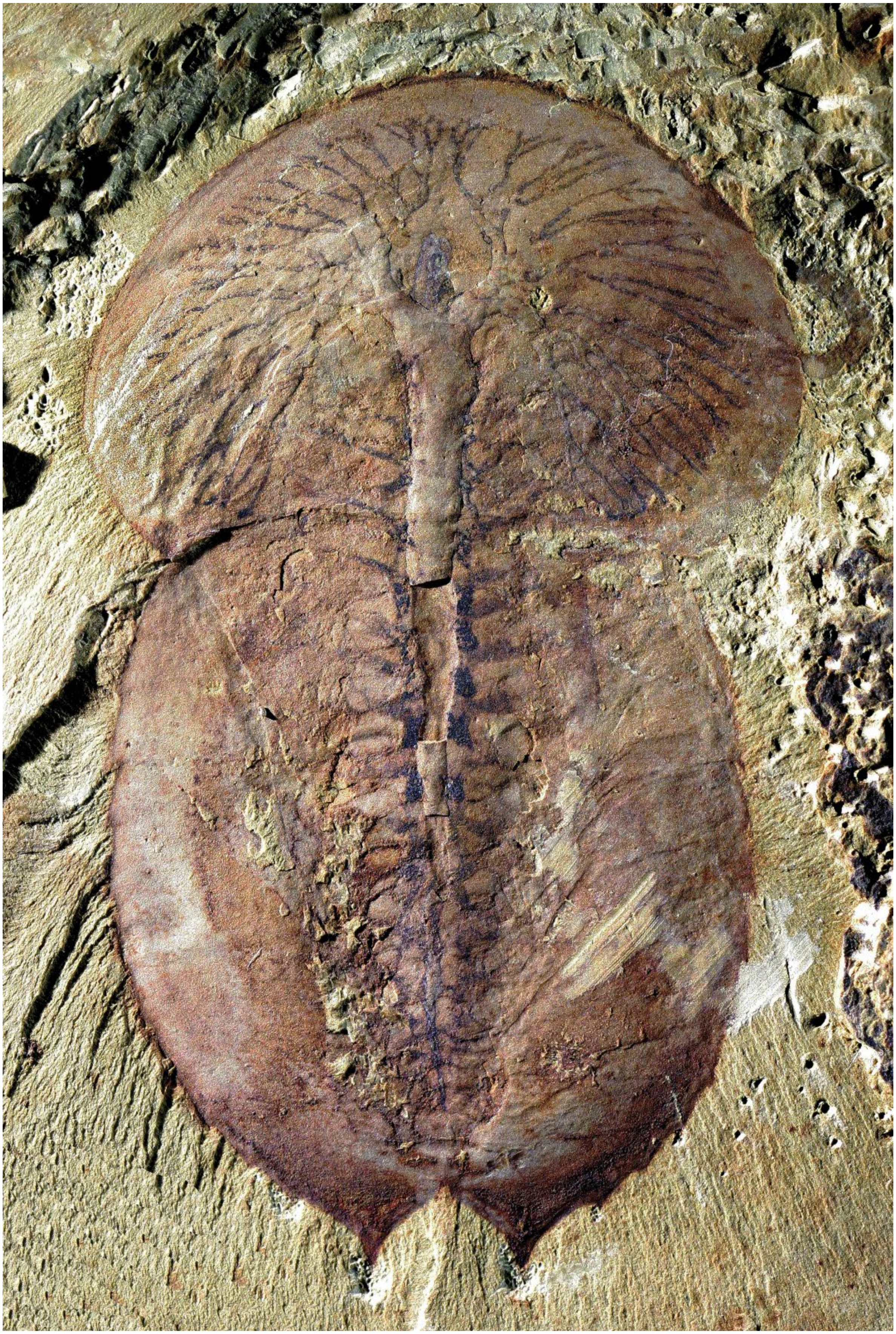
The Cambrian Fossils of Chengjiang, China

The Flowering of Early Animal Life



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The Flowering of Early Animal Life

Second Edition

Hou Xian-guang, David J. Siveter, Derek J. Siveter, Richard J. Aldridge, Cong Pei-yun, Sarah E. Gabbott, Ma Xiao-ya, Mark A. Purnell, Mark Williams

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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 subsquent 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

(Yunnan Institute of Geological Science, Kunming; *Cathaymyrus* and *Zhongxiniscus*); Andreas Maas and Dieter Waloszek (University of Ulm; *Vestrogothia*, number UB633, Steinmann Institute for Geology, Mineralogy and Palaeontology, Bonn University); Latha Menon (Oxford University; Ediacaran biota at Mistaken Point); Stewart Molyneux (British Geological Survey; Ediacaran acritarch); Ou Qiang (China University of Geosciences, Beijing; *Antennacanthopodia*); and Jean Vannier (Université Claude Bernard, Lyon; *Treptichnus*, *Protosagitta*, and *Cambrosipunculus*). In Figures 2.1 and 29.1 several of the silhouettes are reproduced from Phylopic.org, some under Creative Commons licences; credits: Noah Schlottman (Ctenophora), Michelle Site (Porifera, Entoprocta, Brachiopoda, Tardigrada, Nematomorpha, Hemichordata, Urochordata), Mali'o Kodis (Cnidaria), Bruno Vellutini (Priapulida), Caleb Brown (anomalocaridids), Ralf Janssen, Nikola-Michael Prpic, Wim Damen, Michael Keesey (Myriapoda), Hans Hillewaert (Pancrustacea, Echinodermata), 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 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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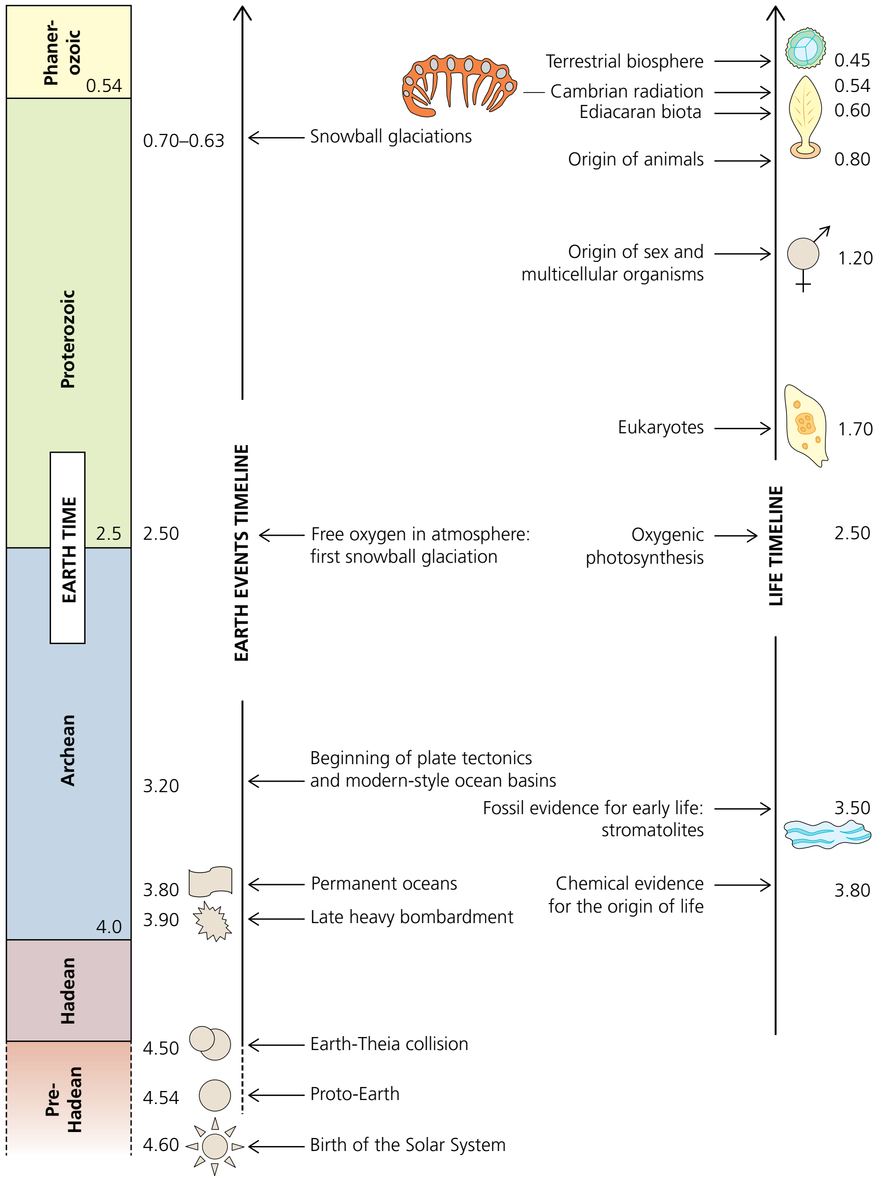
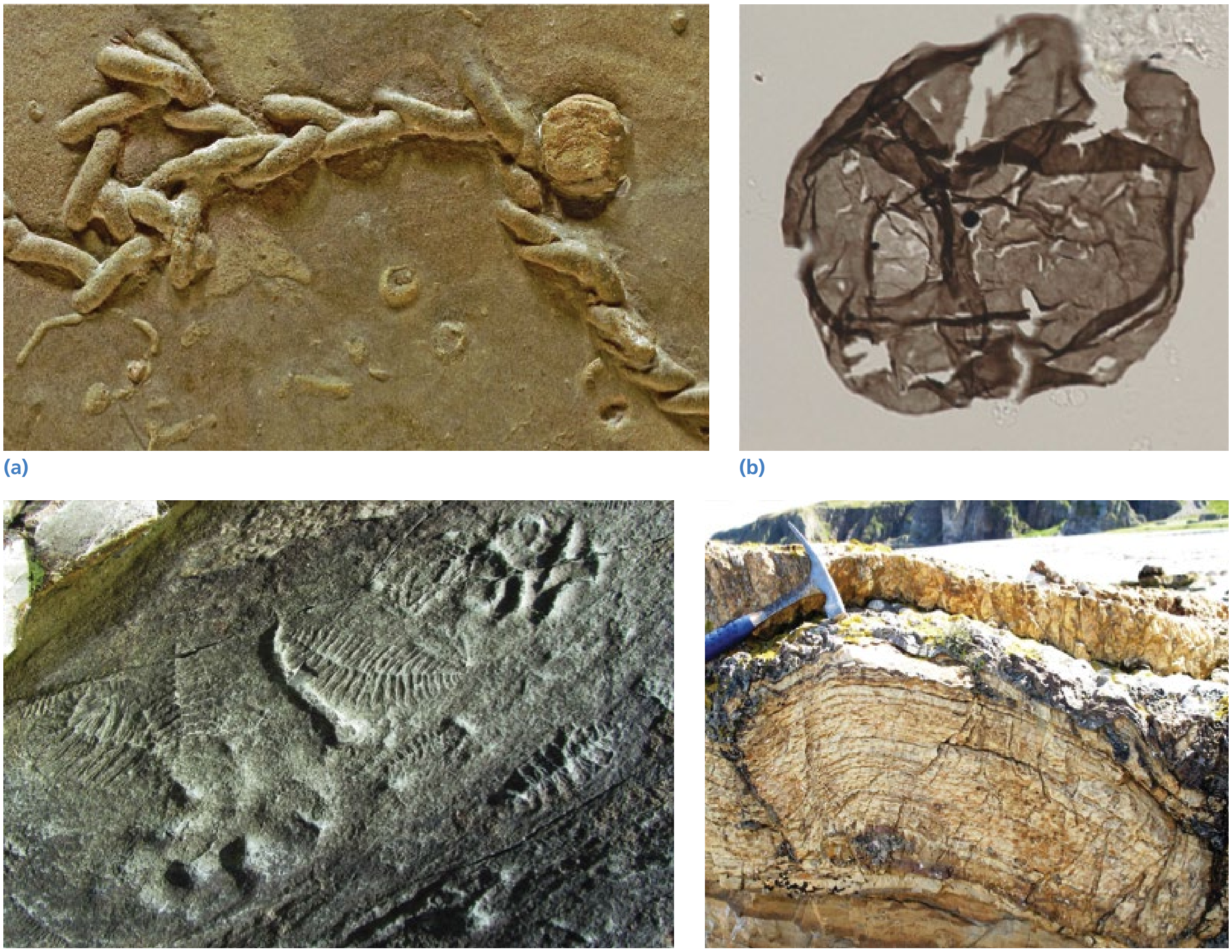


Figure 1.1 Some major events in the history of the Earth and early life.

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



(a) (b) (c) (d)

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.

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

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Figure 2.1 Phylogenentic 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

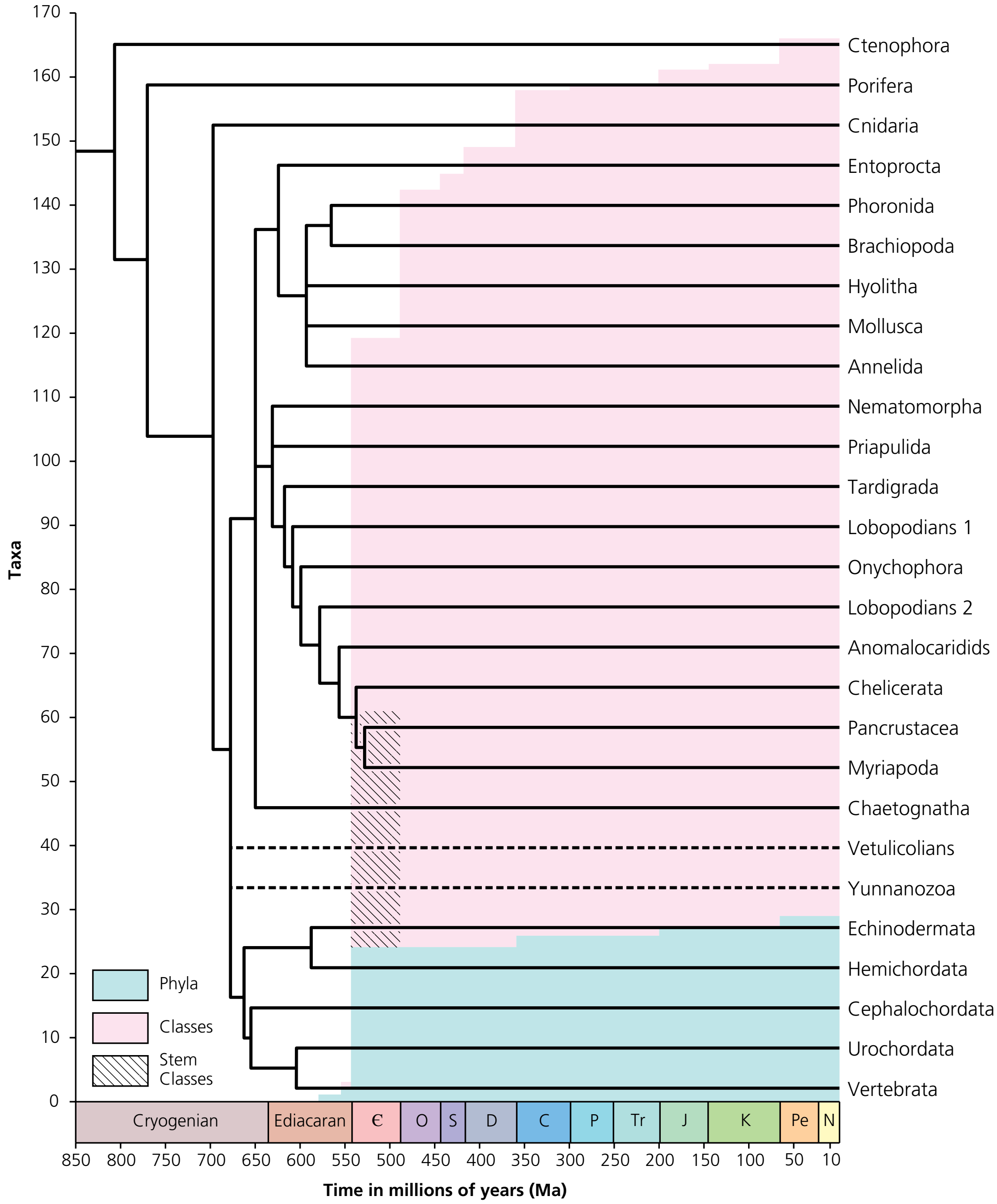


Figure 2.2 Time of origin of the major animal clades. The date of the branching points in the cladogram (hypothesis of relationships as in Fig. 2.1) is based on molecular clock analysis. The colored blocks show the establishment of anatomically distinct, higher level taxa (phyla and classes) as revealed 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. *Myllokunmingia*) 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

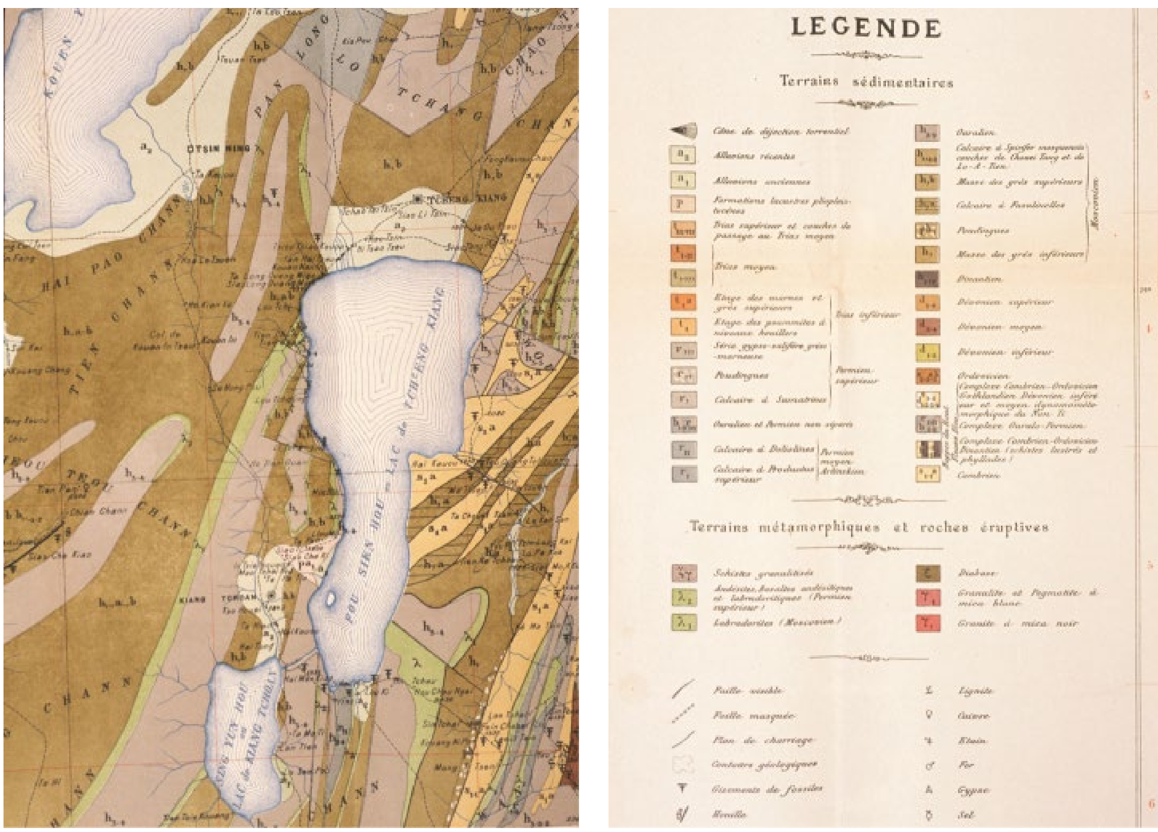
Almost 30 years after its discovery the Chengjiang fossil site was inscribed to the UNESCO World Heritage List at a meeting in St Petersburg in June 2012 (Fig. 3.1). The nominated property is a relatively small oblong area comprising about 512 hectares surrounded by a narrow buffer zone. Its western 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 badoriids (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).

The Cambrian Fossils of Chengjiang, China: The Flowering of Early Animal Life, Second Edition. Hou Xian-guang, David J. Siveter, Derek J. Siveter, Richard J. Aldridge, Cong Pei-yun, Sarah E. Gabbott, Ma Xiao-ya, Mark A. Purnell, Mark Williams.

Figure 3.1 The inscription of the Chengjiang fossil site to the UNESCO World Heritage List, at a meeting of the International Union for Conservation of Nature, St. Petersburg, 2012.



(a) (b)

Figure 3.2 **(a)** The geology of the Chengjiang area, as presented by the French pioneer geologists Deprat and Mansuy (from Deprat 1912). **(b)** Geology legend to the Deprat and Mansuy map.

(a) (b) (c)

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

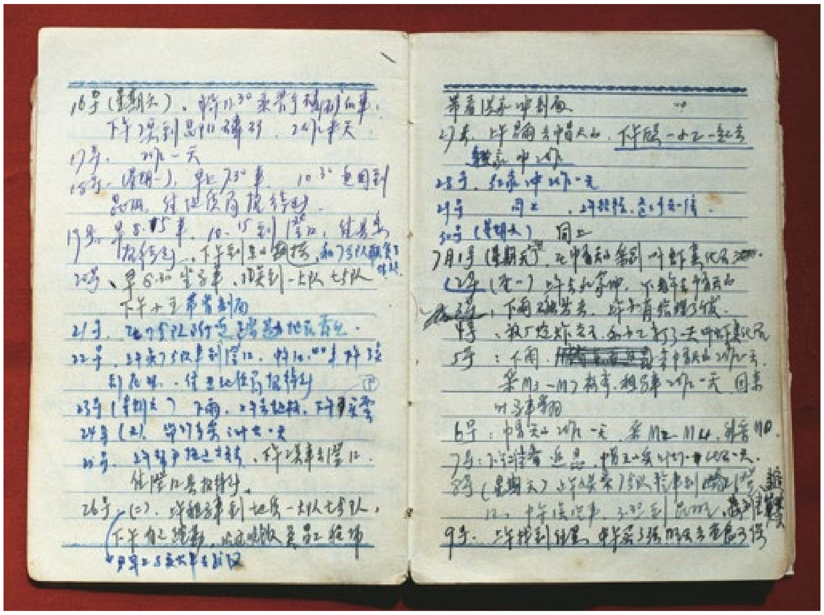
Figure 3.4 View, in 2006, from the lower Cambrian section at Hongjiachong, looking south to Fuxian Lake.

