 2011). This is summarized in Figure 2.2, which shows the time of origin of major clades of animals, and rapid Cambrian rise in the number of metazoan phyla and classes present in the fossil record.

Research to minimize the problems and errors inherent in determining the time of origin of major clades is ongoing, and Chengjiang fossils have a role to play in providing calibration points for the forks in the tree – the points at which new clades originate. For example, the fundamental split between

deuterostomes (including vertebrates and echinoderms) and all other bilaterians (Fig. 2.1) cannot have occurred more recently than the time of the Chengjiang, because the occurrence of what are generally accepted to be the earliest fossil vertebrates (e.g. *Mylokunmingia*) provides a minimum age date for the divergence of deuterostomes (i.e., it cannot have been more recent; see Benton & Donoghue 2007).

The debate concerning divergence times and the reality of the Cambrian explosion was characterized for many years by disagreements between proponents of molecular-based and fossil-based analyses, followed by the realization

that combining the available data gives the best results. Much the same can be said about the use of molecular and morphological/fossil data for reconstructing hypotheses of relationship and the nature of the tree of life. The dichotomy of molecules versus morphology still exists to some extent, and the utility of the respective datasets depends on the nature of the question being asked, but systematic analyses provide good evidence that the impact of morphological data from fossils is equivalent to that from extant taxa, and that excluding them can have a marked negative impact on phylogenetic hypotheses (e.g., Cobbett *et al.* 2007). Chengjiang fossils thus play an important role in disentangling the deep relationships between major clades of animals.

In all of this, the distinction between stem and crown groups of clades is critical. Crown groups are defined by the phylogenetically most basal *extant* branch of a clade, and the crown group comprises this clade and all the branches that sit above it. To use a familiar example, monotremes (mammals that lay eggs) define the mammal crown group as they are the most basal *living* members of the clade. Stem clades comprise extinct taxa that are more closely related to a particular crown group than to any other clade (e.g., fossil mammals that sit outside the mammal crown group, by virtue of them branching off before monotremes, are stem mammals). In the context of molecular clocks, stems and crown groups are important because molecular data are generally available only for extant taxa, and this approach can date only the point at which extant clades diverged. Thus, by dating the split between the most basally branching clade and all the members of the crown group, the origin of the crown group can be dated. By determining the time of split between one crown group and the sister crown group – mammals and reptiles, for example – the origin of the total group (the crown plus the stem) can be dated. The fossil taxa of stem groups are nonetheless critical because not only do they provide the calibration points for clock-based analysis (see above), but also by filling the gaps between crown groups with correctly placed fossils they provide our only evidence of the pattern of character acquisition, and the assembly of crown group body plans. Chengjiang fossils are particularly significant in this context as they include a number of fossil taxa that would otherwise be unknown, and that together constitute large parts of the stem lineages of phylum-level crown groups. Panarthropods and euarthropods provide particularly striking examples; without Chengjiang fossils our view of how and when these clades acquired their distinctive anatomical characteristics would be significantly diminished (e.g., Edgecombe & Legg 2014). Similarly, much attention has focused on the putative, and in some cases controversial, stem deuterostomes of the Chengjiang biota, because of their potential to shed light on the somewhat cryptic origins of a clade to which we, as vertebrates, belong (Shu *et al.* 2010; but see Donoghue & Purnell 2009).

Looking at the same data in a slightly different way illuminates the origins of particular mechanical and organ systems: prey apprehension or sensory systems, for

example. The presence of paired eyes in stem vertebrates from the Chengjiang biota illustrates this point: they place the origins of visual systems in vertebrates before the origin of the crown group (Lamb 2013). Similarly, anatomical details of the compound eyes and the presence of structures interpreted as remains of the nervous system in Chengjiang anomalocaridids (stem panarthropods) shed new light on the sensory capabilities of Cambrian organisms, in addition to providing new evidence for homology of anterior appendages, and the ecological context and sequence in which these systems were assembled (Cong *et al.* 2014).