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

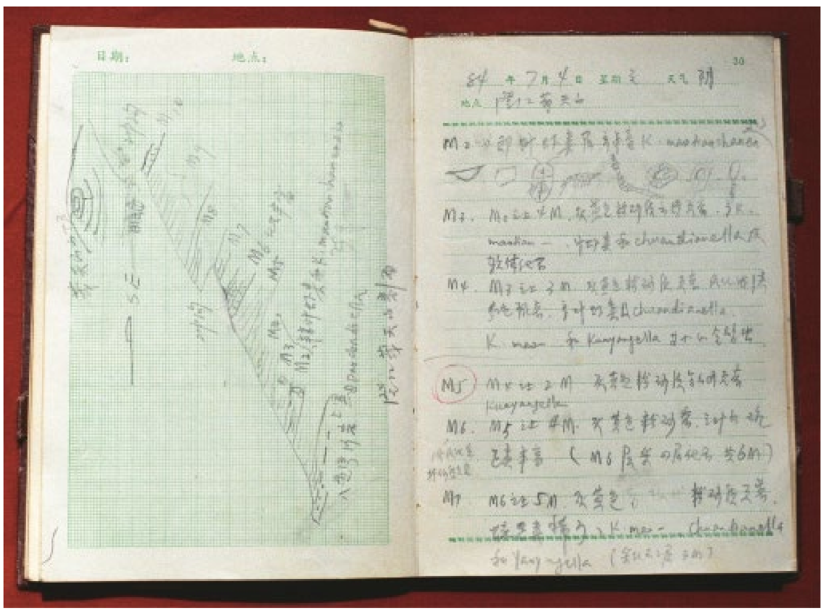
Work at Maotianshan was notably easier than at Dapotou and Hongjiachong, because the rock was more strongly weathered. Hou's field diary for Sunday 1 July 1984 signaled the significance of his discovery of soft-bodied fossils at Maotianshan by alluding to comparable material from the Burgess Shale: "The 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, Leanchoilia, 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

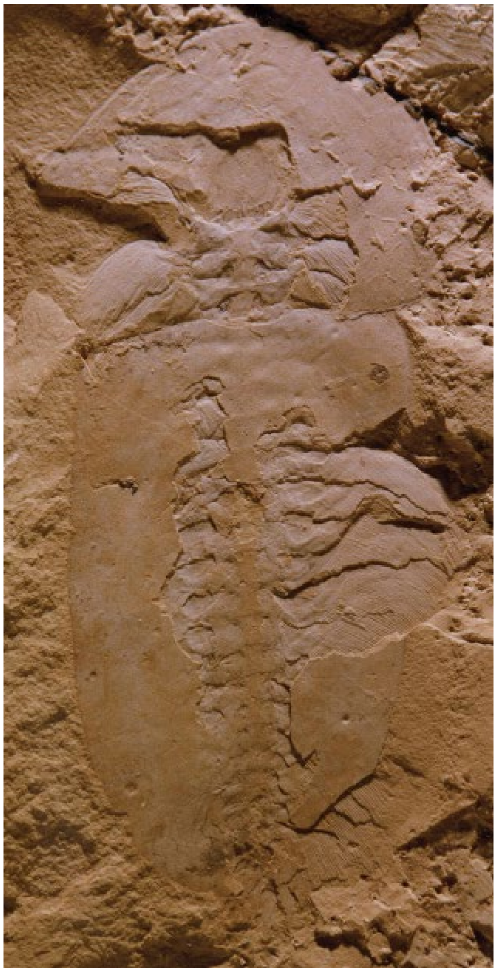


Figure 3.7 The specimen of the arthropod *Misszhouia longicaudata* (×2,8) that marked the discovery of soft-bodied fossils at Chengjiang.

references therein). Subsequent to the early phase of study, Chengjiang fossils have been found even wider afield in Yunnan Provence and also have been studied by Chinese paleontologists and other scientists from many countries, generating hundreds of publications. In particular, Chen Jun-yuan (formerly of Nanjing Institute of Geology and Palaeontology) and Shu De-gan (North-west University, Xian) and their collaborators made considerable additions to the literature on the biota (see References). Furthermore, the discovery and description of abundant lower Cambrian soft-bodied fossils from exposures at Ercaicun, Mafang, and other localities in the Haikou area (Fig. 3.10), to the west of Dianchi Lake, southwest of Kunming, confirmed that the Chengjiang Lagerstätte occurs across a sedimentary basin covering thousands of square kilometers (see Fig. 4.3). In addition to the Yunnan Key Laboratory for Palaeobiology at Yunnan University, fossils of the Chengjiang Lagerstätte are on display locally in the Chengjiang County Museum, Chengjiang (Fig. 3.11), and at the field station at Maotianshan (Fig. 3.12). There is also a representative exhibition in Yuxi City Museum, and plans are in place for a new purpose-built museum, to be sited near the northern shore of Fuxian Lake, which will focus on the Chengjiang biota.

Many methods and techniques are used to reveal the anatomy and paleobiology of Chengjiang fossils. Most Chengjiang fossils are preserved as flattened part and counterpart specimens, though slight three-dimensional preservation is not uncommon, particularly of parts of the digestive system. Mechanical preparation under a binocular microscope using fine needles is the normal method employed to clean away the clay-rich sedimentary matrix from the fossils. This simple but skillful and time-consuming work is essential in revealing important

Figure 3.8 Transporting fossils in 1989 near Fengkoushao.

Figure 3.9 Collecting at Haikou, Kunming in 2015.

Figure 3.10 Collecting at Ercaicun, Haikou, Kumming in 2001. This locality has yielded the world's oldest known vertebrate specimens.

Figure 3.11 Part of the exhibition of the Chengjiang biota at Chengjiang County Museum.

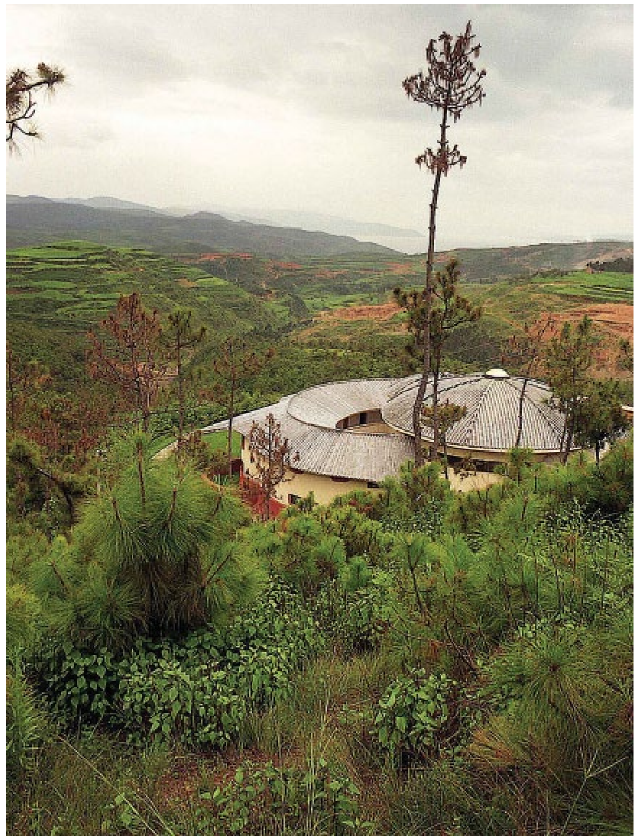


Figure 3.12 The geological field station at Maotianshan, with Fuxian Lake in the distance.

anatomical details such as the appendages of arthropods. Elemental mapping is typically undertaken by energy-dispersive X-ray within a scanning electron microscope (see Fig. 5.2). That method, combined as necessary with microstratigraphic data from millimeter-scale logs of cores, yields the composition of the host sediment and the fossils, in addition to elucidating the key taphonomic pathway(s) of the Chengjiang biota (e.g., Gabbott *et al.* 2004; Gaines *et al.* 2008, 2012a). The innovative use of X-ray computed tomography and elemental analysis on specimens preserved with weak three-dimensionality has furnished especially important morphological results and interpretations, with bearings on phylogenetic relationships and evolution, as, for example, in the reconstruction of the paleobiology of arthropods (e.g., Tanaka *et al.* 2013; Cong *et al.* 2014; Liu Yu *et al.* 2015), and the sclerotome of chancelloriid-like metazoans (Hou *et al.* 2014).

Incident light and polarized light macrophotography (e.g., see Siveter 1990) is the method generally used to secure images of Chengjiang fossils. Fluorescence microscopy has also been used for image capture (e.g., Liu Yu *et al.* 2014). In some cases the specimen is immersed in a liquid such as ethanol to enhance the oxidized fossil against the typically yellowish-colored rock matrix.

4 The Distribution and Geological Setting of the Chengjiang Lagerstätte

Paleogeographical Setting

The geography of the Cambrian world was very different from that of the present, and was dominated by Gondwana, a supercontinent that united present-day South America, Africa, Antarctica, India and Australia, and which straddled southern latitudes from the geographical South Pole to the northern hemisphere tropics (Fig. 4.1). To the north and west of Gondwana lay, from west to east, the ancient continents of Laurentia (modern North America), Baltica (modern Scandinavia), Siberia, North China, and South China. South China formed a discrete continental block, situated to the west of the Gondwana supercontinent – possibly adjacent to its Indian segment, and within the northern subtropics (Cocks & Torsvik 2013). Three sedimentary provinces have been identified within the South China continent during the Cambrian (Zhang Wen-tang *et al.* 2003), from northwest to southeast these being the Yangtze Platform, the Jiangnan Belt, and the Southeast China Fold Belt. The Yangtze Platform extended from the area of modern Shanghai in the northeast, to the Kunming area of Yunnan Province in the southwest (Fig. 4.2). During the Cambrian the geography of this sedimentary basin was associated with small land areas and extensive epicontinental seas, with carbonate and clastic platforms to the northwest, and mudstone deposits of the deep shelf to basin slope to the south and east. It is within the clastic deposits of the shelf platform of the south-western Yangtze Platform that the Chengjiang biota is located.

Localities with exceptionally preserved Chengjiang biota are known from several areas across central and eastern Yunnan (Fig. 4.3), encompassing Chengjiang, Jinning, Anning, Wuding, Yilang, Malong and Qujing counties and the Kunming District (Steiner *et al.* 2005; Zhang Xing-liang *et al.* 2008). However, the best-preserved fossils and most productive exposures are those of Chengjiang County to the east of the eponymous county town (e.g., Maotianshan, Ma'anshan, and Xiaolantian), and localities to the west of Dianchi Lake, as at Ercaicun, Jianshan, and Mafang in the Haikou area.

Stratigraphical Context

The fossils of the Chengjiang biota occur in mudstones of the Yu'anshan Member, Chiungchussu Formation, which falls within the *Eoredlichia-Wuyangaspis* trilobite biozone, Nangaoan Stage, of the early Cambrian (Figs 4.4 and 4.5). At outcrop the Yu'anshan Member deposits weather to a buff yellow color, but in fresher, borehole material the mudstones are gray to dark gray. The color alteration from gray to yellow is a consequence of recent weathering, which has oxidized much of the organic carbon and iron sulfides. Strata of the lower Cambrian are well developed in eastern Yunnan, and sedimentary deposits of equivalent age to the Chengjiang biota are extensively distributed. Common macrofossils in these deposits are trilobites and other arthropods.

The Yu'anshan Member is informally divided stratigraphically into four lithologically and paleontologically distinctive parts (Zhu *et al.* 2001). The lowermost strata comprise dark-gray siltstones that contain the earliest trilobites in the Cambrian of eastern Yunnan, together with the bradoriid arthropods *Hanchiangella*, *Liangshanella*, and *Nanchengella*. These sedimentary deposits fall within the *Hupeidiscus-Sinodiscus* trilobite biozone of South China (Figs 4.4 and 4.5). Above this lithological interval, black siltstones and mudstones yield trilobites such as *Tsunyidiscus* and *Wutingaspis*, and the bradoriids *Hanchungella* and *Emeillopsis*, with trilobites and bradoriids being the dominant fossils. Stratigraphically above, at outcrop, are yellowish green mudstones interbedded with thin-to-medium

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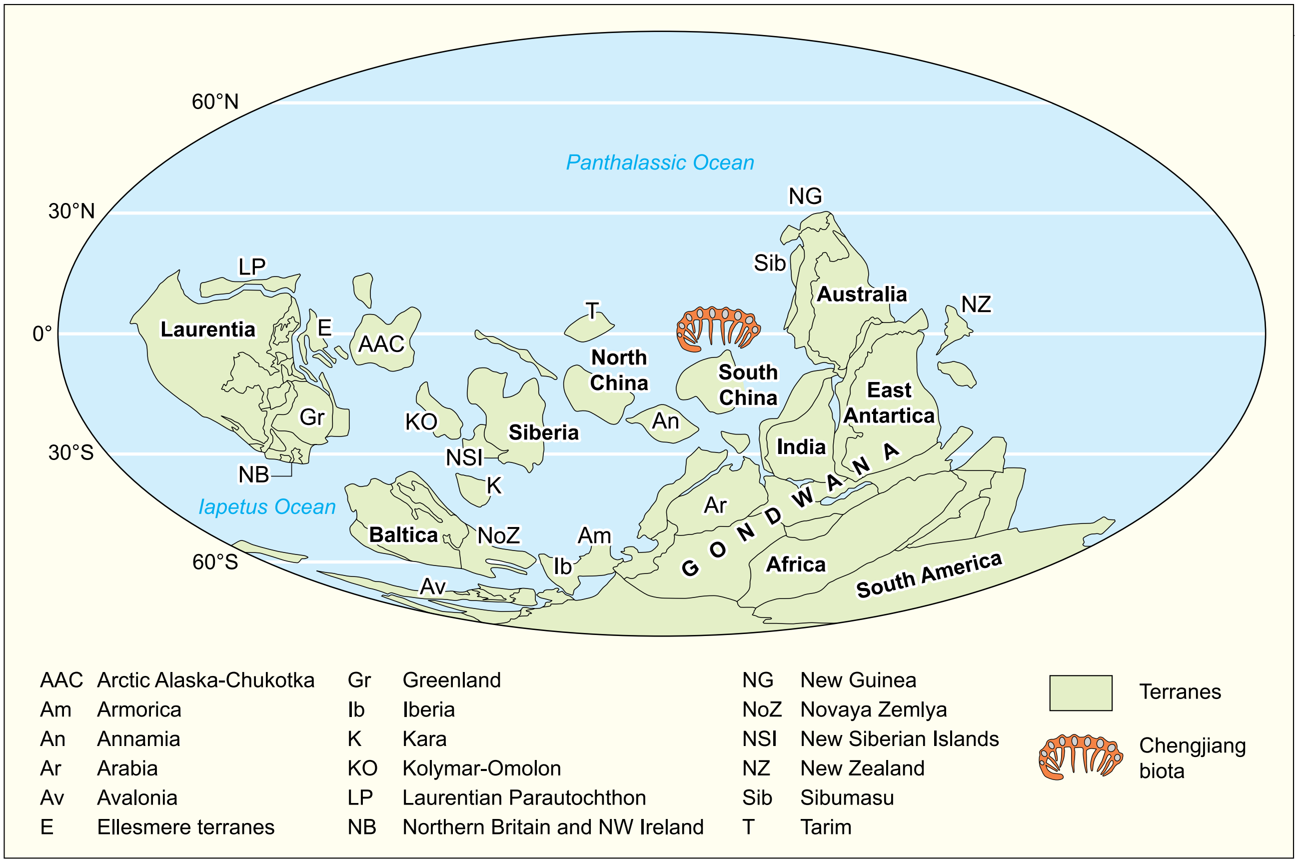


Figure 4.1 Distribution of terranes in the early Cambrian (520 Ma) (modified from Torsvik & Cocks 2013). The Chengjiang biota is on the South China microplate.

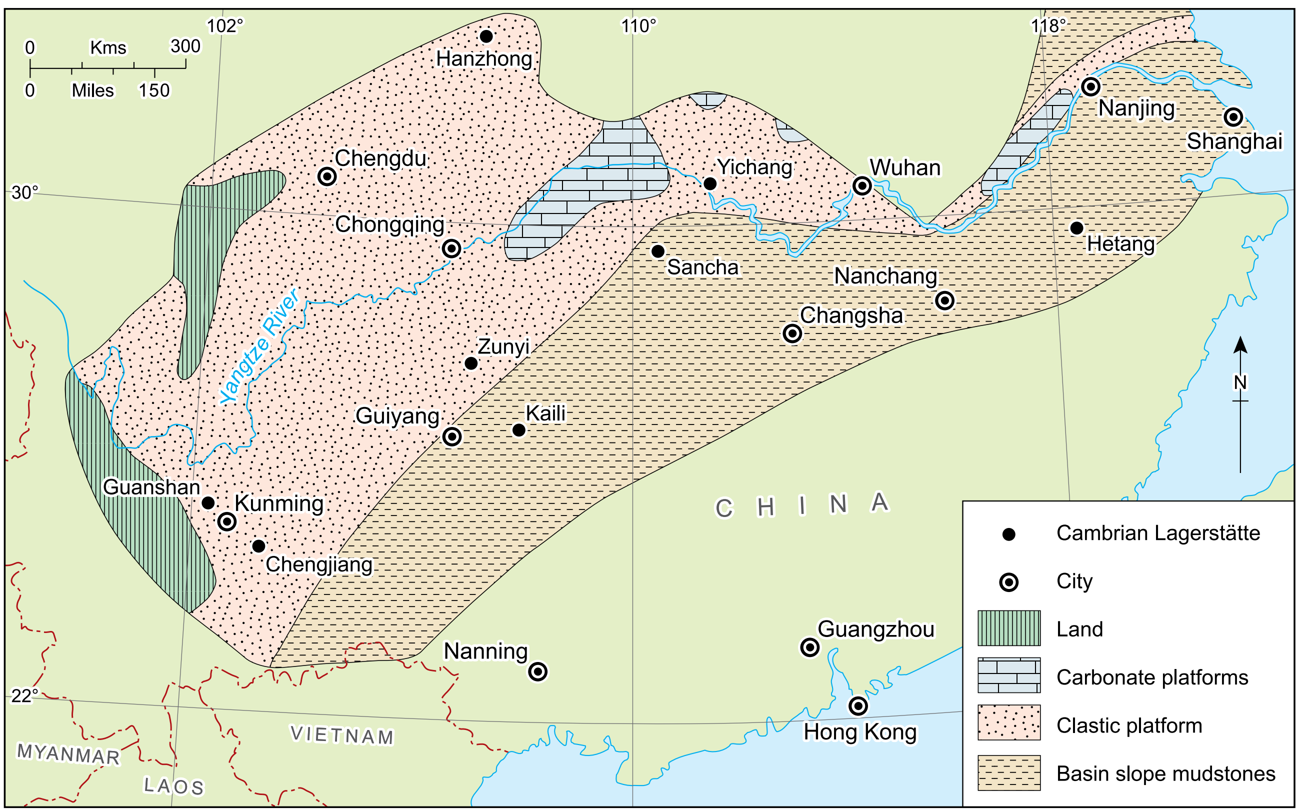


Figure 4.2 Distribution of sedimentary facies and Lagerstätten of the Yangtze Platform of south China during the early Cambrian (modified from Zhang *et al.* 2008).

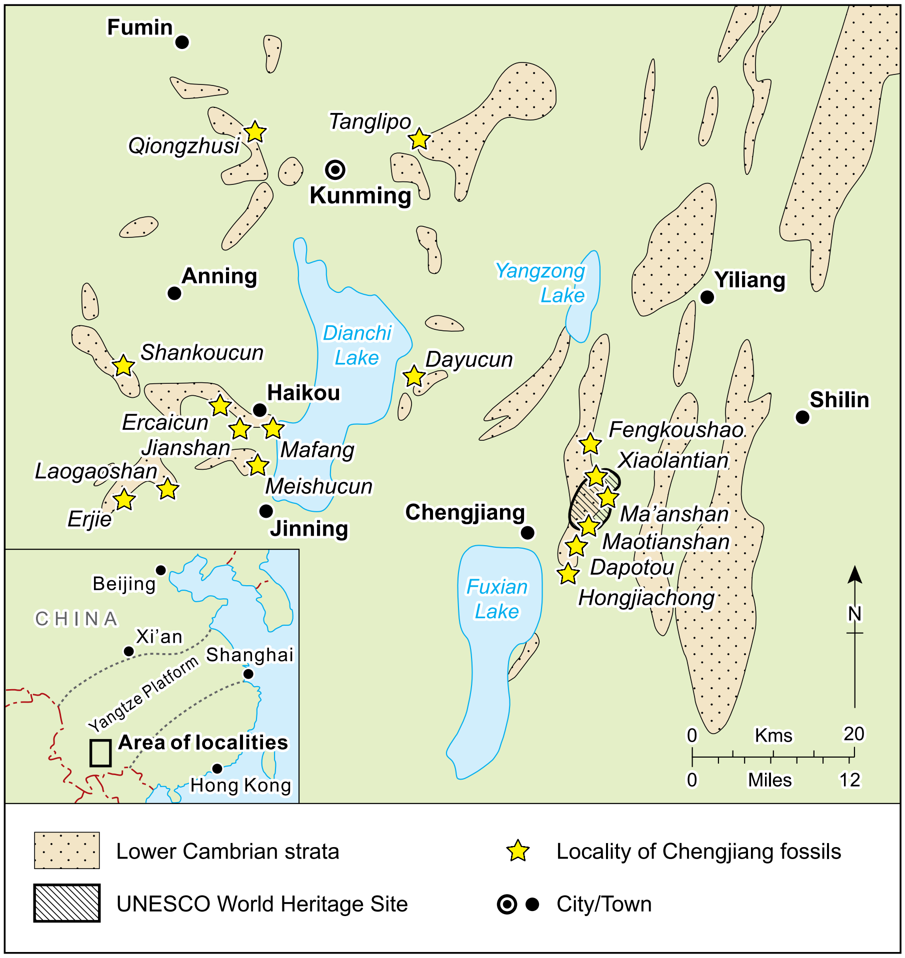


Figure 4.3 Distribution of the main localities of the Chengjiang biota and the Chengjiang Fossil World Heritage Site, Yunnan Province (modified from Zhu *et al.* 2001 and Hu 2005).

(10–20 cm) siltstones and sandstones. These represent the main strata yielding soft-bodied fossils. There are diverse arthropods, such as *Naraoia*, *Leanchoilia*, *Isoxys*, *Kunmingella*, *Eoredlichia*, and *Yunnanocephalus*. This part of the Yu'anshan Member is also rich in lobopodians, eldoniids, worms, and sponges and is 40–50 m thick. At the top of the Yu'anshan Member there are some 113 m of yellow silty sandstone that contains a reduced diversity Chengjiang biota, mainly of trilobites such as *Eoredlichia* and *Yunnanocephalus*, and less commonly *Chengjiangaspis*, bradoriids such as *Kunmingella*, and the brachiopods *Lingulella* and *Lingulepis*. The upper two sedimentary intervals of the Yu'anshan Member also correlate to within the *Ushbaspis* trilobite of South China (Fig. 4.4).

Sedimentology

Broadly, the environment of deposition for the sedimentary deposits hosting the Chengjiang biota was a shallow, gently eastwardly sloping epeiric shelf filled with muds and sands (Hu 2005; Zhang Xing-liang *et al.* 2008). This basin was subject to occasional storm influence. An alternative hypothesis for the depositional environment invokes a tidal setting and is based on the occurrence of light-dark couplets of mudstone on a millimeter scale that may show periodicity (Babcock *et al.* 2001; Zhang Xing-liang *et al.* 2001). However, there is little evidence to support this, and a marine basin influenced by occasional storms is now regarded as the favored model.

To the eye, the main sedimentary host rocks of the Chengjiang biota appear to be fairly uniform, though subtly striped (Fig. 4.6). But under a hand lens a number of distinctive types of layers are revealed. Thin to moderately thick siltstone and claystone beds form the bulk of the fossil-bearing rock, and these can be subdivided into two types of distinct layers. The so-called background beds dominantly comprise organic-rich laminae containing abundant organic debris, particularly algal fragments, fecal strings, small shells, and animal exuviae (Chen Jun-yuan & Erdtmann 1991; Chen Jun-yuan *et al.* 1996; Hu 2005; Steiner *et al.* 2005). There are some more silt-rich laminae within the background beds and bioturbation may be developed but is weak. These sedimentary layers

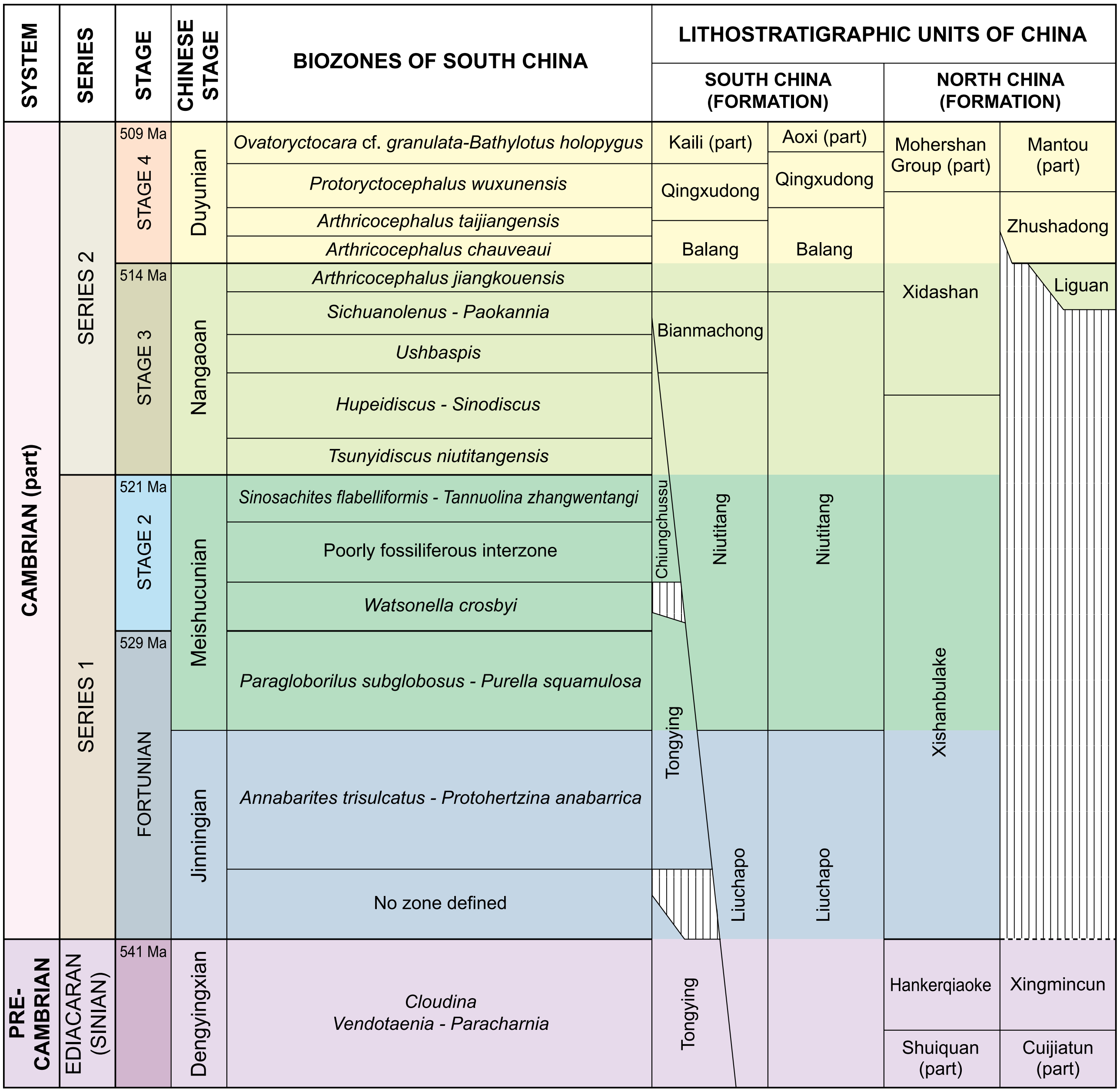


Figure 4.4 Upper Precambrian to lower Cambrian stratigraphy of China (modified from the National Commission on Stratigraphy of China 2015).

reflect slow accumulation over years or even hundreds of years (Hu 2005). Their precise genesis has yet to be explored and they have been variously interpreted as hemipelagites or storm-generated distal nepheloid plumes (Hu 2005). In contrast the so-called event beds when interbedded with the background beds have a sharp base with occasional sole marks or other erosional sedimentary structures (Zhu *et al*. 2001). These beds may occasionally show normal grading but because their grains are so fine the beds are usually structureless (Hu 2005). Their contact with the overlying background beds is usually gradational and irregular and they most often form couplets with the background beds. It is within these beds, each of which is thought to represent a single event, that most of the exceptionally preserved fossils occur. Chaotic orientations of contained fossils also evidence a single event. The event beds are thought to represent distal mud tempestites, where each bed is deposited under storm influence and represents a single depositional event of hours or days in duration (Hu 2005).

The so-called event beds and background beds capture the broad pattern of sedimentology for the Chengjiang biota (Fig. 4.6). However, within these units there is more complexity, and a full description and elucidation of the details of Chengjiang shale sedimentology is awaited.

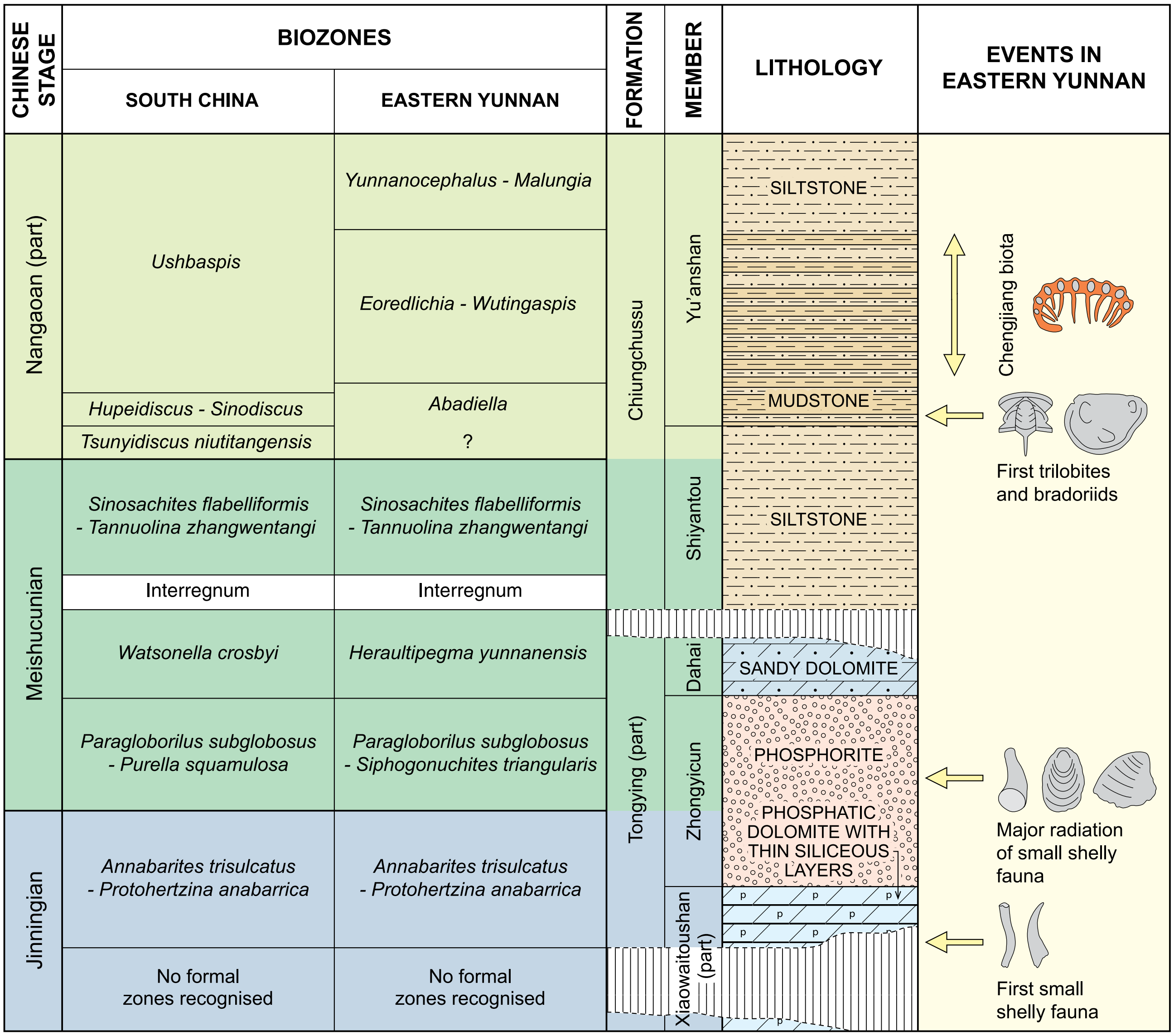
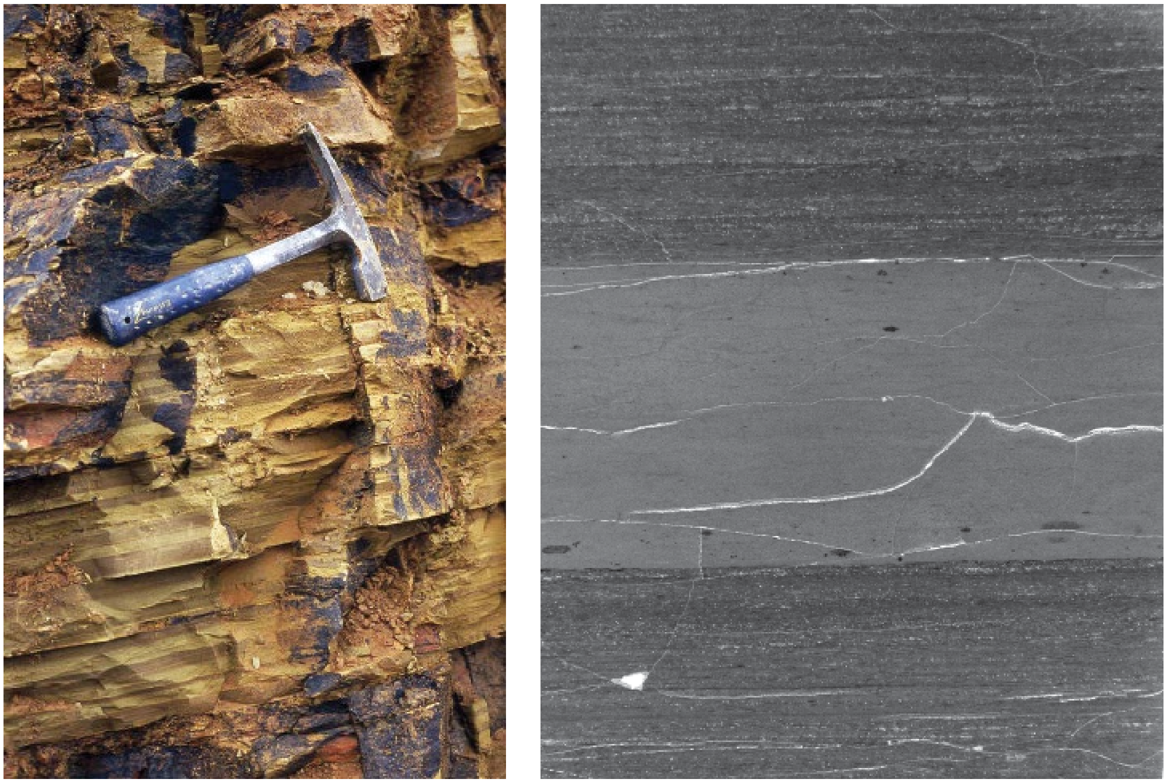


Figure 4.5 Lower Cambrian stratigraphy of eastern Yunnan, showing the position of the Chengjiang biota and other faunal events (modified from the National Commission on Stratigraphy of China 2015).



(a) (b)

Figure 4.6 Sedimentary deposits associated with the Chengjiang biota. **(a)** A typical exposure of the Yu'anshan Member, showing bedding; Maotianshan. **(b)** A photomicrograph of a thin section showing an event bed (1 cm thick) in the center with background beds above and below.

5 The Taphonomy and Preservation of the Chengjiang Fossils

The remarkable quality and fidelity of preservation of Chengjiang fossils can be seen, for example, in the morphology of the proboscis and gut in worms such as *Cricocosmia* and *Palaeopriapulites*, the details of appendages in arthropods such as the bradoriid *Kunmingella*, the complex alimentary system in the arthropod *Naraoia*, and the delicacy of the supposed gills in the enigmatic *Yunnanozoon* (Fig. 5.1). Vertebrates, such as *Myllokunmingia,* preserve gills, serial structures interpreted as myomeres and gonads, and structures within the head. This quality of preservation enables us to investigate the anatomy of early animals on the basis of exceptional evidence. However, hand-in-hand with interpretation of fossil anatomy must be an understanding of the taphonomy of each individual fossil and, on a broader scale, the rock deposit as a whole.

Taphonomy, the study of the physical, biological, and chemical processes that occur from the death of an organism through to discovery of a fossil, involves consideration of transport, decomposition, burial, and diagenesis. Understanding taphonomy is especially important where soft-bodied remains are concerned because although exceptionally well preserved, such fossils have been modified from how they appeared in life. Most obviously, the majority of fossils occurring in sediments are almost completely two-dimensional and this transformation generally occurs very rapidly after death as the tissues decay and collapse. Determining the nature and sequence of that loss, in particular by experimental decay of animals in laboratory conditions, is extremely important for anatomical and phylogenetic interpretation (e.g., Briggs 1995; Sansom *et al*. 2010b). Broadly speaking, soft-tissue remains of animals in the marine fossil record occur as either organic remnants, or are mineral replacements of the soft tissues, or both (Briggs 2003).

Most of the exceptionally preserved fossils in the Chengjiang biota are found in so-called event beds, and most occur parallel to lamination surfaces (see Fig. 4.6), although some retain low three-dimensional relief and chaotic orientations also occur. Because fossils in the event beds come to rest with their flattest surface parallel to bedding, it has been suggested that transport was, at least at times, relatively gentle (Hou *et al*. 2004a; Zhang Xi-guang & Hou 2007). As well as the generally well-articulated nature of most Chengjiang fossils, there are several fossil associations that suggest minimal transport, such as both adult and juvenile *Fuxianhuia* occurring in close proximity. Conversely, other bedding planes do contain size-sorted taxa such as *Leanchoilia* and *Yunnanocephalus*, suggesting concentration events and some transport (Zhang Xi-guang & Hou 2007). A comprehensive investigation of the sedimentological and quantitative taphonomic analyses of both background and event beds in the Chengjiang biota reveals that in general lateral transport seems to have been limited, and that fossil communities therefore likely reflect accurately *in vivo* communities. The event beds, showing minimal post-mortem transport or decay bias, are considered to capture a more accurate representation of the living community than the background beds (Zhao Fang-chen *et al.* 2009, 2012).

The laminated so-called background beds (see Fig. 4.6) are typically characterized by preservation of organic hash and poorly preserved disarticulated arthropod and sponge remains (Zhao Fang-chen *et al.* 2009). In many cases fossils in the background beds show evidence of decay; for example, nearly all priapulids in these layers lack their proboscis even though their guts are preserved, demonstrating they are not molts (Hu 2005). Mass occurrences of the bradoriid *Kunmingella* in butterfly orientation – with valves agape – are common in the background beds, and are thought to reflect time-averaged assemblages. Despite the fact that the background beds generally yield poorly preserved, more cuticular material, some of the most spectacular examples of soft part preservation in the fossil record have been recently discovered in these units,

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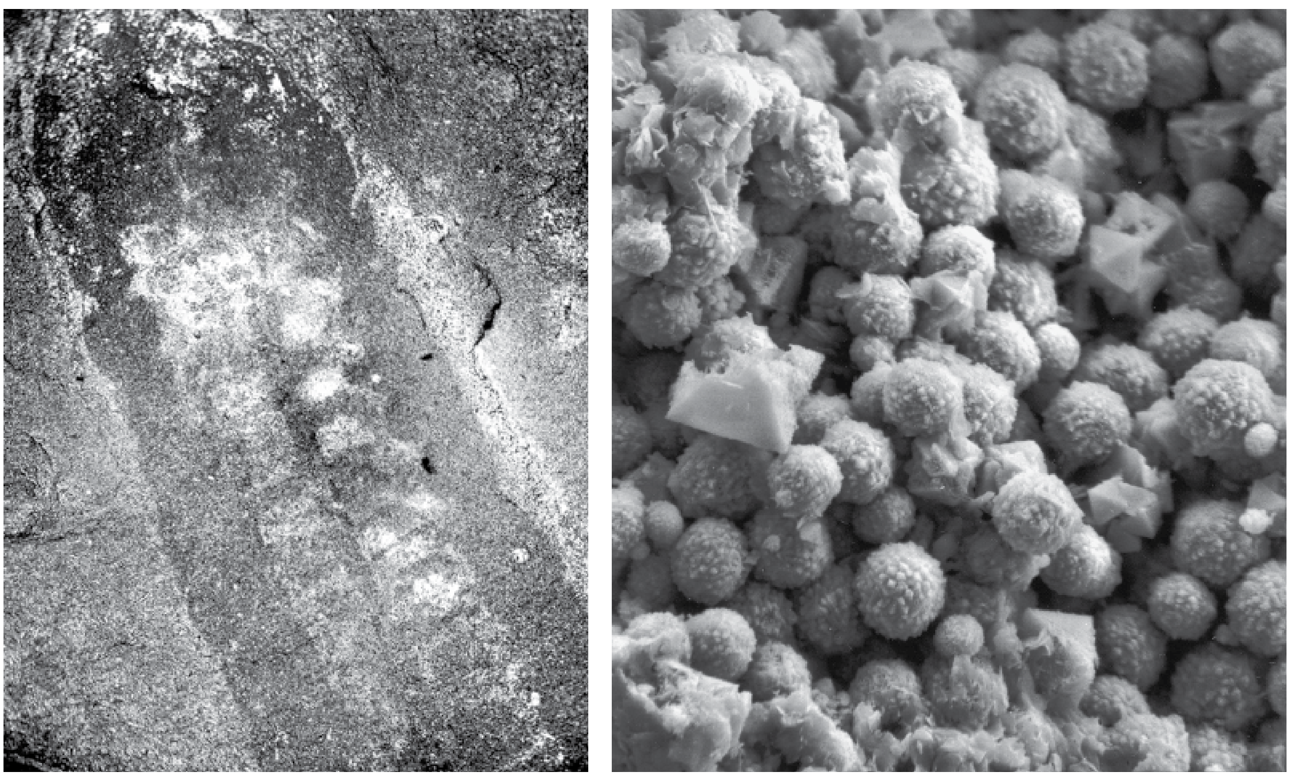
Figure 5.1 Examples of the fidelity of preservation of Chengjiang fossils. **(a)** *Kunmingella douvillei*, dorsal view of posterior part of an open carapace with appendages, RCCBYU 10258, ×19.0; Ercaicun, Haikou, Kunming. **(b)** *Naraoia spinosa*, dorsal view of cephalic area with cheek diverticulae, YKLP 13803, ×4.3; Ercaicun, Haikou, Kunming. **(c)** *Yunnanozoon lividum*, lateral view showing detail of anterior arches with gills, RCCBYU 10310, ×6.6; Ercaicun, Haikou, Kunming. **(d)** *Fuxianhuia protensa*, showing head region with paired eyes, an antenna, brain, optic capsule, and optic neuropils, YKLP15006, ×7.7; Mafang, Haikou, Kunming.

including aspects of the cardiovascular system, such as the heart and arteries of the arthropod *Fuxianhuia protensa* (Ma *et al*. 2014b). In the same taxon (Ma *et al.* 2012b), and in the great appendage arthropod *Alalcomenaeus* (Tanaka *et al*. 2013), and in an anomalocaridid (Cong *et al*. 2014) aspects of the central nervous system and brain are preserved. Here, remarkable preservation of soft tissues is revealing anatomical details of arthropods that were previously only known from extant material.

Upon death, the usual fate of soft-bodied animals is that they are scavenged upon and then any remains are rapidly decomposed by enzymes within the tissues or by bacteria. In the Chengjiang biota rapid burial in event beds may have protected carcasses from scavenging, and in the early Cambrian the diversity and complexity of burrowing organisms may have been less than after the Cambrian (e.g., Allison & Briggs 1993; Orr *et al*. 2003). However, perhaps more important in prohibiting bioturbation was sustained anoxia in the sediment, which established conditions therein that were inhospitable to scavenging animals. That the Chengjiang lithology comprises continuous laminations and that soft-bodied fossils are never found alongside evidence of burrowing suggests that bioturbators were prohibited from churning through the sediment. The dark-gray to almost black color of the rock when fresh attests to the presence, at least intermittently, of a low oxygen or completely anoxic environment, although oxygenated bottom waters also occurred (Forchielli *et al.* 2014). However, anoxia cannot stop the destructive march of enzymes and bacteria. Something else had to occur in order for the organic tissues of Chengjiang carcasses to bypass the normal process of being recycled. The processes responsible are complex and remain controversial.

Nearly all examples of published Chengjiang fossils are from the surface or subsurface, from sedimentary layers that have been subjected to extensive weathering. That both sedimentary rocks and fossils have been altered from their fresh state makes comprehensive taphonomic analyses difficult. Chemical analyses have recorded a variety of modes of preservation of soft parts. Most commonly they occur as thin organic carbon films and also as iron oxides (Gabbott *et al.* 2004; Zhu *et al.* 2005). The carbonaceous films may appear black when fresh, but as weathering progresses these films lose their carbon (Forchielli *et al.* 2014) and take on a whitish and ghost-like appearance. The iron minerals associated with the fossils have crystal morphologies that demonstrate they were precipitated as pyrite (fool's gold; Fig. 5.2), partially coating some of the organic tissues (Gabbott *et al.* 2004). Subsequent weathering of the pyrite formed iron oxides. It is the association of iron oxides with fossils that produces the characteristic aesthetically attractive and highly distinctive red and orange hues of the Chengjiang biota (Gabbott *et al.* 2004). This accounts for why Chengjiang fossils look different from other Cambrian, mudstone-hosted, exceptionally preserved sedimentary deposits, which all effectively share carbonaceous films as the dominant mode of preservation (Gaines *et al.* 2008). As well as these modes of preservation, instances of authigenic iron-rich clay minerals and calcium phosphate have been recorded (Zhu *et al.* 2005).

Whilst the role of iron in Chengjiang fossil preservation is not yet fully understood, the retention of organic films is perhaps even more of a conundrum. This style of preservation, of organic biomolecules as films less than 1 micron thick in marine clastic rocks – the so-called Burgess Shale-type preservation – is typified by whole assemblages of refractory and labile tissues displaying precise anatomical detail (Butterfield 1990; Gaines 2014). It has now been recorded from most Cambrian marine mudstone Lagerstätten, such as the Sirius Passet biota of Greenland, the Kaili Formation of Guizhou Province, China, and from various black mudstones in the United States such as the Marjum, Spence and Wheeler formations of Utah. Carbonaceous preservation does occur throughout the fossil record but after the Cambrian typically only selected, more refractory tissues, such as graptolite periderm, algae, or eurypterid cuticle is preserved (Butterfield 1990; Gaines 2014). Any explanation of this preservation mode must



(a) (b)

Figure 5.2 The Chengjiang vermiform species *Cricocosmia jinningensis*. **(a)** Scanning electron microscope back-scattered image of anterior region showing the body margins and sclerites, evident as bright areas, composed of iron oxides, RCCBYU 10340, ×18.0; Haikou, Kunming. **(b)** Iron oxides associated with the body margin showing typical framboidal texture, RCCBYU 10340, ×2200; Haikou, Kunming.

therefore also account for its dominantly Cambrian occurrence (Allison & Briggs 1993; Butterfield 1995): most such deposits occur in the early and middle Cambrian (Series 2 and 3), although some are in the late Cambrian (Series 4) and early Ordovician (Van Roy *et al*. 2010; Gaines 2014).

There is a stream of theories to explain how organic biomolecules can survive the process of decomposition (e.g., Butterfield 1995; Petrovitch 2001). Anoxia may slow down decay but it is insufficient to halt it as many bacteria and the enzymes in the tissues themselves still work well in oxygen-deficient environments. An idea that is gaining ground, because it is supported by multiple lines of evidence and can account for the time-restricted nature of the Burgess Shale-type preservation, is that the seafloor was rapidly sealed by calcium carbonate, effectively entombing carcasses and retarding decay. In this model rapid cementation at the seafloor prohibited bacteria from sourcing oxidants required to decompose organic matter (Gaines *et al*. 2012b). Rapid carbonate precipitation requires an alkaline ocean. This was possibly the result of chemical weathering of massive tracts of the then recently exposed reactive continental crust (Peters & Gaines 2012).

Whatever the precise mechanisms for preservation, the range of tissues preserved in the Chengjiang biota is impressive. Non-mineralized anatomy ranges from fairly tough organic material, such as chitin in arthropods, through to tissues that decay rapidly after death such as the heart, liver, and even nerve tissue and cardiovascular circulatory structures. These tissues are extremely labile and their preservation attests to the ability of the Chengjiang environment to capture precise details of animal anatomy. However, whilst the organic remains of fossils in the Chengjiang biota are well preserved, their original, biomineralized hard part component (shelly material) is lost to the fossil record. For example, the silica of sponges and the calcium carbonate or calcium phosphate shells of brachiopods occur as molds within the sediment. The extensive weathering of the deposit is the likely cause, especially because where iron sulfide (pyrite) is oxidized to form iron oxides sulfuric acid is produced and this may have contributed to the dissolution of biominerals.

6 The Paleoecology of the Chengjiang Biota

Paleoecological investigations can be undertaken on a single species, or they may examine the interactions of animals and plants that are preserved as fossil communities. One of the central goals of such paleoecological studies is the interpretation of where fossils lived in their environment and how they fed. Paleontologists use multiple sources of evidence to reconstruct the paleoecology of an individual animal and the interactions of that animal within its community. The exceptionally well-preserved fossil biota of Chengjiang provides one of the most important windows on the complexity of the ecosystem involving early metazoans (Vannier 2009).