Understanding the biology of exceptionally preserved organisms of the Chengjiang biota tells us more than how particular clades evolved. By understanding the sensory capabilities, locomotory modes, and mechanisms of feeding and defence of Chengjiang animals, much can be inferred about the ecosystem and how it functioned. And because of the exceptional preservation we can be confident that most of the macroscopic components of the ecosystem are preserved, and our view is thus more complete. In other words, by understanding the phylogenetic affinities and functional morphology of Chengjiang organisms, supplemented with direct evidence from gut contents, for example, these fossils reveal the mode of life of ancient organisms and how they interacted. They provide the only direct evidence we have for the nature and complexity of ecosystems at this critical period in Earth history. This reveals that although they were not as sophisticated as later ecosystems, Cambrian ecosystems at the time of the Chengjiang biota were already far more complex than their Ediacaran counterparts or anything from the previous 3 billion years (Bambach *et al.* 2007).

Phylogenetic Structure

The organization of chapters in this book, many of which correspond to what are generally accepted as phyla, reflects the evolutionary relationships between major clades of organisms (Fig. 2.1). Apart from algae, all of the elements of the Chengjiang biota are assigned to Metazoa (animals), and most of these belong to a handful of major clades: Ctenophora (comb jellies), Porifera (sponges), Cnidaria, and Bilateria. Like the modern world, most of the animals in the Chengjiang biota are assigned to clades within the Bilateria – animals that share major aspects of the body plan, such as bilateral symmetry. This clade is in turn divided into two – the protostomes and deuterostomes – subdivisions that are well supported as monophyletic groupings on the basis of molecular evidence, and are also distinguished by differences in early embryonic development. As is evident from Figure 2.1 and the chapters that deal with these animals, deuterostomes and protostomes are diverse, both in terms of body plans and numbers of taxa. With only one or two exceptions, the bilaterian taxa of the Chengjiang are consistently and reliably placed within either protostomes or deuterostomes, but recent reviews have highlighted controversies concerning relationships between other clades of metazoans (Edgecombe *et al.*

2011b; Dohrmann & Worheide 2013; Nosenko *et al.* 2013; Dunn *et al.* 2014), with the relationships of sponges (Porifera) and ctenophores being among the most contentious. The issue with sponges concerns whether they are monophyletic, or constitute a paraphyletic grade (i.e., a series of clades, some of which are more closely related to other animals). This has yet to be determined with confidence, but Nosenko *et al.* (2013) were of the view that increased taxon sampling in future analyses is likely to increase the stability of sponges as a clade. That sponges (Porifera) are a clade was also advocated by Dunn *et al.* (2014), and this view is followed herein. Ctenophores have recently been placed either as the sister group to all other metazoans (e.g., Dunn *et al.* 2008), or as sister group to the Cnidaria (e.g., Nosenko *et al.* 2013), but phylogenetic

analyses based on whole ctenophore genomes (Ryan *et al.* 2013; Moroz *et al.* 2014) support their placement at the base of the Metazoa, as shown herein. In general, the phylogenetic scheme for animals of the Chengjiang biota used here (Fig. 2.1) follows the consensus presented by Dunn *et al.* (2014). Clades within Euarthropoda and the relationships between them follow Legg *et al.* (2013) and Edgecombe & Legg (2014).

Another aspect of uncertainty concerns the confidence with which a number of Chengjiang animals can be placed within major clades, either because there is a lack of definitive evidence, or because alternative interpretations assign the same fossils to different clades. These difficulties are indicated herein using the phrase “of uncertain affinity,” which equates with the taxonomic concept of *incertae sedis*.