Assemblages of fossils, even if exceptionally well preserved like that of Chengjiang, will likely not reflect the original composition of the fauna. This is in part because some organisms may end up being transported to or from the assemblage by marine currents. Furthermore, different organisms have different degrees of preservation potential. Paleoecological studies can determine, through quantitative detailed studies, to what extent fossil assemblages represent original communities. Arthropods dominate the Chengjiang biota, comprising more than one-third of species, followed by sponges and priapulid worms and relatives, each representing some 10% of species (Fig. 6.1). Following preliminary paleoecological studies (e.g., Dornbos & Chen 2008) the most detailed investigation to date uses some 10,000 fossil specimens collected from Mafang (Zhao Fang-chen *et al*. 2014a) from a narrow 2.5-meter interval of rock that comprises couplets of so-called event beds and background beds (see Chapter 4). The fossils recovered suggest that a single recurring marine community is preserved through the original sediment layers in the section, though it is uncertain exactly how much time is represented by the rock interval. In the slowly deposited background sedimentary deposits that interpose the event beds there is a preponderance of organic matter and fecal or algal strings with just a few mostly poorly preserved soft-bodied animals: these sediments provide evidence of the train of organic debris reaching the seabed from the actions of the animals above. By contrast, the rapidly deposited mudstones of the event beds literally capture the animals of the Chengjiang biota *in vivo*, so that they may more or less accurately reflect the original composition and structure of the early Cambrian marine community of the South China paleocontinent (Zhao Fang-chen *et al*. 2009, 2014a). In general the ecological structure of the Chengjiang biota is comparable to that of the middle Cambrian Burgess Shale of British Columbia (Zhao Fang-chen *et al*. 2014a).

The animals of the Chengjiang biota occupied a wide range of ecological niches from floating or swimming in the water column, to living on or just above the seafloor, to being within the sediment (Figs 6.2 and 6.3). Feeding strategies are similarly diverse, and the range of ecological strategies represented indicates the development of a sophisticated community with an integrated food web that laid the foundation for modern marine food webs (Vannier 2007). The Chengjiang biota includes a diverse array of animals that would have spent their lives in the water column. Those that actively swam and could control their movement and position in the water column (nekton) include ctenophores, chaetognaths, and a range of arthropods including those with a bivalved carapace that covered much of their soft anatomy, such as *Isoxys*, and *Zhenghecaris*. Other swimmers probably included the vertebrate *Myllokunmingia* and also the vetulicolians, which have a body morphology that suggests forward propulsion. Certainly the largest predators at the time were the spectacular anomalocaridids, some of which such as *Anomalocaris* and *Amplectobelua* have a set of laterally positioned paddle-like flaps that were probably used for swimming. Eldoniids, such as *Rotadiscus* and *Eldonia*, look like jellyfish and have traditionally been interpreted as pelagic (Zhu *et al*. 2002; Vannier & Chen 2005). They

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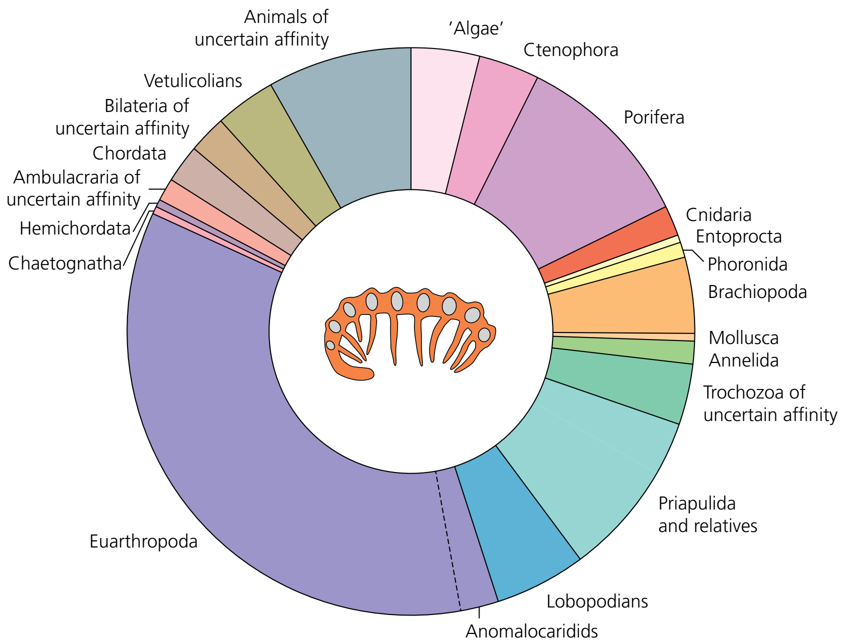


Figure 6.1 The composition of the Chengjiang biota (see the taxonomic list given in Chapter 28).

possess circumoral tentacles and are thought by some authors to have been mid-water predators. However, to account for their occurrence in some cases as mass accumulations on bedding surfaces it has been suggested that they may have been capable of benthic incursions – indeed, Dzik *et al.* (1997) argued for a benthic mode of life – and were "poisoned" before being buried (Caron & Jackson 2008). In short, the pelagic realm of the Chengjiang biota was inhabited by a range of animals, and analyses reveals three, possibly four trophic levels that were predicated on phytoplankton at the base of the food web (Hu *et al.* 2007).

Similar to marine communities today, most Chengjiang animals probably lived at, or just above the seafloor (see Figs 6.2 and 6.3). An estimated more than 90% of Chengjiang species lived as epibenthos (Vannier 2007). Indeed, the seafloor was replete with life and supported several sessile organisms that either rested directly on, or were anchored to the substrate. Tiering of bottom-living organisms was also clearly a feature of early Cambrian life. Sponges were the most diverse animals exploiting this lifestyle; some grew just above the seafloor, such as choiids and hamptoniids, whilst the majority grew between 5 and 15 cm above the seafloor. However, two species, *Halichondrites elissa* and *Quadrolaminiella diagonalis*, reached between 15 and 30 cm above the seafloor (Wu *et al.* 2014). The abundance of sponges suggests an environment with a ready supply of microscopic particles raining down from the overlying water column. Other sessile benthic organisms include the enigmatic and scaly chancelloriids and the jelly-like tunicates (sea squirts). This seafloor landscape was home to a huge variety of epibenthic arthropods and organisms that left a variety of trace fossils, indicating that the sediment was crawled over and in some cases dug into by these animals. Likely candidates for this niche include artiopodan arthropods such as *Acanthomeridion*. Others, such as the bivalved arthropods *Kunmingella* and *Clypecaris*, may have swam just above, frequently coming to rest on the seafloor where they may have fed.

Whilst arthropods ploughed through the surface of the sediments, only a few taxa lived deeper within (Fig. 6.2), and the exact nature of some of these lifestyles are still debated. For example, lingulid brachiopods have a very long pedicle and today occur in burrows centimeters below the seafloor; however, Chengjiang lingulids have been interpreted as perhaps living on the seafloor, or even attached to other animals that lived in the water column. The infaunal lifestyle of priapulid worms in the Chengjiang biota is less controversial because their morphology in the Cambrian is strikingly similar to Recent counterparts, which use coordinated peristaltic movements along their bodies to move on and through sediment (Vannier *et al.* 2010). A discovery of priapulid worms preserved within their lined burrows demonstrates that they were able to make a dwelling tube within the sediment (Huang 2005; Zhang Xi-guang *et al.* 2006). Other infauna, such as sipunculans (Huang *et al.* 2004a) and *Facivermis* (Hou Xian-guang *et al.* 2004a; Huang 2005) were much rarer components of the fauna (or were less likely to be preserved) but were probably very shallow burrowers. Today the top few centimeters of seafloor sediment is occupied by meiofauna, a major ecological category of animals, which are small, being approximately 0.1–1 mm long, and live between the sediment grains. In the Chengjiang biota there are tiny arthropods such as *Ercaia* (Chen Jun-yuan *et al.* 2001) and possible loriciferans (Huang 2005) that may have possessed a meiofaunal habit, but these animals are too large to conform to the strict definition of today's meiofauna (Vannier 2007).

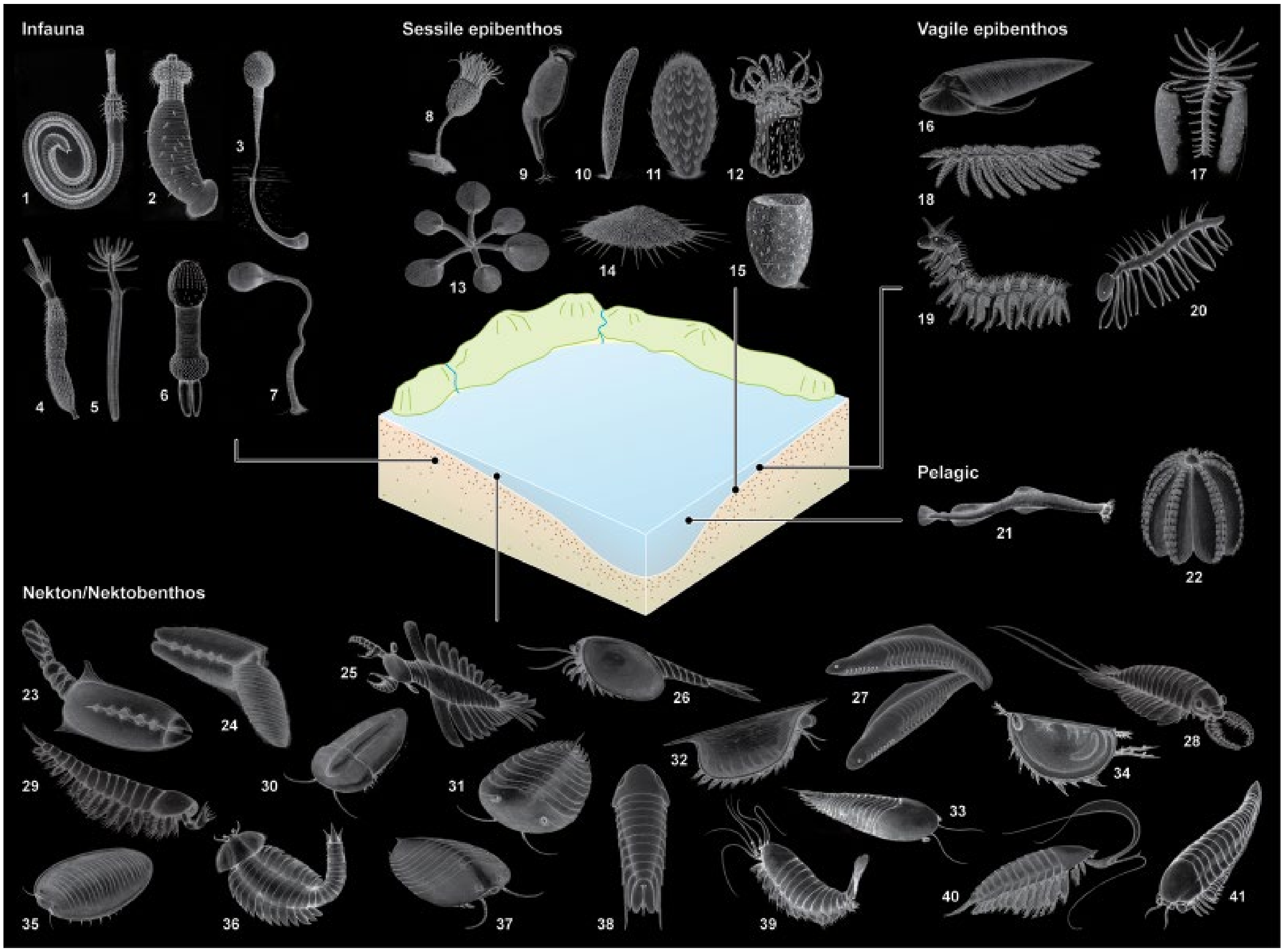


Figure 6.2 Early Cambrian Chengjiang marine fauna and their niches.

Infauna: 1. *Cricocosmia jinningensis*; 2. *Eximipriapulus globocaudatus*; 3. *Yuganotheca elegans*; 4. *Corynetis brevis*; 5. *Facivermis yunnanicus*; 6. *Xiaoheiqingella peculiaris*; 7. *Lingulellotreta malongensis*.

Sessile epibenthos: 8. *Cotyledion tylodes*; 9. *Shankouclava anningense*; 10. *Paraleptomitella dictyodroma*; 11. *Allonnia phrixothrix*; 12. *Archisaccophyllia kunmingensis*; 13. *Longtancunella chengjiangensis*: 14. *Choia xiaolantianensis*; 15. *Paradiagoniella xiaolantianensis*.

Vagile epibenthos: 16. *Linevitus opimus*; 17. *Luolishania longicruris* (on sponge); 18. *Diania cactiformis*; 19. *Onychodictyon ferox*; 20. *Hallucigenia fortis*.

Pelagic: 21. *Protosagitta spinosa*; 22. *Maotianoascus octonarius*.

Nekton: 23. *Vetulicola cuneata*; 24. *Heteromorphus confusus*; 25. *Lyrarapax unguispinus*; 26. *Chuandianella ovata*; 27. *Myllokunmingia fengjiaoa*; 28. *Anomalocaris saron*.

Nektobenthos: 29. *Haikoucaris ercaiensis*; 30. *Misszhouia longicaudata*; 31. *Xandarella spectaculum*; 32. *Isoxys auritus*; 33. *Cindarella eucalla*; 34. *Kunmingella douvillei*; 35. *Saperion glumaceum*; 36. *Fuxianhuia protensa*; 37. *Kuamaia lata*; 38. *Acanthomeridion serratum*; 39. *Alalcomenaeus* sp.; 40. *Leanchoilia illecebrosa*; 41. *Chengjiangocaris longiformis*.

Not surprisingly, given the diverse range of niches that Chengjiang animals inhabited, their feeding strategies and interactions mirror this complexity. The burst of new body plans and anatomical innovations evidenced in Chengjiang taxa was accompanied by the rapid development of new strategies for feeding and predator avoidance. There is no record of phytoplankton in the rocks of the Chengjiang Lagerstätte, but they must have been abundant as they form the basis of primary production in the marine food chain. Primary producers were likely to be groups such as acritarchs and cyanobacteria, which have been recorded from the Yu'anshan Member of eastern Yunnan. Being at the base of the food chain these were eaten by micro- and meso-zooplankton, which in turn were preyed upon by larger pelagic predators. However, evidence for these smaller zooplankton, of animals typically less than 2 cm in size, is virtually absent in the Chengjiang biota. Chaetognaths, if feeding the same as they do today, may have predated on smaller zooplankton in the water column using their grasping spines to catch small prey (Chen Jun-yuan & Huang 2002; Vannier *et al*. 2007).

Figure 6.3 An artistic impression of the Chengjiang biota showing some of the ecological niches (excluding infaunal niche) occupied by early Cambrian life.

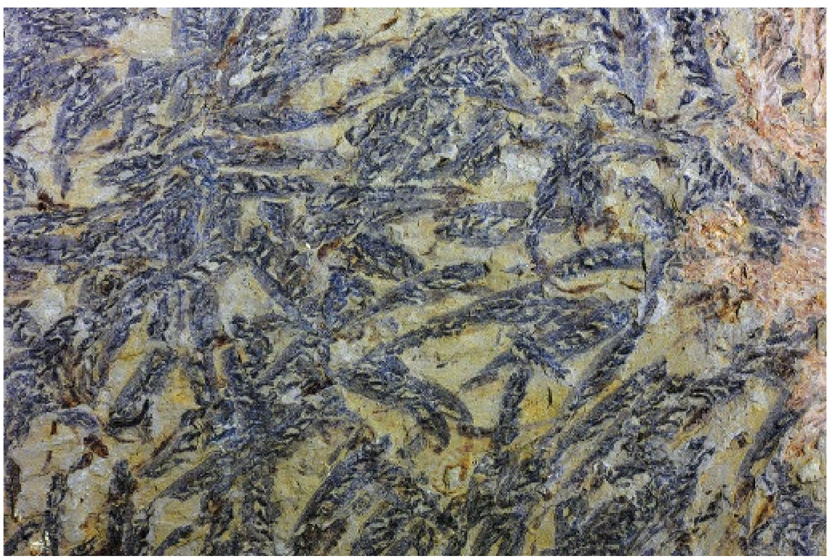
Other animals in the water column such as *Vetulicola*, ctenophores, and possibly eldoniids also probably fed on phytoplankton or zooplankton. Sponges and other sessile animals living on the seafloor probably filter fed on the rain-down of phytoplankton and zooplankton from the upper levels of the water column. Also on the seafloor a range of vagrant animals were able to scavenge dead carcasses and exploit the flux of particles that was sinking from the water column and collected onto the seafloor as nutrient-rich marine snow. Animals such as sipunculans, hyolithids, and many arthropods were likely efficient recyclers of this material (Vannier 2007).

Predation was advanced in the Chengjiang biota, with predators such as the diverse priapulids living in the sediment and catching small epibenthic prey that strayed across their burrows. A host of arthropods were predatory just on or above the seafloor, whilst others ventured further up into the water column to hunt, such as *Isoxys* and the anomalocaridids. Anomalocaridids are perhaps the best candidates for carnivores that ate other carnivores, which would indicate an even more complex food chain. Perhaps they were apex predators, though gut contents are required to be certain (Vannier 2007).

As well as investigating the autecology of individual taxa and their faunal associations, mass occurrences of species, where fossil abundance is extraordinarily high, are not uncommon in the Chengjiang biota (Fig. 6.4). These include mass occurrences of a single species such as the worm *Cricocosmia jinningensis*, which can reach 4000 individuals per square meter. Brachiopods, priapulids, and even yunnanozoans also occur en masse in single event beds (Han *et al.* 2006a). In addition, concentrations of the exoskeletons of other animals are also preserved in hundreds to thousands of often a single species, in most cases of hyolithids, bradoriids, or "waptiids" (Vannier & Chen 2005). Whether these accumulations are a reflection of a true population bloom owing to favorable conditions, transport sorting, or a behavioral event such as mass molting, is unknown. These accumulations can be distinguished from coprolites, because the latter are characterized by a consistent size range (0.5–7cm), definable edges, and a distinct shape that is commonly round or ribbon-like. Inside the supposed coprolites exoskeletal material may be closely packed, or even stacked (Vannier & Chen 2005). Interestingly, fewer than 10 species are found in these aggregates and they include bradoriids, waptiids, *Isoxys*, trilobites, hyolithids, and supposed medusoid animals. The original ecological niches of the groups in the coprolites demonstrate that predation occurred at all levels in the water column and within the sediment (Vannier & Chen 2005).

There are notable absences from the Chengjiang biota too. Thus, only a few species of putative echinoderms are recognized. Echinoderms are typically stenohaline, requiring normal salinities, and their absence has been attributed

(a)



(b)

Figure 6.4 Mass assemblages of Chengjiang fossils. **(a)** *Cricocosmia jinningensis*, YKLP 13801, ×2.6; Jianshan, Haikou, Kunming. **(b)** *Yunnanozoan lividum*, YKLP 13802, ×1.1; Mafang, Haikou, Kunming.

to abnormal salinity (Babcock *et al*. 2001) or possibly due to the absence of hard substrates on the Chengjiang seabed (Zhu *et al*. 2001). Their absence is probably not a taphonomic artifact as other animals with a calcitic (e.g., trilobites) or phosphatic (e.g., brachiopods) skeleton are present. The dearth of echinoderms may be due to ecological factors, rather than being a consequence of abnormal salinity controls. Because echinoderms are found in similar age carbonate rocks in the same area of the Yangtze Platform in southern China it has been argued that echinoderms first radiated during early Cambrian times in proximal, shallow, and carbonate environments and that they took some time to radiate into more siliciclastic environments such as those of Chengjiang (Clausen *et al*. 2010).

7 Cambrian Lagerstätten

Chengjiang is one of several Cambrian sites, including the celebrated Burgess Shale of Canada, which preserves an abundance of important soft-bodied fossils. Worldwide there are more than 40 localities in the Cambrian where Burgess Shale-type faunas have been recorded. These Lagerstätten preserve taxa, or closely allied forms, found in the Burgess Shale usually as carbonaceous compressions of the non-mineralized parts of animals, as well as shelly fossils. The deposits are typically shales, which accumulated under rapid burial and/or anoxia in the sediment. The Chengjiang biota ranks amongst the foremost of these Burgess Shale-type faunas.

The Chengjiang Lagerstätte contains by far the most diverse and disparate fauna – paleocommunity – known from the lower Cambrian, although there are other lower Cambrian sites that have additional taxa with soft-tissue preservation and therefore contribute to the total story of global early Cambrian biodiversity. Almost all of the Chengjiang soft-bodied species are unknown elsewhere, although a few genera are also found in other lower Cambrian sites around the world. The diversity and quality of preservation of the fauna at Chengjiang means that it would undoubtedly be regarded as the "type locality" for early Cambrian life.

Other important fossil Lagerstätten from the Cambrian include, for example, Sirius Passet in North Greenland, the Emu Bay Shale of Australia, and fossils of Orsten-type preservation originally described from material from Sweden (Fig. 7.1). In addition, small carbonaceous fossils (SCFs), recovered from mudstones by using hydrofluoric acid (Fig. 7.1), are adding significant information on Cambrian ecology and evolutionary dynamics (Butterfield & Harvey 2012).

Sirius Passet, North Greenland

The Sirius Passet fauna was discovered in the 1980s in J.P. Koch Fjord, North Greenland. The fossils with soft-bodied preservation occur in dark-colored lower Cambrian black slates that were mapped as the Transitional Buen and interpreted as fine-grained turbidites (Peel & Ineson 2011). The fossil-bearing deposits were originally shales that were subsequently metamorphosed, as indicated by the presence of chloritoid porphyroblasts. Sirius Passet, which dates to 520–535 Ma (Babcock 2005), has yielded important soft-bodied taxa. So far it has revealed some 50 species including trilobites, sponges, worms, halkieriids, lobopods, and arthropods. One of its most significant fossils is *Halkieria evangelista*, which was the first complete, articulated member of its group to be described (Conway Morris & Peel 1990, 1995), halkieriids being previously known only from isolated sclerites. *H. evangelista* is slug-like in shape, typically 1–8 cm long, is covered in approximately 2000 overlapping sclerites, and has a shell-like plate with prominent growth lines and ornamentation near both anterior and posterior ends of the body. The evolutionary relationships of halkieriids have generated much debate centered on their possible affinities with mollusks, annelids, brachiopods, and chancelloriids.

Lobopodians, vetulicolians, and a new filter-feeding anomalocaridid and other soft-bodied animals have also been recovered, but currently the known diversity of forms is relatively low (e.g., Vinther *et al.* 2011, 2014). However, this will certainly increase as research on new collections is undertaken.

Emu Bay Shale

Exceptionally preserved fossils from the Emu Bay Shale were originally described by Martin Glaessner (1979) and have been reviewed, *inter alia*, by Nedin (1995) and Paterson *et al.* (2015b). The deposit, located at Kangaroo Island in South Australia, has many faunal elements in common with the Burgess Shale, for example, *Anomalocaris, Isoxys*, *Tuzoia*,

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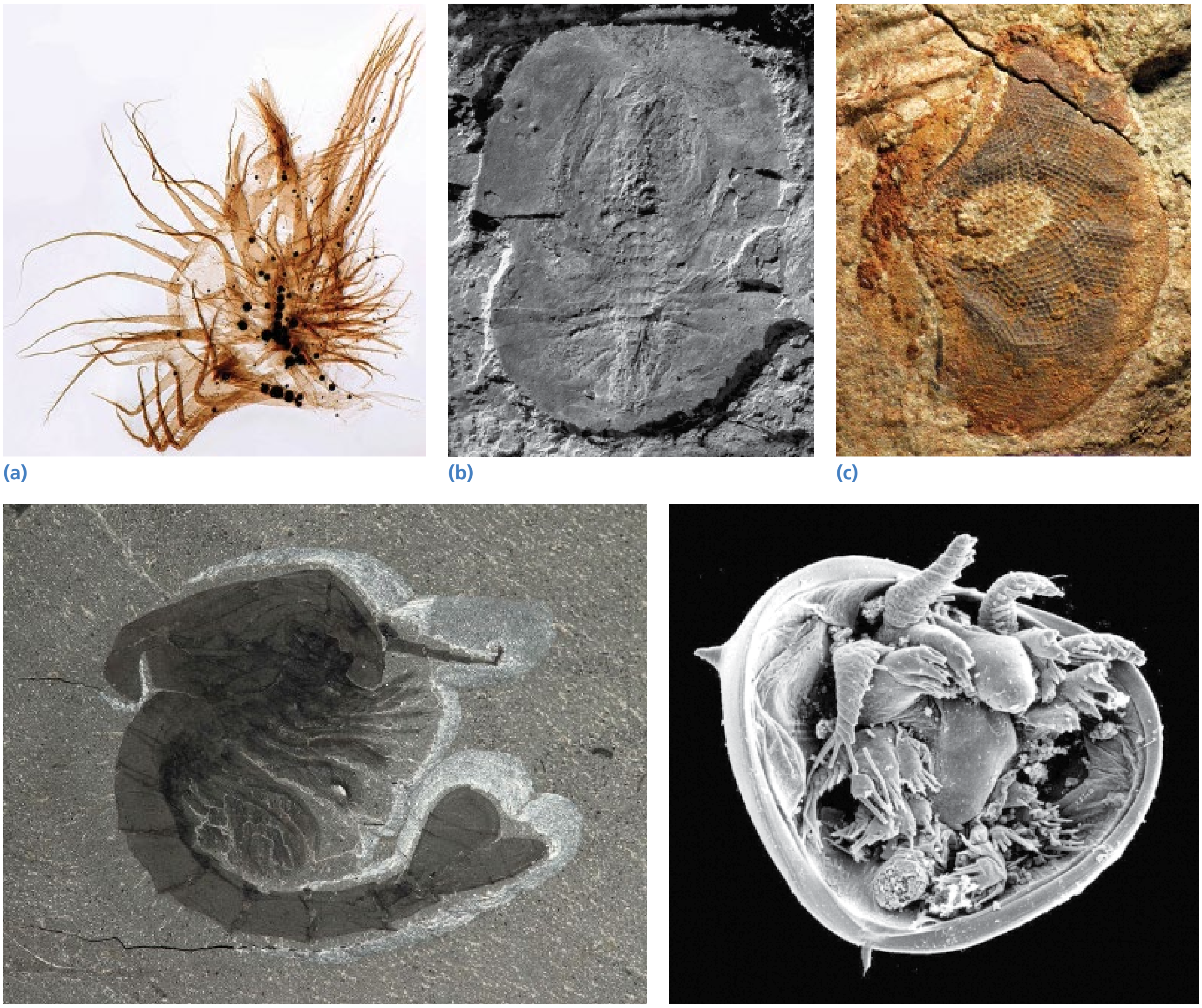

(a) (b) (c) (d) (e)

Figure 7.1 Exceptionally preserved fossils from Cambrian deposits. **(a)** A carbonaceous branchiopod crustacean appendage lobe, ×48; Earlie Formation, Saskatchewan, Canada. **(b)** The arthropod *Arthroaspis bergstroemi*, ×0.4; Buen Formation, Sirius Passet, Greenland. **(c)** Unnamed arthropod, eye, ×8.0; Emu Bay Shale, South Australia. **(d)** The arthropod *Waptia fieldensis*, ×2.1; Burgess Shale, British Columbia, Canada. **(e)** The phosphatocopid arthropod *Vestrogothia spinata,* ×165; Orsten deposits, Billingen, Västergötland, Gotland.

and *Paleoscolex*. It is dated at approximately 515 Ma and so is intermediate in age between the Chengjiang biota and Burgess Shale. The sedimentary deposits are dark gray to black micaceous mudstones, which were deposited in an isolated basin with mainly oxygenated water, but at the seafloor and below the sediment conditions were anoxic (Gehling *et al.* 2011). Fossils are preserved as carbonaceous compressions with some associated iron pyrite and calcium phosphate. Although considered as preserving taxa with lower preservation quality than fossils of the Chengjiang and Burgess Shale, more recent discoveries from the new Bucks Quarry rival preservation in these deposits. For example, stalked eyes, digestive structures, and details of appendages in arthropods have been recorded (García-Bellido 2009a, 2009b). Some of the arthropod eyes reveal the presence of modern optics in early Cambrian animals (Lee, M.S.Y. *et al.* 2011). The preservation of eyes in *Anomalocaris* is so detailed that 16,000 hexagonally-packed ommatidial lenses can be discerned in a single eye, indicating sophisticated visual acuity and suggesting a highly mobile predator (Paterson *et al.* 2011). One of the more common fossils is also one of the most problematic: *Myoscolex ateles* has a segmented, elongated body and preserves the world's oldest phosphatized muscle tissue and was initially interpreted as an annelid, and more recently as an *Opibinia*-like animal (Briggs & Nedin 1997). As at Chengjiang and Burgess Shale, arthropods dominate the Emu Bay Shale biota, with trilobites being amongst the most common fossils.

The Burgess Shale

This celebrated Lagerstätte (Briggs *et al.* 1994) was discovered over 100 years ago in the Canadian Rockies and has generated countless research publications. Stephen Jay Gould's book *Wonderful Life* (1989) gave the fossils of the Burgess Shale worldwide, popular attention. The middle Cambrian shales that host the fossils occur over a wide area, and new fossil localities, for example Marble Canyon in Kootenay National Park, are frequently being added to the first exploited sites, such as Walcott's Quarry and Raymond's Quarry. The Burgess Shale strata comprise intercalated beds of very fine-grained claystone and siltstone and carbonates. In the fine beds, where preservation quality is best, sedimentary structures only discovered by looking at thin sections of the rock reveal that the sediment was deposited as a fairly thick slurry moving across the seafloor (Gabbott *et al.* 2008), and not as a persistent rain down of particles. The slurries engulfed animals and this accounts for their frequent chaotic orientation in the layers.

Broadly speaking the preservation modes of the Chengjiang and Burgess Shale are similar. Both comprise carbonaceous compressions, but iron oxides after pyrite frequently coat these organic films in the Chengjiang (there is also similar pyritization in some Burgess Shale fossils but it is infrequent and pyrite is not oxidized). The Burgess Shale also has preserved guts in several taxa that are phosphatized, thereby revealing remarkable details of the animal's last meal (Butterfield 2002; Vannier 2012). Some late stage metamorphic clay mineralization imparts a silvery patina to some of the Burgess Shale fossils (Butterfield *et al.* 2007; Page *et al.* 2008). The principal reason that the fossils from the Chengjiang biota and Burgess Shale appear very different is the distinct post-depositional histories of each deposit, especially that the Chengjiang deposits have experienced deep weathering and the Burgess Shale was subject to greenschist facies metamorphism (Powell 2003).

The Chengjiang and the Burgess Shale faunas complement each other in providing two different windows in time on the Cambrian explosion, and both are essential for our understanding of this benchmark episode in the history of life. The Chengjiang site represents Cambrian life some 12 million years earlier than that of the Burgess Shale; because of the evolutionary changes during this interval, this time difference is highly significant. The fauna at the two sites shows some differences at phylum level, and a very considerable difference at generic level, and an almost complete difference in terms of species.

Whilst taxa differ between the Chengjiang and Burgess Shale faunas the ecological structure is comparable; for example, as at Chengjiang, arthropods dominate the Walcott Quarry fauna in both abundance and species diversity. Both deposits are dominated by epifauna but in the Burgess Shale vagile deposit feeders and sessile suspension feeders, mostly arthropods and sponges, dominate (Caron & Jackson 2008). In the Chengjiang, epibenthic, vagrant, hunting or scavenging, sessile suspension feeders, and infaunal vagile hunters or scavengers dominate, represented by arthropods, brachiopods, and priapulids, respectively (Zhao Fang-chen *et al.* 2014a). Both biotas have fewer pelagic taxa. Overall though, the diversity levels, ecological niche occupation, and community structure are similar, suggesting that soft-bodied benthic communities in subtidal siliciclastic settings seemed to have persisted and have been stable until at least the middle Cambrian (Zhao Fang-chen *et al.* 2014a).

Orsten Fossils

Fossils of Orsten-type were discovered by Klaus Müller in the mid-1970s by laboratory preparation of limestone nodules from the late Cambrian bituminous Alum Shales of southern Sweden. The fossils consist of tiny (typically sub-millimeter) but, crucially, three-dimensional specimens preserved by secondary phosphate replacement, and are recovered from their calcareous nodule by dissolution in weak acetic acid. The fossils preserve soft tissues and hard parts but the mode of preservation appears to have captured only cuticle-bearing metazoans, especially arthropods and also cycloneuralian nemathelminths (Maas *et al.* 2006). Another bias is size, with no fossil being more than about 2 mm in overall dimension. However, the fidelity of preservation is truly remarkable. For example the arthropods show delicate features such as hairs and bristles on the limbs, details of eyes, and minute pores in the cuticle (Waloszek 2003a, 2003b). Such high-fidelity, three-dimensional preservation has provided a rich source of evidence on the morphology, ontogeny, ecology, and early evolution of the Arthropoda, especially the Crustacea (e.g., Waloszek 2003a, 2003b; Waloszek *et al.* 2014). The Orsten fauna has been interpreted as a meiofauna – a community of very small animals that lived in a microenvironment similar to the flocculent bottom layer in aquatic regimes today. Examination of Orsten fossils by synchrotron radiation X-ray tomographic microscopy has revealed details of internal soft tissues such as muscles and digestive system. This allows comparison of preserved fossil organs with those of equivalent structures in extant crustaceans and is providing new insights on life habits and functional morphology of early animals (Eriksson *et al.* 2012). The Orsten-type preservation type is now known to be more widespread in both time and space than initially assumed, with such fossils occurring in a broad stratigraphic range including within the Neoproterozoic and across several continents (Maas *et al.* 2006).

Part Two
Chengjiang Fossils

8 Algae

Algae refers to an unnatural polyphyletic assemblage that is difficult to classify. The term is most often used to define an algal mode of life, and most algae contain chloroplasts and are photosynthetic. Modern algae live in a variety of habitats and vary from microscopic single-celled organisms to complex multicellular forms, such as giant kelps tens of meters in length. They exhibit a wide range of reproductive strategies, from asexual division to complex forms of sexual reproduction. Green algae are very closely related to, and probably the ancestors of, the higher plants.

Algae represent the base of the food chain that is preserved in the Chengjiang biota, occurring as thread-like, two-dimensional structures on bedding plane surfaces. These remains are one of the most common fossil forms in the Lagerstätte, but because little distinctive morphology is preserved it can be difficult to determine whether they are algae, cyanobacteria, or even fecal strings. Some Chengjiang taxa that were originally regarded as algae, such as *Fuxianospira gyrata* Chen & Zhou, 1997 and *Megaspirellus houi* and *Yuknessia* of Chen & Erdtmann, 1991, have been reassessed by some authors to be strings of fecal material (Steiner *et al.* 2005). Moreover, *Yuknessia simplex* Walcott, 1919, a species described from the Burgess Shale, has been reinterpreted as a pterobranch based on the presence of fusellae (LoDuca *et al.* 2015). This demonstrates the challenge of placing alga-like fossils within the correct group.

Genus *Fuxianospira* Chen & Zhou, 1997

Fuxianospira gyrata Chen & Zhou, 1997

Fuxianospira gyrata comprises an unbranched, cylindrical filament of uniform diameter that can reach 1.2 mm in size. It is tightly helicoidal along its length, and so when flattened has a beaded appearance. This species is the most abundant supposed alga of those occurring at Chengjiang. Some specimens, at least, have been figured under the name *Yuknessia* (Chen Jun-yuan *et al.* 1996; Hou *et al.* 1999). That genus was described originally on the basis of the species *Yuknessia simplex* from the Middle Cambrian Burgess Shale (Walcott 1919), the macroscopic form of which resembles some modern tubular green algae (Conway Morris & Robison 1988) but is now thought to be a pterobranch (LoDuca *et al.* 2015). Although originally described as an alga, *F. gyrata* is now regarded by some authors as a coprolite (e.g., Steiner *et al.* 2005).

Key references

Chen Jun-yuan & Erdtmann 1991; Chen Jun-yuan *et al.* 1996; Chen Jun-yuan & Zhou 1997.

Figure 8.1 ***Fuxianospyra gyrata.*** RCCBYU 10211, x2.7; Ercaicun, Haikou, Kunming.

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Genus *Megaspirellus* Chen & Erdtmann, 1991

Megaspirellus houi Chen & Erdtmann, 1991

Megaspirellus is not as common as other supposed algae in the Chengjiang biota, but it is one of the most distinctive forms.

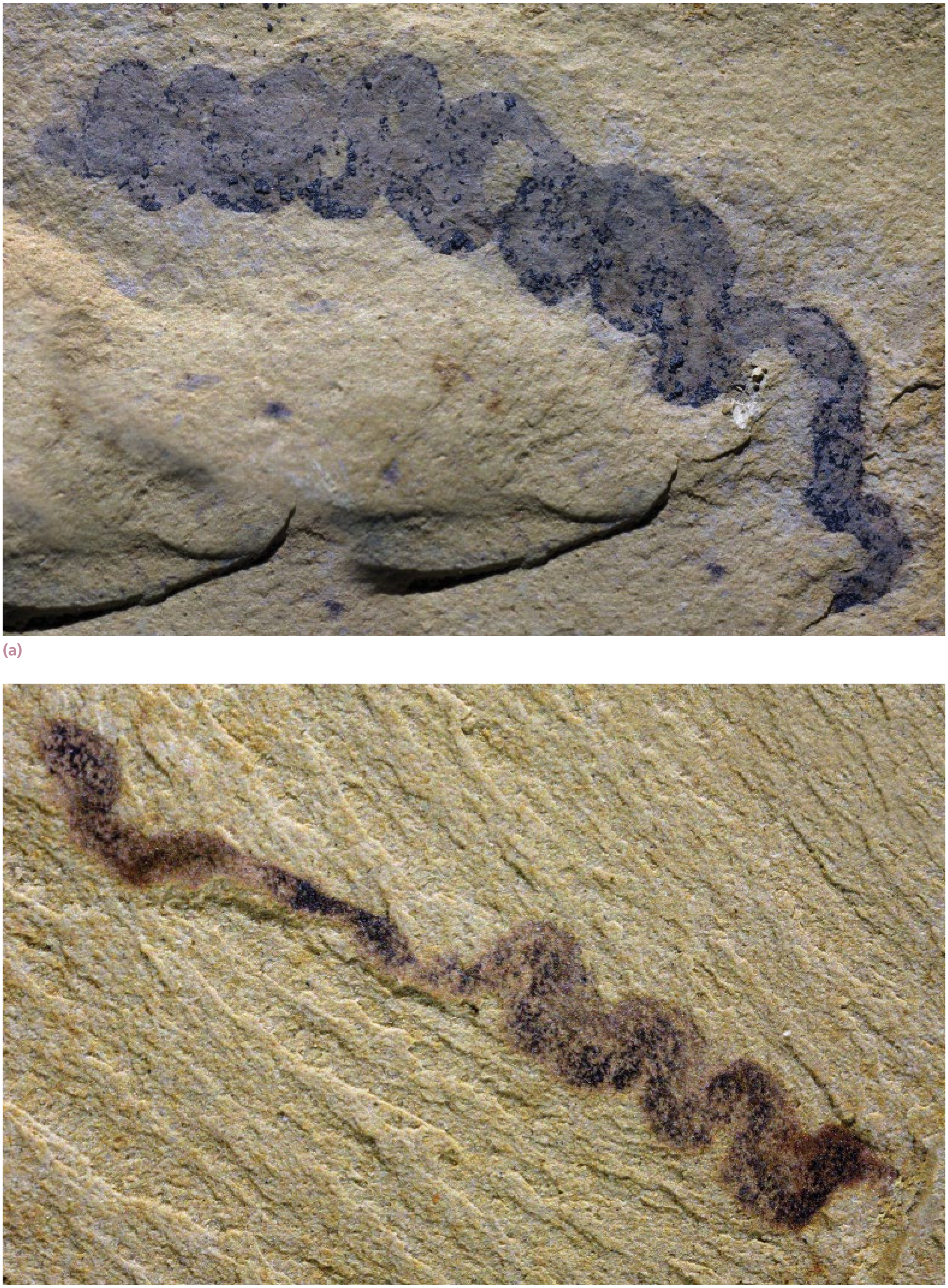
Typically *M. houi* has a filament approximately 2.4 cm long and 0.5 mm wide, most of which forms an open, nearly parallel-sided helical coil, which terminates at one end with a straight extension of the filament about 6 mm in length. The coil has a maximum width of 3 mm and comprises 19 whorls. There is no indication of cell structure along the sheath, which suggests it was substantial (Chen Jun-yuan & Erdtmann 1991).

The biological affinity of this taxon remains obscure. It is suggested on the basis of general morphological similarity with the modern *Spirulina* that an affinity with cyanobacteria may be likely (Chen Jun-yuan & Erdtmann 1991). However, several aspects of this fossil are more consistent with it being a fecal string. For example, some remains are three-dimensional and in some cases contain sediment pellets, and it never displays branching or holdfasts typical of cyanobacteria (Steiner *et al.* 2005).

Key references

Chen Jun-yuan & Erdtmann 1991; Steiner *et al.* 2005.

Figure 8.2 ***Megaspirella houi***. **(a)** YKLP 13804a, ×7.7; Ercaicun, Haikou, Kunming. **(b)** YKLP 13805, ×18.5; Ercaicun, Haikou, Kunming.



(a)

(b)

Genus *Sinocylindra* Chen & Erdtmann, 1991

Sinocylindra yunnanensis Chen & Erdtmann, 1991

This Chengjiang alga is relatively rare. Specimens appear as a dark, smooth, thread-like ribbon that maintains a thickness of about 0.3 mm along its entire length of up to 2 cm. It is unbranched and often appears in an open, looping, irregular coil. It may have been an effective floater and was certainly highly flexible. The macroscopic features of the alga resemble some members of the Oscillatoriaceae, but it is too large for a bacterial affinity (Chen Jun-yuan & Erdtmann 1991). The lack of branching and the relatively loose coiling suggest similarities with modern brown algae.

Key references

Chen Jun-yuan & Erdtmann 1991; Chen Jun-yuan *et al.* 1996; Hou *et al.* 2004a.

Figure 8.3 ***Sinocylindra yunnanensis***. **(a)** RCCBYU 10212, ×5.8; Maotianshan, Chengjiang. **(b)** YKLP 13806, ×11.3; Ercaicun, Haikou, Kunming.

(a)

(b)

Genus *Yuknessia* Walcott, 1919

Yuknessia sp. of Chen & Erdtmann, 1991

This is the dominant supposed alga of the Chengjiang biota and appears abundantly on countless bedding planes.

The thallus is small, consisting of only a few stipes, which are long, flexible, and slender with no branching or jointing. The height of the thallus is 1–2 cm and the width of the stipes increases gradually from 0.5 mm to 1 mm.

The algal affinity of this form is controversial. It is considered by some authors to be a coprolite (Steiner *et al*. 2005). The Chengjiang material closely resembles *Yuknessia simplex* Walcott, 1919 from the Burgess Shale in the dimensions of the thallus and stipes, but there are far fewer stipes in the thallus. The Burgess Shale taxon, long regarded as a green alga (Walcott 1919; Conway Morris & Robson 1988), has recently been reinterpreted as a pterobranch based on the presence of fusellae (LoDuca *et al*. 2015).

Key references

Chen Jun-yuan & Erdtmann 1991; Steiner *et al*. 2005.

Figure 8.4 ***Yuknessia*** sp. **(a)** YKLP 13807, ×5.7; Ercaicun, Haikou, Kunming. **(b)** YKLP 13808, ×1.7; Ercaicun, Haikou, Kunming.

(a)

(b)

9 Ctenophora

Ctenophores have a descriptive array of common names including comb jellies, sea combs, sea walnuts, or sea gooseberries. All extant forms are marine and have a delicate, transparent, gelatinous bag-like body. The discovery of sclerotized and lightly armored ctenophores from the Chengjiang Lagerstätte reveals that more robust forms occurred in the past, perhaps reflecting intensified ecological interactions in the early Cambrian ecosystem (Ou *et al.* 2015). The most distinctive feature of ctenophores is their combs, which are borne in longitudinally arranged bands (known as ctenes or comb rows), each with transverse lines of cilia (combs) that are used for swimming. The comb rows of most planktonic ctenophores produce a rainbow effect, which is caused not by bioluminescence but by the scattering of light as the combs move.

The placement of ctenophores close to the root of the animal tree of life is unquestionable but there is some disagreement over their precise position, particularly in relation to the Porifera (sponges) and cnidarians. Widespread acceptance that Porifera are at the root to all other animals has been thrown into question because recent sequencing of the genomes of two ctenophores has indicated that Porifera are more closely related to cnidarians and bilaterians, leaving ctenophores at the base of the animal tree (Ryan *et al.* 2013; Moroz *et al.* 2014).

Despite their generally low preservation potential at least eight species of ctenophore are known from the Chengjiang Lagerstätte, which represents the earliest and most diverse known fauna of fossil ctenophores. The affinity of the Chengjiang species *Batofasciculus ramificans* Hou *et al.*, 1999 was originally considered to be uncertain (Hou *et al.* 1999, 2004a). However, this species has recently been reinterpreted as having eight externally directed longitudinal lobes with regular spines and to be a ctenophore (Hu *et al.* 2007; Ou *et al.* 2015), as has *Trigoides aclis* Luo & Hu *in* Luo *et al.*, 1999 (Ou *et al.* 2015). Three further ctenophores recently recorded from the Chengjiang biota are *Gemmactena actinala* Ou *et al.*, 2015; *Thaumactena ensis* Ou *et al.*, 2015; and *Galeactena hemispherica* Ou *et al.*, 2015, thus adding significantly to the Cambrian diversity of the group. All extant ctenophores are carnivores, mostly using long tentacles to ensnare prey. However, Chengjiang ctenophores seemingly lack tentacles and may have engulfed prey in a similar manner to that suggested for Burgess Shale ctenophores (Conway Morris & Collins 1996) that also lack tentacles.

There are other putative Chengjiang ctenophores that have either been reassigned or remain questionable owing to poor preservation and lack of ctenophore characters, including *Petalilium latus* Luo & Hu *in* Luo *et al.*, 1999 (= *Nectocaris pteryx* Conway Morris, 1976; see discussion of that species). The Chengjiang biota also includes *Stromatoveris psygmoglena* Shu *et al.*, 2006, a frond-like fossil with supposed ctenophore affinities.

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Genus *Galeactena* Ou, Xiao, Han, Sun, Zhang, Zhang & Shu, 2015

Galeactena hemispherica Ou, Xiao, Han, Sun, Zhang, Zhang & Shu, 2015

Several specimens of *Galeactena hemispherica* are known.

This species is characterized by an octaradial body with a vaulted hemispherical shape, which seemingly resists twisting and distortion, suggesting a degree of structural integrity. The apical organ is elongate and tapers aborally to a blunt end within which the carbonaceous remains of a spheroidal statolith occur. There is a central tube preserved in positive relief that tapers aborally and terminates beneath the statolith; this is interpreted as the aboral canal (Ou *et al.* 2015). Eight longitudinal lobes stretch almost the entire body length. Each lobe gently thins centrifugally into a median ridge, which may represent a lightly sclerotized spoke. Two longitudinal rows of ctenes flank each longitudinal lobe. A constriction separates the central body from a short oral skirt. There are no tentacles evident.

G. hemispherica is the only known species of *Galeactena*. A ctenophore affinity is based on a suite of features; for example, the oral-aboral axis, the aboral organ, and the presence of ctenes in octaradial rows. Phylogenetic analysis resolves this species as a close relative of the Chengjiang ctenophore *Maotianoascus octomarinius* (Ou *et al.* 2015).

The aboral structure may have acted as a sense organ, and this along with the presence of octaradial comb-rows suggests a nektonic mode of life. Locomotion was enabled by ciliary ctenes.

The species is known only from the lower Cambrian Chengjiang biota, at the Jianshan section, Haikou, and the Xiaolantian section, near Chengjiang, Yunnan Province.

Key reference

Ou *et al.* 2015.