3 The Discovery and Study of the Chengjiang Lagerstätte

Almost 30 years after its discovery the Chengjiang fossil site was inscribed to the UNESCO World Heritage List at a meeting in St Petersburg in June 2012 (Fig. 3.1). The nominated property is a relatively small oblong area comprising about 512 hectares surrounded by a narrow buffer zone. Its western boundary is 5 km east of the county town of Chengjiang and its southern boundary is about 4 km northeast of Fuxian Lake (see Fig. 4.3). Maotianshan, the site of the initial finds of Chengjiang soft-bodied fossils, is in the center of the southern part of the nominated property. Whilst the Burgess Shale in Canada was already recognized as a World Heritage site, Chengjiang offered a compelling case for equivalent status. Evaluation of the nomination of Chengjiang to the World Heritage List noted that the site presents an exceptional record of the diversification of life on Earth during the early Cambrian period, when almost all major groups of animals appeared in the stratigraphic record for the first time. It also accredited “the property to be a globally outstanding example of a major stage in the history of life, representing a paleobiological window of great significance” (IUCN 2012). Its fossils were recognized to be of the highest quality of preservation and to convey the earliest record of a complex marine ecosystem.

The Chengjiang-Kunming area of Yunnan Province is one of the best-known, richly fossiliferous and long-studied geological regions of China. The area has traditionally been taken as a standard for the stratigraphy and correlation of the Cambrian in the Southwest China (Yangtze) Platform and throughout China and beyond. More than one hundred years ago the Frenchmen Henri Mansuy (1907, 1912), Honoré Lantenois (1907) and Jacques Deprat (1912) undertook pioneering research on the geology and

paleontology of the region (Figs 3.2 and 3.3). The local Cambrian was also extensively examined in the 1930s and 1940s as a part of mapping and other general geological survey work (see Hou *et al.* 2002b). In spite of such endeavor it was not until 1984 that the first soft-bodied fossils of the Chengjiang Lagerstätte were discovered, by Hou Xian-guang.

Already in 1980 Hou Xian-guang had collected Cambrian bradoriid arthropods at the Qiongzhusi section in Kunming City, as part of his Masters degree based at the Nanjing Institute of Geology and Palaeontology of the Chinese Academy of Sciences. The Kunming-Chengjiang area was known to be rich in bradoriids through the work in the 1930s of Professor Yang Zui-yi, of Zhongshan University (see Ho 1942). This university had relocated, because of hostilities within China, from Guangzhou City in Guangdong Province to Chengjiang County, and Yang’s Department of Geology had been re-sited at the village of Donglongtan, 1.5 km west of Maotianshan. In June 1984 Hou Xian-guang arrived in Kunming to begin his second period of fieldwork hunting for bradoriids (Hou *et al.* 2002b). He undertook sampling in Jinning County, southwest of Kunming, and then traveled to Chengjiang town and on eastwards to nearby Dapotou village (see Fig. 4.3). There, prospecting for phosphorite deposits in the lower Cambrian, were staff of the Geological Bureau of Yunnan Province, who provided Hou Xian-guang with general fieldwork assistance. Hou Xian-guang assessed several nearby lower Cambrian localities and at first collected bradoriids from near Hongjiachong village (Fig. 3.4). However, as the section proved to be incomplete a sequence on the west slope of Maotianshan was ultimately chosen for detailed logging and systematic fossil collection (Fig. 3.5).



(a)



(b)



(c)

Figure 3.3 Cambrian fossils from and near the Chengjiang area figured by Mansuy (1912), as (a) *Obulus damesi*, $\times 6.4$; (b) *Redlichia carinata*, $\times 2.9$; and (c) *Bradoria douvillei*, $\times 6.7$.



Figure 3.4 View, in 2006, from the lower Cambrian section at Hongjiachong, looking south to Fuxian Lake.