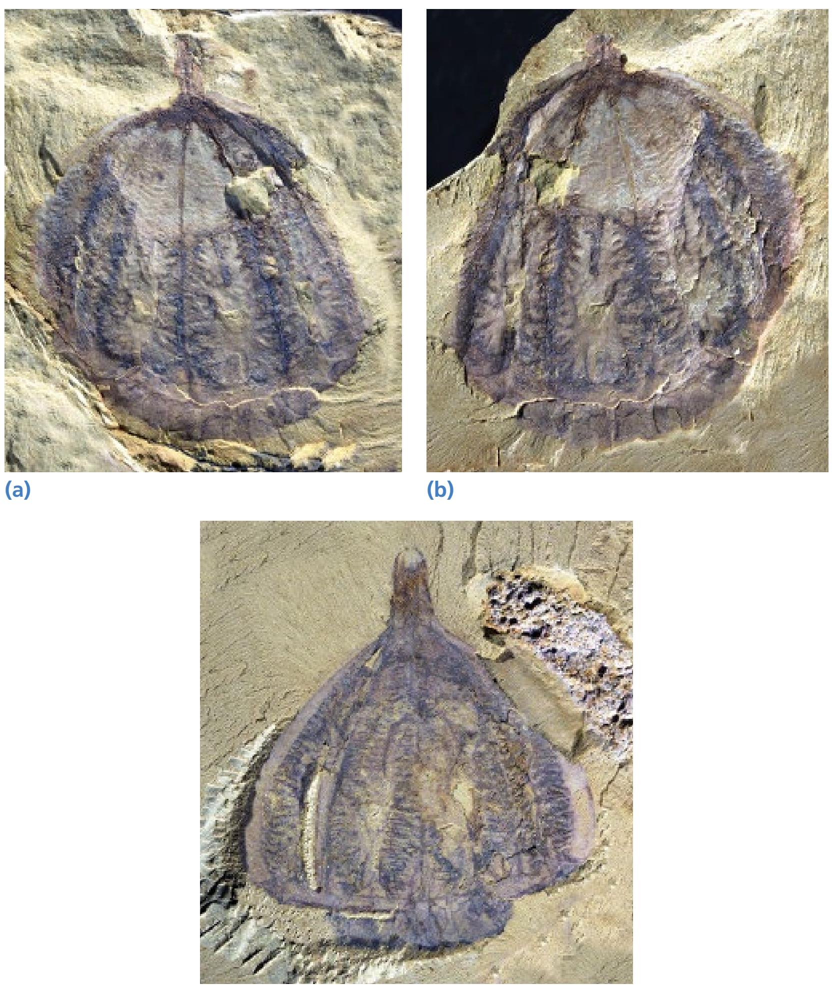


Figure 9.1 ***Galeactena hemispherica***. **(a)** YKLP 13809a, ×2.2; Xiaolantian, Chengjiang. **(b)** YKLP 13809b, ×2.3; Xiaolantian, Chengjiang. **(c)** YKLP 13810, ×2.8; Ercaicun, Haikou, Kunming.

Genus *Maotianoascus* Chen & Zhou, 1997

Maotianoascus octonarius Chen & Zhou, 1997

Just a handful of specimens of *Maotianoascus octonarius* are known.

The octaradial body is subcircular in shape. The body comprises eight longitudinally extending petaloid lobes, which have a ring-like arrangement about the axis, implying radial symmetry. Each lobe has a narrow strip that faces outward. Each strip is divided by a median-line or fold, either side of which is a longitudinal strip of fine, transversely orientated ridge-and-furrow-like structures flanked by smooth longitudinal areas. These seemingly delicate structures are interpreted as the combs of comb rows, of which there are 16. The apical organ is dome-like and houses a spherical statolith (Ou *et al.* 2015). The oral region is skirt-like. Tentacles are absent.

This fossil strongly resembles extant ctenophores except in the number of comb rows, which in living forms is characteristically eight. Other Cambrian ctenophores also have more than eight comb rows. For example, *Ctenorhabdotus capulus* and *Xanioascus anadensis* from the Burgess Shale each have 24, whilst *Fasciculus vesanus* from the same deposit may have up to 80 comb rows (Conway Morris & Collins 1996).

Similar to extant ctenophores, *M. octonarius* was probably pelagic and achieved locomotion by action of the multitude of tiny cilia on each comb row. As it lacks tentacles it may have captured food directly into its mouth in a similar manner envisaged for *C. capulus*.

M. octonarius is known only from the Chengjiang biota, at Maotianshan, and the Sanjiezi section at Jinning, Yunnan Province.

Key references

Chen Jun-yuan & Zhou 1997; Hou *et al.* 1999, 2004a; Chen Jun-yuan 2004; Ou *et al.* 2015.

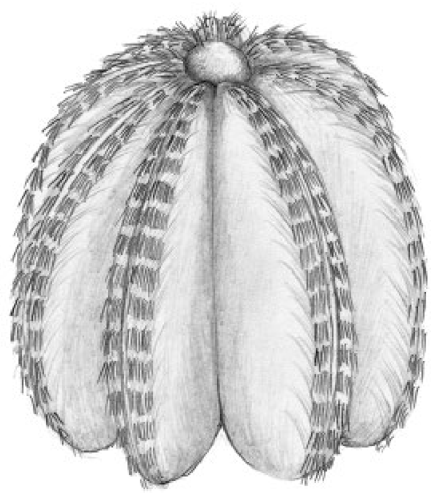
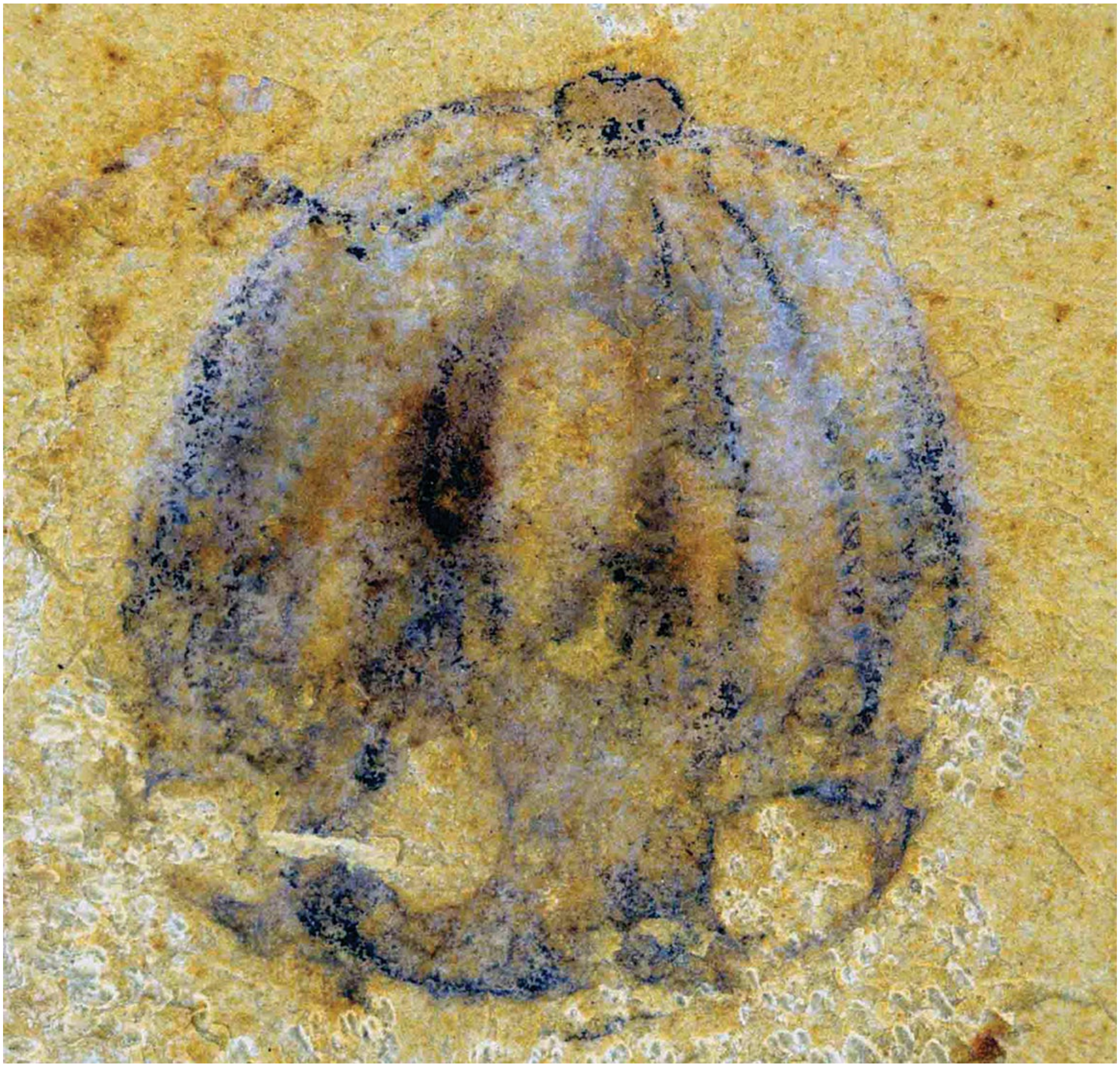


Figure 9.2 Reconstruction of ***Maotianoascus octonarius***.

Figure 9.3 ***Maotianoascus octonarius.*** RCCBYU 10217, ×21.6; Maotianshan, Chengjiang.



Genus *Batofasciculus* Hou, Bergström, Wang, Feng & Chen, 1999

Batofasciculus ramificans Hou, Bergström, Wang, Feng & Chen, 1999

Material of *Batofasciculus ramificans* is quite rare. Only about 20 specimens are known.

The body has octaradial symmetry and bears eight rigid branches (spokes; Ou *et al.* 2015). Each spoke has a line of at least 20 regularly spaced, outwardly pointing thorn-like spines. The spines reach maximum size at about mid-length of each spoke and gradually decrease in size both orally and aborally. There are eight soft-tissue flaps that radiate from the oral-aboral axis, each framed by a spoke. The oral region is surrounded by apiculate lappets. The aboral region comprises a pointed dome formed by eight rigid plates, which enclose a statolith (Ou *et al.* 2015). There are no tentacles or ctene rows, although absence of the latter may be due to poor preservation.

When this species was originally described its affinity was a mystery, and it drew comparison with a range of solitary and colonial organisms (Hou *et al*. 1999, 2004a). A ctenophore affinity is based on features such as the oral-aboral axis, aboral organ, possession of eight soft-tissue flaps, and a close resemblance to other Chengjiang ctenophore taxa (Hu *et al.* 2007; Ou *et al*. 2015).

B. ramificans resembles the Chengjiang ctenophore *Gemmactena actinala* in having a pointed dome-like apical organ walled by plates, and like *Gemmactena* it was probably nektonic.

The species is known only from the Chengjiang biota. It has been collected at sections at Jinning, Maotianshan, Haikou, and Anning.

Key references

Hou *et al.* 1999; Hu *et al.* 2007; Ou *et al*. 2015.

Figure 9.4 ***Batofasciculus ramificans*.** **(a)** NIGPAS 115442a, ×2.0; Maotianshan, Chengjiang. **(b)** NIGPAS 115442b, ×2.0; Maotianshan, Chengjiang. **(c)** RCCBYU 10302, ×3.3; Maotianshan, Chengjiang.


(a)
(b)
(c)

Genus *Yunnanoascus* Hu, Steiner, Zhu, Erdtmann, Luo, Chen & Weber, 2007

Yunnanoascus haikouensis Hu, Steiner, Zhu, Erdtmann, Luo, Chen & Weber, 2007

Only a few specimens of *Yunnanoascus haikouensis* have been found.

The body is 2 cm long and divided into an aboral part that is 1 cm long and disk-like in outline with some plate-like structures. The oral part has 16 comb rows preserved. The space between adjacent comb rows ranges from 0.5 mm at the base to 1 mm in the middle of the body and 1.5 mm at the oral end.

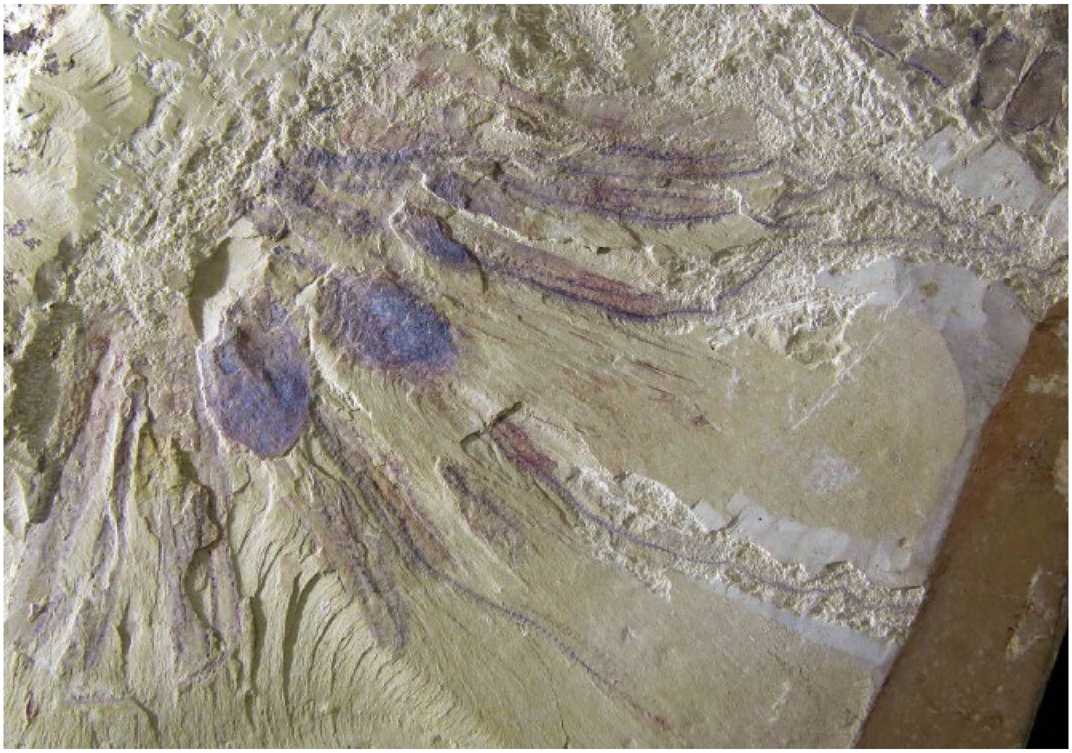
A ctenophore affinity is based on the presence of comb rows. This taxon differs from the Chengjiang species *Maotianoascus octonarius* because it appears to lack a skirt-like structure.

The species is known only from Ercaicun in the Haikou area, Yunnan province.

Key reference

Hu *et al*. 2007.

Figure 9.5 ***Yunnanoascus haikouensis*****.** **(a)** YKLP 13811a, ×1.7; Maotianshan, Chengjiang. **(b)** YKLP 13811b, ×2.1; Maotianshan, Chengjiang.



(a)

(b)

10 Porifera

Sponges are multicellular organisms that lack the sophisticated organization of other Metazoa. Organs and a nervous system are absent and the few types of cells that they have are not organized into tissues. The skeleton consists of a colloidal jelly, or of the horny material spongin, and/or a framework of siliceous or calcareous spicules that in some species is augmented with, or may consist entirely of, a calcareous skeleton. Their form varies from simple bag-shaped to stalked and elaborately branching colonies. In life they are sedentary and benthic. They filter food from water currents pumped through minute holes (ostia) that lead to cavities lined with flagella-bearing cells (choanocytes) and thence to an interior cavity or water canal system (spongocoel or atrium); water is passed out via an apical opening (osculum). Most poriferans are shallow marine dwellers; some species are also known from deep water or fresh water. Today the latter include most of the hexactinellids, the glass sponges with their skeleton of opaline silica spicules. Sponge spicules and skeletons are common as fossils from the Cambrian onwards. Some research has challenged the traditionally regarded basal phylogenetic position of sponges, suggesting that in some features they hint at a more cnidarian-like or ctenophore-like precursor (Halanych 2015).

Sponges are a diverse component of the Chengjiang biota. Most of the described species are thought to be demosponges, a group in which the rays of the siliceous spicules usually diverge at 60° or 120°. A few species, such as *Paradiagoniella xiaolantianensis,* have been considered as representatives of hexactinellid sponges. Detailed studies on the morphology of Chengjiang sponges and the topological relationships of the spicules are few. A recently completed thesis (Chen Ai-lin 2015) comprehensively documents Chengjiang sponges but the study is largely unpublished.

Genus *Paradiagoniella* Chen, Müller, Hou & Xiao, 2014

Paradiagoniella xiaolantianensis Chen, Müller, Hou & Xiao, 2014

This is a rare species of the Chengjiang biota. Some specimens of *Paradiagoniella xiaolantianensis* are preserved superimposed on exoskeletons of the arthropod *Naraoia*. Spicules are well exposed in the holotype specimen.

The sponge body is ovoid in outline and relatively small, only some 3.2–3.3 cm high and 1.8–2.4 cm wide. It has a round base and possibly a round osculum. The maximum width occurs near the oscular end. The skeleton is mainly composed of stauractines (spicules with four rays) and rare oxeas (spicules with two rays). The four rays of the stauractines are of equal lengths, smooth and distally sharp. Up to six ranks of stauractines can be distinguished, each of which is not arranged parallel to the other ranks. The first order of stauractines can form sub-quadrules in the body wall, with smaller stauractines nested inside. Oxeas are interlocked with stauractines.

The affinity of *P. xiaolantianensis* is uncertain. It has been assigned to the family Protospongiidae, which has been considered to be a member of the Hexactinellida (Finks & Rigby 2004; Carrera & Botting 2008). However, some authors think that the Protospongiidae might be paraphyletic and may include both hexactinellids and stem siliceans (Botting & Butterfield 2005; Botting *et al.* 2014).

The ecology of *P. xiaolantianensis* is unknown.

P. xiaolantianensis is only known from Xiaolantian near Chengjiang town.

Key reference

Chen Ai-lin *et al.* 2014.

The Cambrian Fossils of Chengjiang, China: The Flowering of Early Animal Life, Second Edition. Hou Xian-guang, David J. Siveter, Derek J. Siveter, Richard J. Aldridge, Cong Pei-yun, Sarah E. Gabbott, Ma Xiao-ya, Mark A. Purnell, Mark Williams.

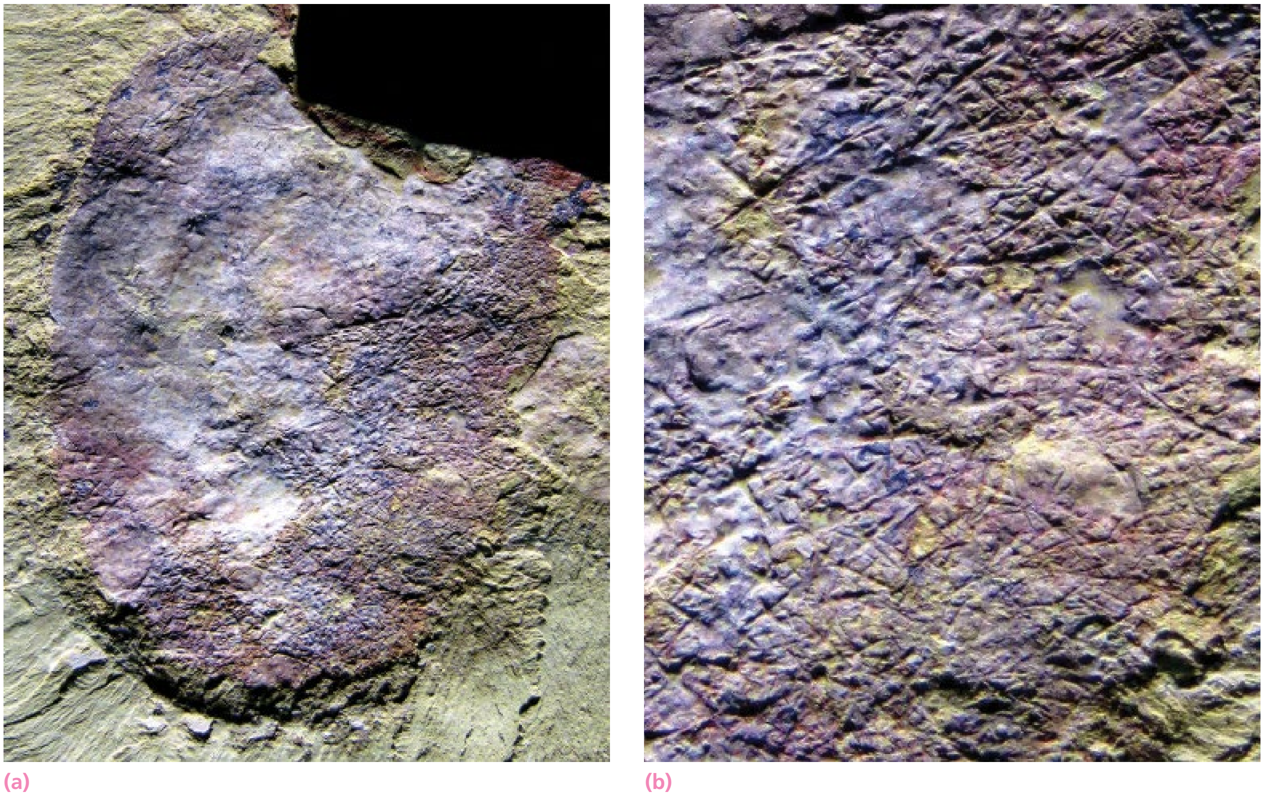


Figure 10.1 ***Paradiagoniella xiaolantianensis***. (a) CFM S-001a, ×2.9; Xiaolantian, Chengjiang. (b) CFM S-001b, ×7.5; Xiaolantian, Chengjiang.

Figure 10.2 Reconstruction of ***Paradiagoniella xiaolantianensis*** (after Chen Ai-Lin *et al.* 2014).

Genus *Triticispongia* Mehl & Reitner *in* Steiner *et al.*, 1993

Triticispongia diagonata Mehl & Reitner *in* Steiner *et al.*, 1993

Characteristically *Triticispongia diagonata* is preserved as flattened iron oxide and moldic impressions. It is a common sponge within the Chengjiang biota.

Specimens are small, some 0.6–1.5 cm high. The sponge body is oval to rounded and thin walled, with spongocoel constituting most of the space. Some specimens display scattered basal root tuft spicules, and spicule rays occur around the flattened oscular margin, which appears as a more or less subhorizontal termination of the skeleton. The skeleton contains two moderately well organized series of small, delicate spicules with rectangular patterns. One series of spicules has its prominent spicule axes parallel and normal to the principal axis of the sponge, and the second series has a more diagonal arrangement.

This species is considered to be an early reticulosid hexactinellid sponge.

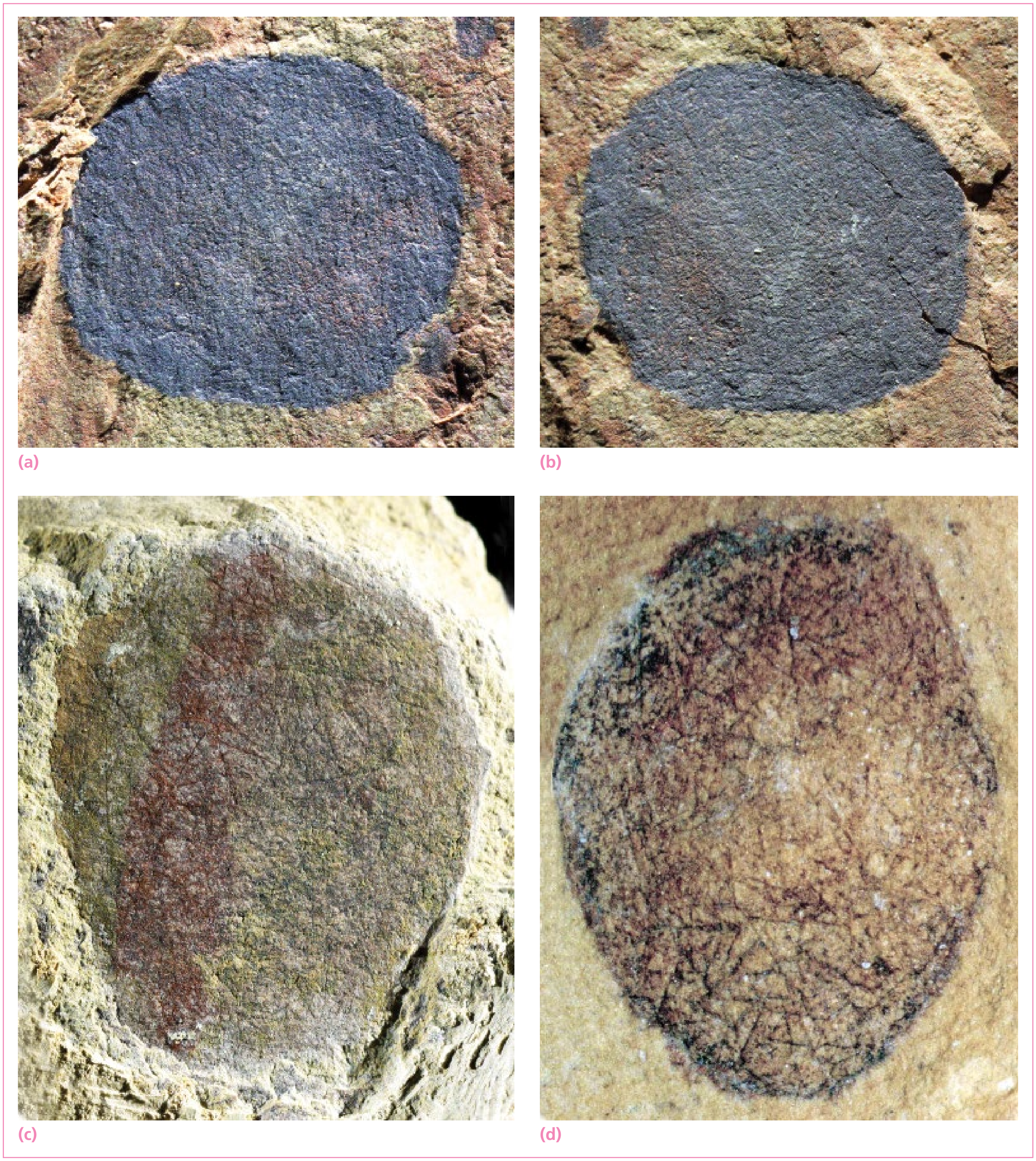
Its root tuft presumably anchored the body to the substrate, as is characteristic of many living forms of glass sponge.

T. diagonata was originally described from the Cambrian of Hunan Province, China. It occurs at many localities of the Chengjiang biota.

Key references

Steiner *et al.* 1993; Rigby & Hou 1995; Hou *et al.* 1999, 2004a.

Figure 10.3 ***Triticispongia diagonata***. **(a)** YKLP 13812a, ×8.5; Ercaicun, Haikou, Kunming. **(b)** YKLP 13812b, ×8.5; Ercaicun, Haikou, Kunming. **(c)** YKLP 13813, ×6.2; Ercaicun, Haikou, Kunming. **(d)** NIGPAS 115320, ×13.6; Xiaolantian, Chengjiang.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Genus *Saetaspongia* Mehl & Reitner *in* Steiner *et al.*, 1993

Saetaspongia densa Mehl & Reitner *in* Steiner *et al.*, 1993

Specimens of *Saetaspongia densa* from Yunnan Province are preserved as impressions, in low bas-relief. The generic name of this relatively common Chengjiang sponge alludes to its thin, hair-like spicules.

This sponge has a moderately small, well-defined, almost circular body up to 3 cm by 4 cm in diameter. An oscular opening is not evident, though a flattened part of its outline may be the margin of the osculum. The skeleton consists mainly of very narrow diactine spicules, 1–2 mm long and about 0.025 mm in diameter. The spicules occur as dense, semi-parallel, almost plumose bundles, and do not project beyond the outer margin of the sponge body. Less common, somewhat thicker spicules, up to 0.1 mm in diameter, are intermixed. The spicules may include three-, four-, or even six-rayed (hexactine) forms.

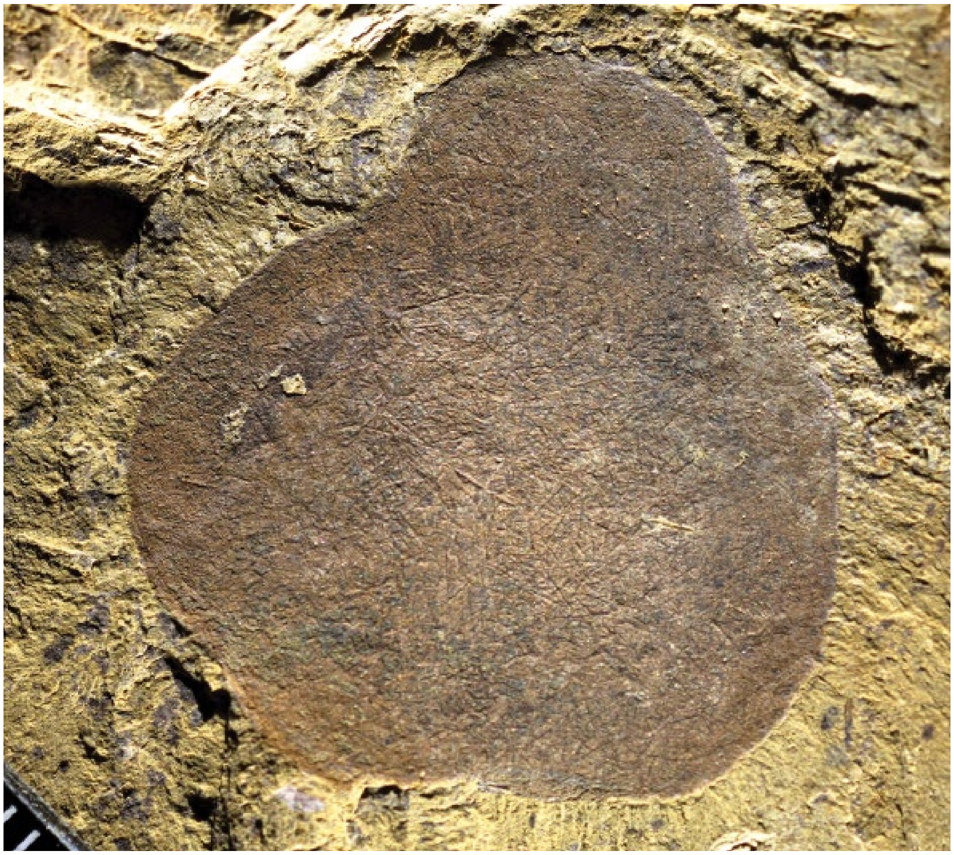
S. densa is the only known species of *Saetaspongia*. The presence of small, probable hexactine spicules in specimens from Yunnan Province suggests that it may belong to the Hexactinellida, the glass sponges (Rigby & Hou 1995). Many living hexactinellids have a basal cluster of siliceous fibers for anchorage, but a root tuft is not evident in this species.

The original specimens of *S. densa*, from the lower Cambrian Niutitang Formation of Hunan Province, China, are generally larger than those from the Chengjiang biota.

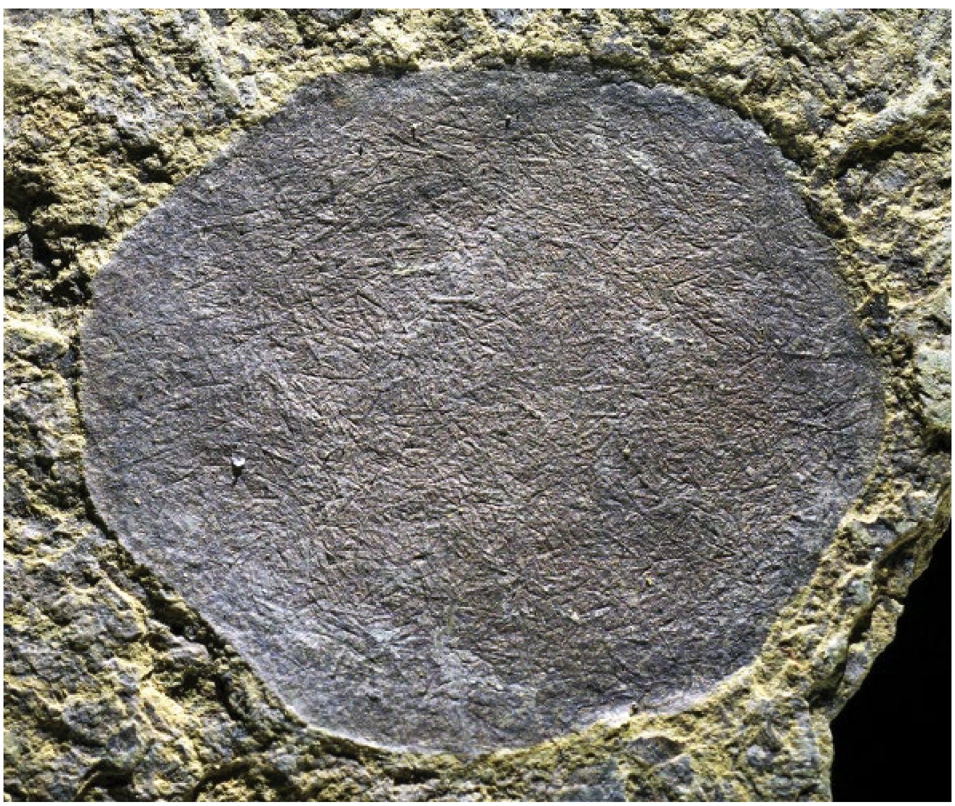
Key references

Steiner *et al.* 1993; Rigby & Hou 1995; Chen Jun-yuan *et al.* 1996; Hou *et al.* 1999, 2004a.

Figure 10.4 ***Saetaspongia densa***. **(a)** YKLP 13814, ×4.2; Ercaicun, Haikou, Kunming. **(b)** YKLP 13815, ×4.2; Ercaicun, Haikou, Kunming.



(a)



(b)

Genus *Leptomitus* Walcott, 1886

Leptomitus teretiusculus Chen, Hou & Lu, 1989

Leptomitus teretiusculus is a moderately common, thin-walled sponge species.

Specimens range up to 11 cm long and about 1.2 cm wide. The body is very elongate, tube-shaped, and possibly composed of two skeletal layers, each with single-axis (monaxon) spicules. The dominant, outer layer consists of a vertical thatch of fine and larger spicules, which in some specimens are slightly smaller in the lower half of the skeleton. The inner skeletal layer consists of tiny, more poorly defined, horizontally arranged spicules. A short fringe of spicules extends beyond the oscular margin.

Leptomitus is considered by some to be paraphyletic (possibly the stock from which a variety of demosponges evolved; Rigby 1986). It is the type genus of the family Leptomitidae.

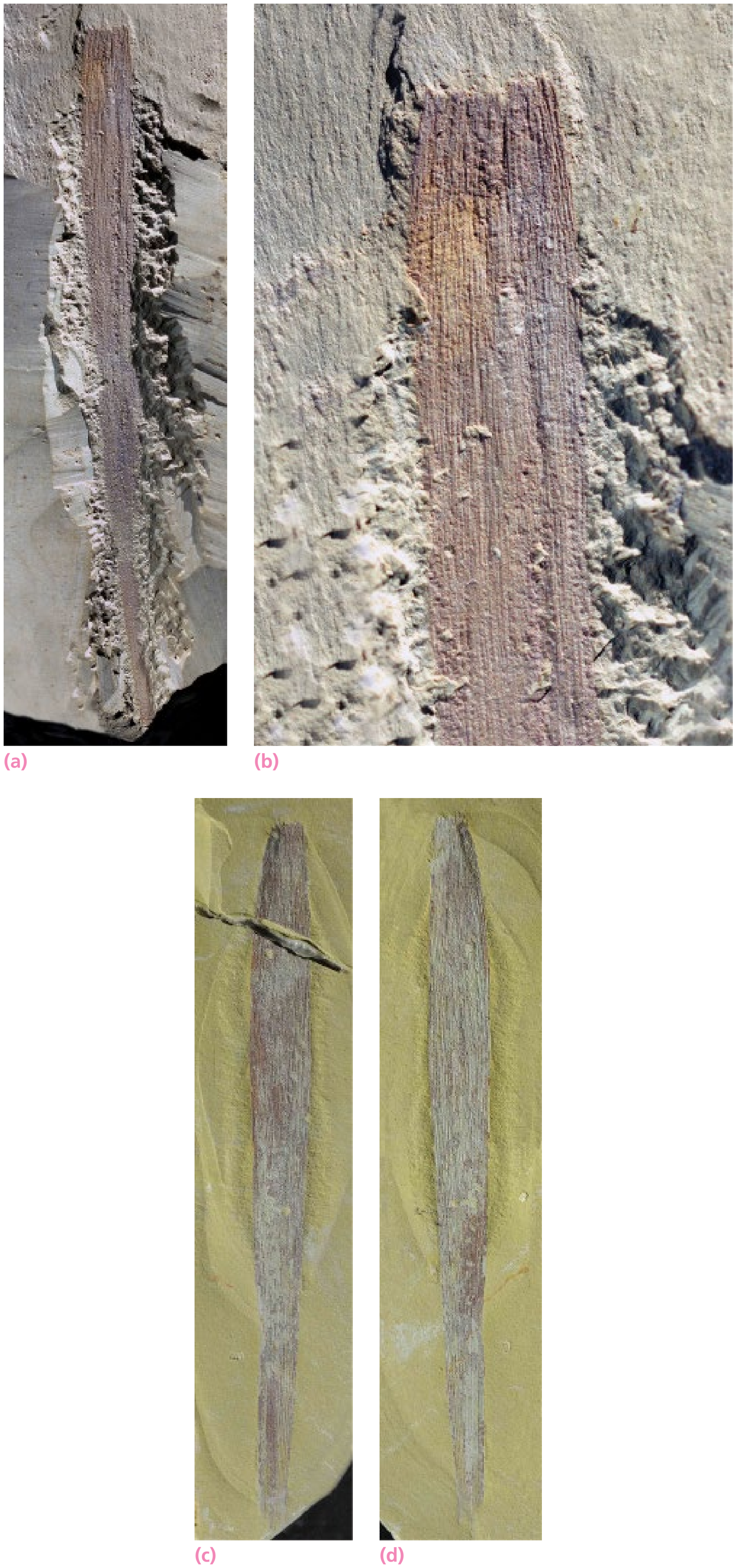
In life *L. teretiusculus* was attached to the substrate by a relatively small surface area, straining food from water pumped through its wall.

A larger *Leptomitus* species occurs in the Burgess Shale (Rigby 1986). Congeneric material has also been reported from the Cambrian of Guizhou Province, China (Zhao Yuan-long *et al.* 1999a, 1999b). *L. teretiusculus* is known only from the Chengjiang biota.

Key references

Rigby 1986; Chen Jun-yuan *et al.* 1989b; Rigby & Hou 1995; Hou *et al.* 1999, 2004a; Chen Jun-yuan 2004.

Figure 10.5 ***Leptomitus teretiusculus***. (a), (b) RCCBYU 10213, ×1.9, ×5.5; Maotianshan, Chengjiang. (c) YKLP 13817a, ×1.2; Ercaicun, Haikou, Kunming. (d) YKLP 13817b, ×1.2; Ercaicun, Haikou, Kunming.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Genus *Choiaella* Rigby & Hou, 1995

Choiaella radiata Rigby & Hou, 1995

The type material of *Choiaella radiata* occurs as iron oxide replacements of thin, spicular, vertically and diagonally flattened skeletons. Specimens are relatively rare.

In overall form the species is small and discoidal to low and broad shield-shaped or funnel-shaped. The skeleton consists essentially of a radiating thatch of small, apparently knobbly, single axis spicules (monaxons) that are generally of one size and which display bundling locally. Other than as a minor fringe, the spicules do not project beyond the margin of the disk.

The genus *Choiaella* is monotypic. It is assigned to the demosponges, the large class that includes most sponge species.

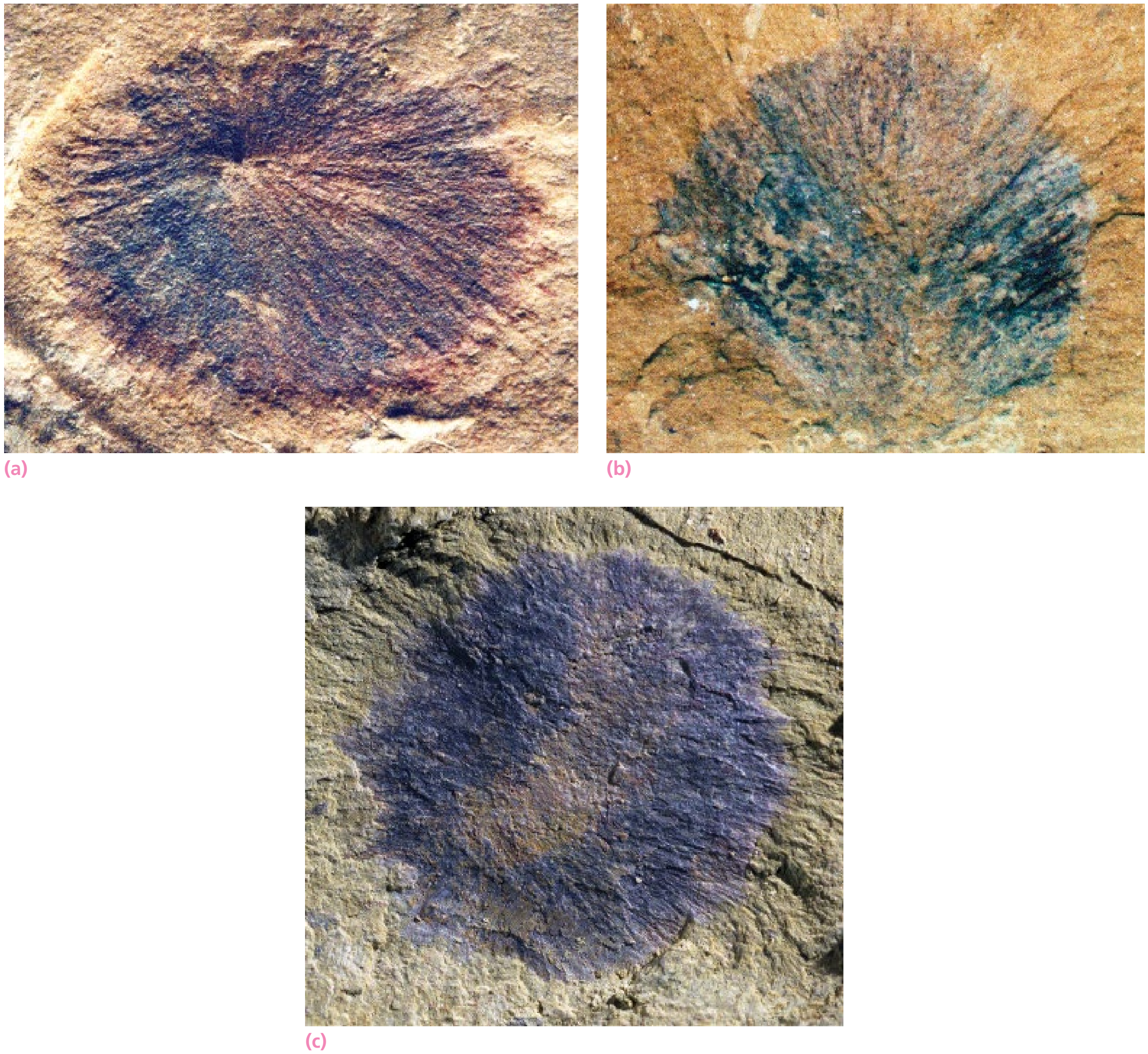
C. radiata is envisaged to be a three-dimensionally outwardly radiating tuft-like or brush-like sponge that emanates from a central point. Comparisons between this skeletal pattern and that of the living sponge *Radiella* suggest that *C. radiata* possibly had a similar, infaunal lifestyle (Rigby & Hou 1995).

This species is known only from localities in the Chengjiang area.

Key references

Rigby & Hou 1995; Hou *et al.* 1999, 2004a; Chen Jun-yuan 2004.

Figure 10.6 ***Choiaella radiata***. **(a)** NIGPAS115324, ×11.4; Xiaolantian, Chengiang. **(b)** NIGP AS 115328a, ×13.8; Maotianshan, Chengjiang. **(c)** YKLP 13818, ×6.6; Ercaicun, Haikou, Kunming.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Genus *Choia* Walcott, 1920

Choia xiaolantianensis Hou, Bergström, Wang, Feng & Chen, 1999

This is a relatively common sponge in the Chengjiang biota. It typically occurs as small, attractively shaped impression fossils.

The body has a low, conical-shaped central disk up to 2 cm in diameter, composed of short, thin monaxon (single axis) spicules that combine to give a thatch-like appearance. Radiating from the disk there is a plethora of slender and discrete monaxon spicules, some of which are longer than the diameter of the disk itself.

Choia is a demosponge and the type genus of the family Choiidae.

The low, hat-like form, together with a lack of any obvious area of attachment, indicates that *Choia* may simply have rested on the substrate, convex side up, filtering food out of water that passed radially in through the disk and out via the central region (Rigby 1986). The Recent infaunal sponge *Radiella*, in which the skeleton is an upward and outward radiating structure, provides a possible model for *Choia*. Another reconstruction has *Choia* resting on the sediment with spicules radiating upward and outward in many directions from the disk, in pin-cushion fashion (Conway Morris 1998).

C. xiaolantianensis is known only from the Chengjiang biota. Congeneric species have been reported from the Cambrian of British Columbia, Utah, and Quebec (Rigby 1986).

Key references

Rigby 1986; Rigby & Hou 1995; Hou *et al.* 1999, 2004a; Chen Jun-yuan *et al.* 2004.

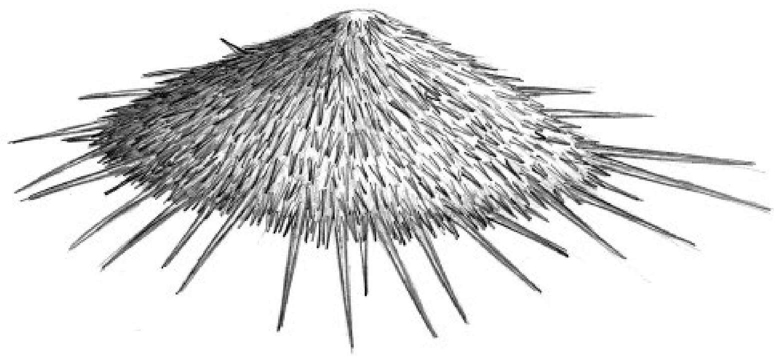
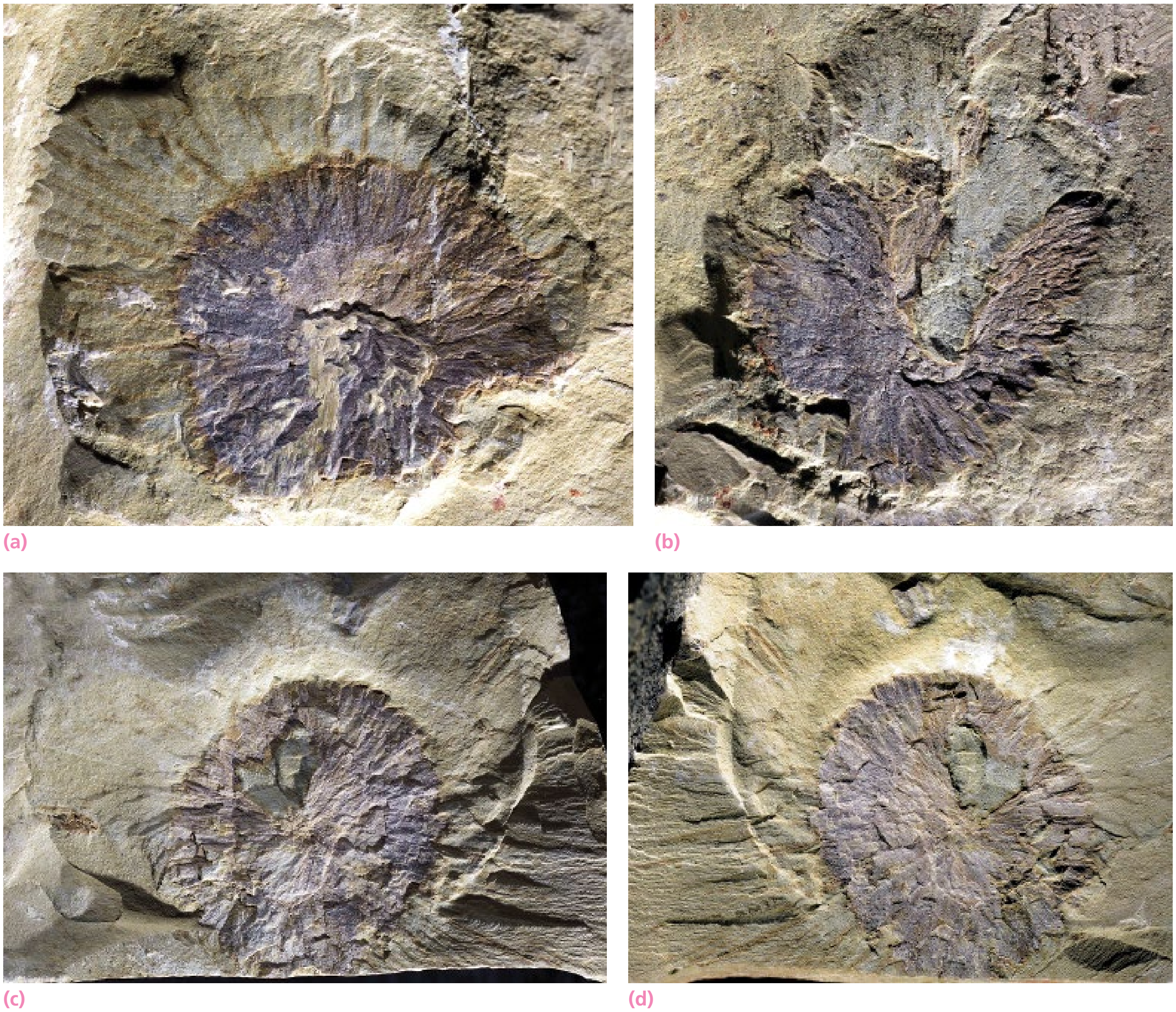


Figure 10.7 Reconstruction of ***Choia xiaolantianensis*** (after Rigby 1986 and Wu *et al.* 2014).