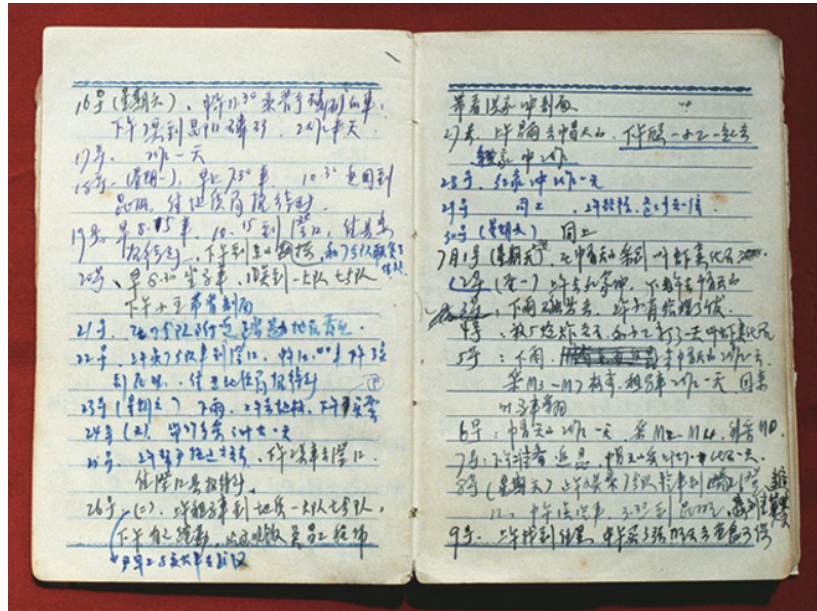
Figure 3.5 Collecting fossils in 1987 at Maotianshan, Chengjiang, where the Chengjiang Lagerstätte was discovered (Hou Xian-guang, center).

Work at Maotianshan was notably easier than at Dapotou and Hongjiachong, because the rock was more strongly weathered. Hou's field diary for Sunday 1 July 1984 signaled the significance of his discovery of soft-bodied fossils at Maotianshan by alluding to comparable material from the Burgess Shale: "The discovery of fossils in the Phyllopod Bed" (Fig. 3.6). In the afternoon that day, a split slab revealed a semicircular white film. Given the realization that this and a second, subelliptical exoskeleton represented a previously unreported species, the rock splitting continued and yielded additional fossils. With the find of a further specimen, an arthropod some 4–5 cm long with limbs preserved, it became clear that the material being collected represented a soft-bodied biota. As Hou Xian-guang has recalled, the specimen with appendages appeared as if it was alive on the wet surface of the mudstone. That fossil was subsequently chosen as the type specimen of a new species of the arthropod *Naraoia* (Fig. 3.7). Work on the section ended when darkness fell.

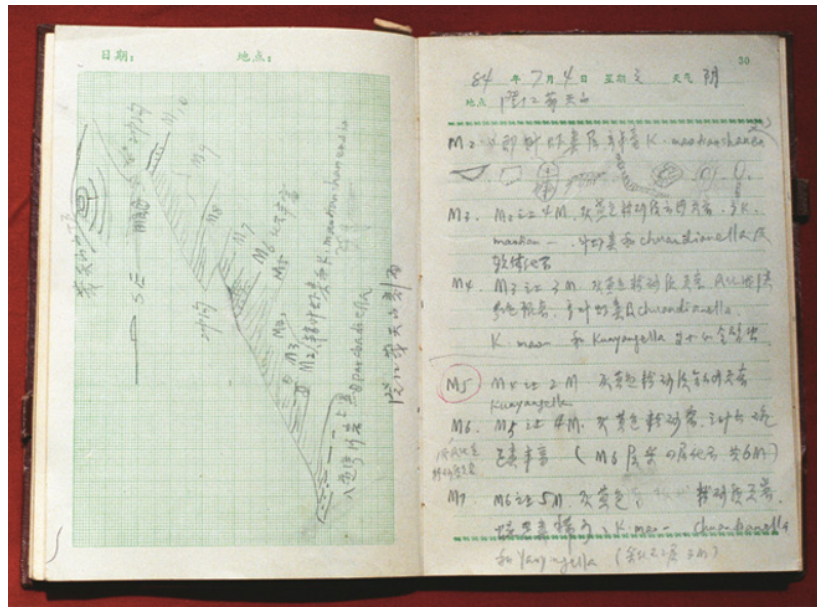
Soft-bodied and other fossils were then collected on a large scale from three broad stratigraphic levels, which later were excavated into quarries. The mudstone of stratigraphic level M2 yielded many species of the Chengjiang fauna. The Geological Bureau team continued to provide valuable support in the field, including blasting trackside exposures on the west slope of Maotianshan. The three stratigraphic levels correspond to at least 10 beds (Hou 1987a), but in fact it proved nigh impossible to determine exactly how many beds of the blocky mudstone bear soft-bodied fossils. After 10 weeks of fieldwork, ending on 17 August 1984, Hou Xian-guang

demonstrated that fossils with soft-part preservation not only occurred at Maotianshan but also are present at many other localities in Chengjiang County and elsewhere in Yunnan Province. Sampling was also made, for example, at Sapushan (Sapu Hill) and Shishan (Shi Hill) in Wuding County, Kebaocun in Yiliang County, and Meishucun in Jinning County. In addition to bradoriids, these sections yielded specimens of soft-bodied and lightly sclerotized and mineralized animals such as worms (*Cricocosmia*), large bivalved arthropods (e.g., *Isoxys*), brachiopods (e.g., *Heliomedusa*) and an isolated sclerite of a lobopodian (*Microdictyon*), more specimens of which were subsequently obtained from Meishucun in 1986 (Hou & Sun 1988). In letters from the field, in 1984, Hou informed his colleagues in Nanjing about the locally rich bradoriid material (in part treated in Hou 1987d), finds of the oldest trilobites at Chengjiang, Wuding and Jinning (some material reported by Zhang Wen-tang 1987a) and other trilobites from Maotianshan (Zhang Wen-tang 1987b), and the discovery and collection of many fossils with preserved soft parts (e.g., Zhang Wen-tang & Hou 1985; Hou 1987a, 1987b, 1987c; Sun & Hou 1987a, 1987b).

With the support of the Nanjing Institute of Geology and Palaeontology, Hou Xian-guang's subsequent fieldwork in the Chengjiang area, from April to June 1985 and throughout October to December 1985, targeted the collection of fossils with soft-part preservation. Chen Luan-sheng, the curator of fossils at the museum of the Nanjing Institute, aided fieldwork, as did a drilling crew of the Geological Bureau of Yunnan Province, who had pitched camp at Maotianshan. Further large-scale collecting took place



(a)



(b)

Figure 3.6 (a) Hou Xian-guang’s field diary, with the record of the discovery of the Chengjiang biota at Maotianshan. (b) Hou Xian-guang’s field notebook with sketches and notes on the geology and drawings of fossils that are now recognized as (from left to right) *Isoxys*, *Branchiocaris*?, *Naraoia*, *Leandroilia*, *Maotianshania*, *Eldonia*, *Heliomedusa*, and *Lingulella*.

from April to September 1987, when work was concentrated mainly at Maotianshan and Jianbaobaoshan near Dapotou village. Chen Jun-yuan, Zhou Gui-qin and Zhang Jun-ming, Hou’s colleagues from Nanjing, joined the fieldwork but they left in early May and June respectively for other duties. Hou Xian-guang made additional collections in November 1989 and April–May 1990 (Fig. 3.8), especially from new sections such as those at nearby Fengkoushao, Xiaolantian and Ma’anshan (see Fig. 4.3). Local farmhands, hired in substantial numbers, became

expert at the labor-intensive task of splitting and examining the large amounts of rock needed to find good yields of fossils. The same fieldwork strategy continues today (Fig. 3.9).

The initial phase of collecting and describing the Chengjiang biota ended when Hou Xian-guang undertook several years of research based at the Natural History Museum in Stockholm. Cooperation with Swedish scientists, especially Jan Bergström, resulted in many papers on a range of Chengjiang taxa (Hou & Bergström 1997 and