Figure 10.8 ***Choia xiaolantianensis***. **(a)** YKLP 13819, ×3.3; Ma'anshan, Chengjiang. **(b)** YKLP 13820, ×1.9; Ma'anshan, Chengjiang. **(c)** YKLP 13821a, ×1.9; Ma'anshan, Chengjiang. **(d)** YKLP 13821b, ×2.0; Ma'anshan, Chengjiang.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Genus *Allantospongia* Rigby & Hou, 1995

Allantospongia mica Rigby & Hou, 1995

This is a rare species. The type material consists of fairly complete and fragmentary iron oxide impression fossils that have replaced thin spicular skeletons.

The body is elongate ovate to sausage-shape in overall form and is relatively small. The holotype measures 1.4 cm by 1 cm. It consists mostly of a radiating hatch of small, single-axis (monaxon) spicules that are locally clumped into tufts. Some parts of the central area of the holotype skeleton are more open-textured. Moderately larger spicules extend outward from around the central thatched area.

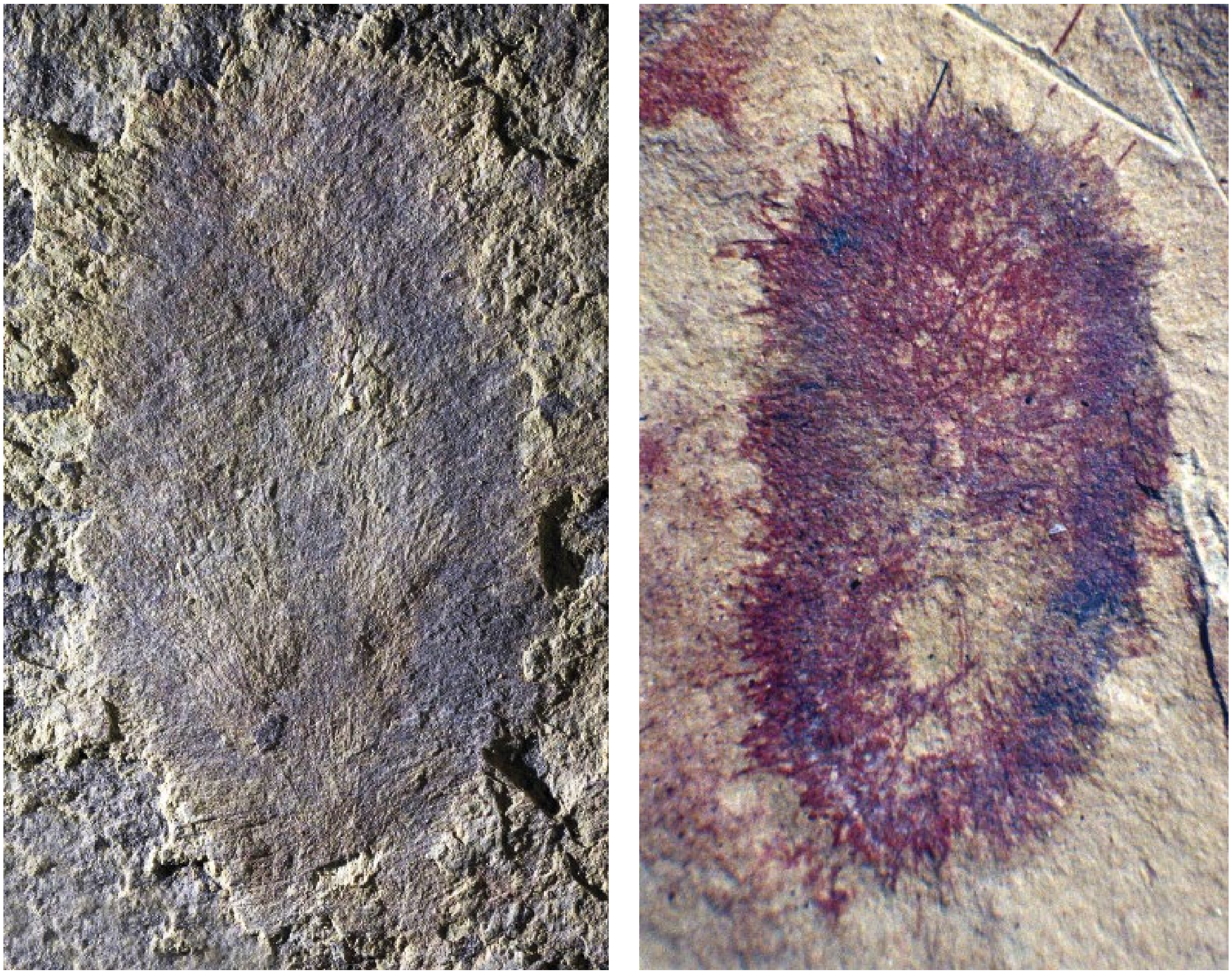
The genus *Allantospongia* is a demosponge and is known from very few species. It is assigned to the family Choiidae. The life orientation of *A. mica* is uncertain.

The species is not recorded outside the Chengjiang biota.

Key references

Rigby & Hou 1995; Hou *et al.* 1999, 2004a.

Figure 10.9 ***Allantospongia mica***. **(a)** YKLP 13822a, ×3.2; Ercaicun, Haikou, Kumming. **(b)** NIGPAS 115322, ×9.2; Xiaolantian, Chengjiang.



(a) (b)

Genus *Leptomitella* Rigby, 1986

Leptomitella conica Chen, Hou & Lu, 1989

This is one of the more common sponge species in the Chengjiang biota.

Specimens are flattened. They have an overall conical shape and are a few centimeters long. The sponge body is thin-walled. The skeleton is composed of single-axis (monaxon) spicules arranged in two layers. The outer layer consists of a vertical thatch of fine spicules and associated vertical rods. The inner layer is formed of both bundled and unbundled horizontally arranged spicules that are slightly finer than those in the outer layer.

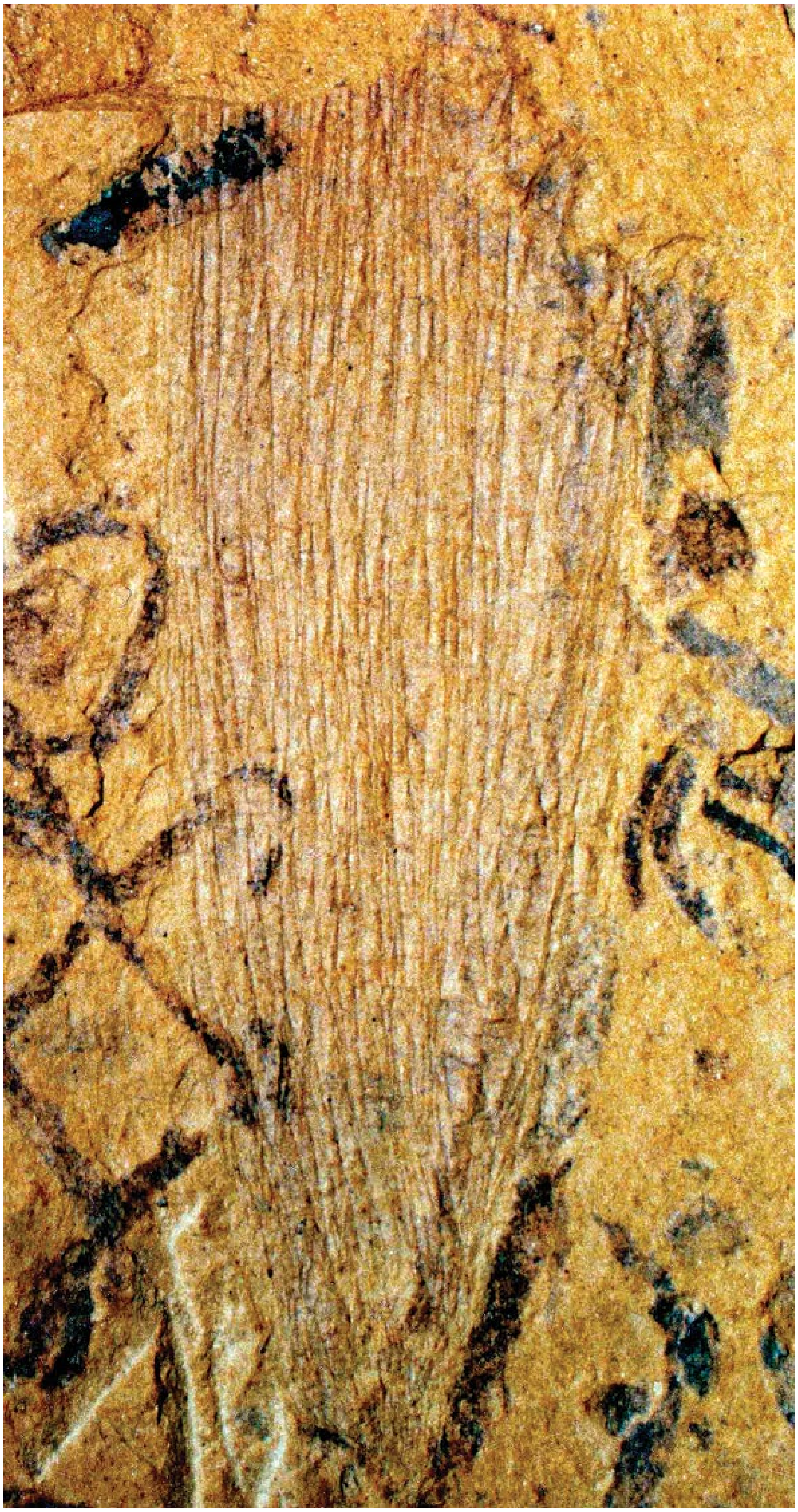
Leptomitella conica is a leptomitid demosponge. In life it was attached to the substrate at its narrow end.

Leptomitella was originally described from the Cambrian of Utah. *L. conica* is known only from the Cambrian of Yunnan Province.

Key references

Rigby 1986; Chen Jun-yuan *et al.* 1989b, 1996; Hou *et al.* 1999, 2004a; Chen Jun-yuan 2004.

Figure 10.10 ***Leptomitella conica.*** NIGPAS 108494, ×10.2; Maotianshan, Chengjiang.



Genus *Paraleptomitella* Chen, Hou & Lu, 1989

Paraleptomitella dictyodroma Chen, Hou & Lu, 1989

Paraleptomitella dictyodroma is a relatively common, tubular, thin-walled sponge that grew to about 10 cm in height. The fossils are flattened, and have a maximum width of about 1.2 cm.

The base of the sponge is narrow, and the oscular margin seems to be rounded. Its double-layered skeleton is formed of single-axis (monaxon) spicules. The outer layer consists of coarse, slightly curved oxeas (monaxons having two rays, with both ends pointed) that interlock with one another to form tapering, elongate areas filled with fine, vertically arranged spicules. Bundles of horizontally arranged spicules make up the inner layer.

P. dictyodroma is the type species of *Paraleptomitella*, a leptomitid demosponge that differs from the closely similar *Leptomitella* in the nature of the fabric of its outer skeletal layer.

It is assumed that *P. dictyodroma* lived anchored to the substrate, but no evidence for a basal tuft structure has been documented. The species has been found only in the Chengjiang biota.

Key references

Chen Jun-yuan *et al.* 1989b, 1996; Hou *et al.* 1999, 2004a; Chen Jun-yuan 2004.

Figure 10.11 Reconstruction of ***Paraleptomitella dictyodroma*** (after Chen Jun-yuan *et al.* 1989b and Wu *et al.* 2014).

Figure 10.12 ***Paraleptomitella dictyodroma***. **(a)** YKLP 13823, ×2.8; Ercaicun, Haikou, Kunming. **(b)** NIGPAS 108489 (left), NIGPAS 108490 (right), ×1.8; Maotianshan, Chengjiang.

(a) **(b)**

Paraleptomitella globula Chen, Hou & Lu, 1989

This is a distinctively shaped, thin-walled sponge, with a maximum height of about 7 cm. The lower part is elongate and tubular, some 5 mm wide, above which it expands into a balloon-like shape of around 1.5 cm maximum width, with a much narrower osculum. Both layers of the skeleton consist of single-axis (monaxon) spicules. The outer layer has an interweaving of slightly curved, coarse oxeas (monaxons having two rays, with both ends pointed), between which there is a network of fine, vertical spicules. The inner skeletal layer comprises fine horizontal spicules arranged in bundles.

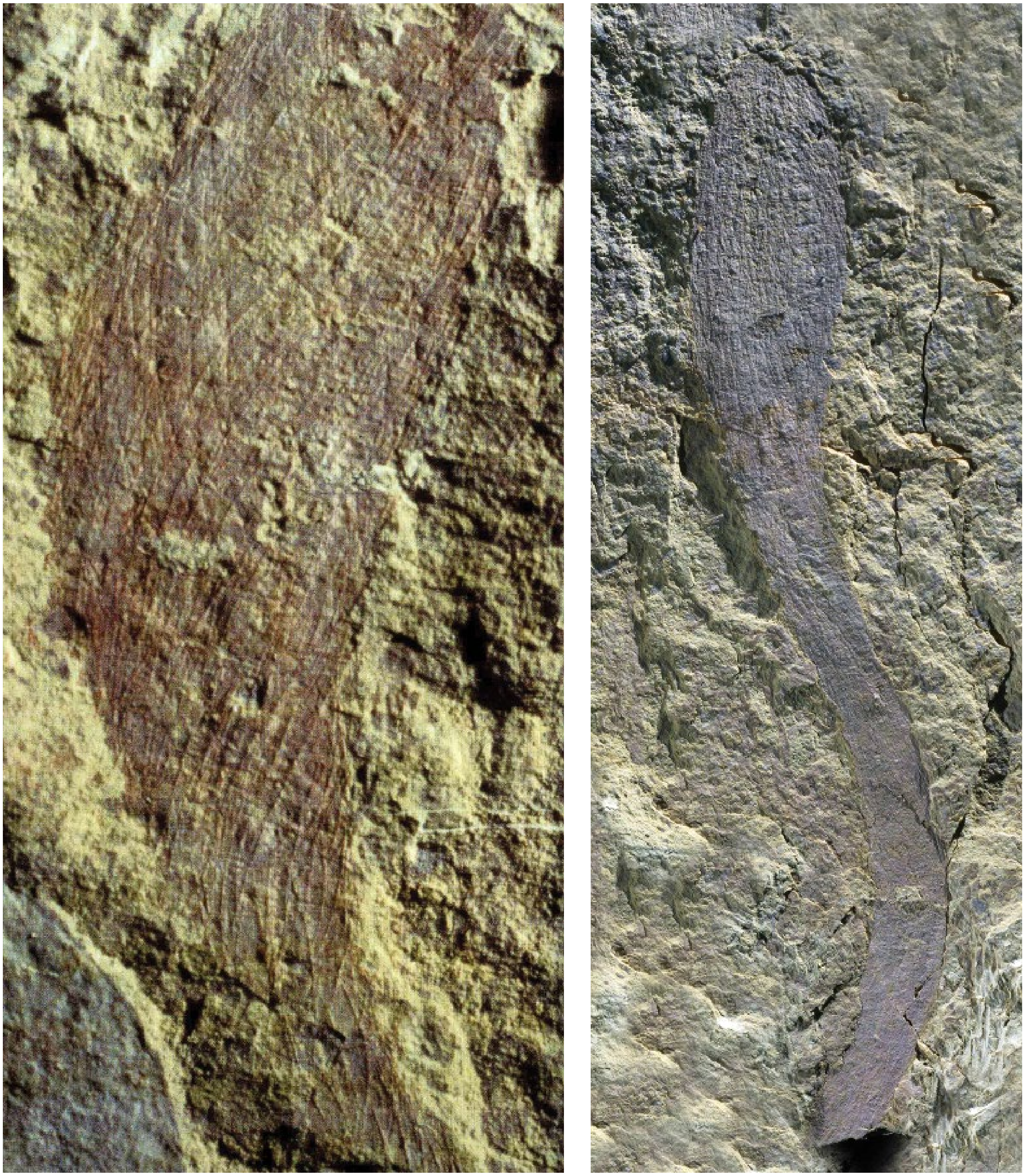
Paraleptomitella globula differs from *P. dictyodroma*, the more commonly found type species of the genus, in the shape of the upper part of its body. It presumably lived attached to the sea floor by its narrow end.

P. globula is known only from the Chengjiang biota.

Key references

Chen Jun-yuan *et al.* 1989b, 1996; Hou *et al.* 1999, 2004a; Chen Jun-yuan 2004.

Figure 10.13 ***Paraleptomitella globula***. **(a)** NIGPAS 108494, ×4.7; Maotianshan, Chengjiang. **(b)** YKLP 13824, ×3.0; Ercaicun, Haikou, Kunming.



(a) (b)

Genus *Quadrolaminiella* Chen, Hou & Li, 1990

Quadrolaminiella diagonalis Chen, Hou & Li, 1990

This large, elongate, ellipsoidal sponge is known from a few tens of specimens.

Q. diagonalis ocurrs as two-dimensional impression fossils up to 30 cm long and about 12 cm wide, narrowing proximally and also distally toward the presumed site of the osculum. The skeleton consists of four layers of single-axis (monaxon) spicules, arranged into two nets each of two layers. The spicules of the outermost layer are coarse, relatively widely spaced and extend virtually the entire length of the sponge; those of the second layer are finer, more closely spaced and horizontal. The spicules of the two layers of the inner net trend diagonally in opposite directions.

Quadrolaminiella is the only known genus of the Quadrolaminiellidae. The genus was originally considered to be a demosponge, possibly derived from *Leptomitus*-like forms by the development of, *inter alia*, a thicker skeleton. *Quadrolaminiella* has also been compared with Cambrian hexactinellids (Reitner & Mehl 1995).

The life position of *Q. diagonalis* was probably vertical, anchored to the substrate at its relatively narrow basal region.

Q. diagonalis is one of two *Quadrolaminiella* species, both of which are found only in the Chengjiang biota.

Key references

Chen Jun-yuan *et al.* 1990, 1996; Reitner & Mehl 1995; Hou *et al.* 1999, 2004a; Chen Jun-yuan 2004.

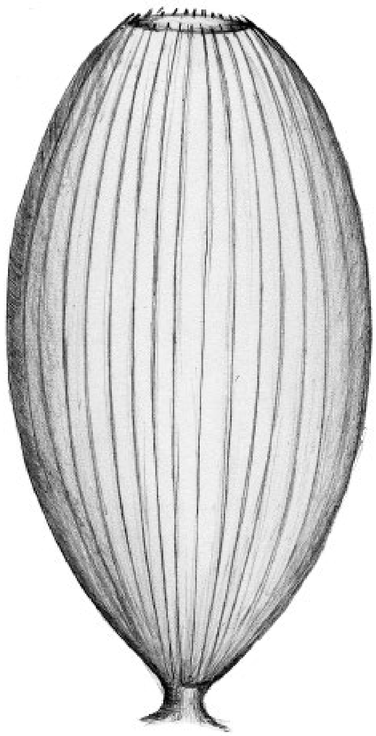


Figure 10.14 Reconstruction of ***Quadrolaminiella diagonalis*** (after Chen Jun-yuan *et al.* 1990 and Wu *et al.* 2014).

Figure 10.15 ***Quadrolaminiella diagonalis.*** RCCBYU 10214, ×1.2; Maotianshan, Chengjiang.

11 Cnidaria

Cnidarians are among the most basal metazoans represented by the solitary and colonial corals, sea anemones and sea pens (anthozoans), jellyfish (scyphozoans), and hydrozoans (e.g., *Hydra*). Cnidarians have radial symmetry and a body wall of only two layers, the endoderm and ectoderm; along with sponges and ctenophores, they sit outside the major clade of bilaterally symmetrical animals, the Bilateria. Cnidarian bodies have a single opening, which functions as both a mouth for ingestion of food and an orifice for waste disposal. Most cnidarians are marine, as adults living anchored to the sea floor with their polyps collecting food with tentacles that ring the mouth. A pelagic larval stage is common. Of the purported cnidarian species known from the Chengjiang biota, two are described here. One of these, *Archisaccophyllia kunmingensis* Hou *et al*., 2005, has been recently reinterpreted as a stem phoronid with actinotroch-like larval characters (Zhang Zhi-fei & Holmer 2014). There are two further Chengjiang species that may also be cnidarians. *Priscapennamarina angusta* Zhang & Babcock, 2001 is a possible sea pen (pennatulacean), and *Cambrohydra ercaia* Hu, 2005 is described as a possible fossil hydroid.

Genus *Archisaccophyllia* Hou, Stanley, Zhao & Ma, 2005

Archisaccophyllia kunmingensis Hou, Stanley, Zhao & Ma, 2005

Archisaccophyllia kunmingensis occurs as a remarkably complete life assemblage on a single bedding plane, 15 m^2 in area, that has yielded over 300 individuals.

The fossils are small, averaging 2 cm in length, with preserved details of the oral disk, column, some tentacles, and attachment disk. A straight column terminates in a crown with a centrally located oval mouth encircled by a single row of straight unbranched tentacles (the estimated number is 12), and the column has six, or possibly seven, longitudinal ridges, between which thin, dark irregular lines suggest mesenteries (although the number and arrangement of mesenteries cannot be precisely counted). As both laterally compressed and horizontally compressed specimens show tapering tentacles of differing length it is suggested that the tentacles were retractable.

A. kunmingensis is classified as a member of the subclass Zoantharia as it bears similarities to extant taxa collectively known as sea anemones (Hyman 1940; Hand 1954, 1955; Brusca & Brusca 1990). Certainly, the simple anatomy coupled with an early Cambrian age has been used to suggest that *A. kunmingensis* may be a possible ancestor to extant anemone and some coral groups. The preserved anatomy is insufficient to assign the species with certainty to a lower taxomonic group. However, based on the evidence for six-fold symmetry, the number of longitudinal ridges, the nature of the mesentries in the compressed column, and a possible acontia, an alliance with some members of the extant Actiniaria is suggested (Hou *et al.* 2005). In contrast, some authors consider that *A. kunmingensis* is not a cnidarian, and it has been recently reinterpreted as a stem-phoronid with actinotroch-like larval characters (Zhang Zhi-fei & Holmer 2014).

The polyps were attached to the sea floor by a pedal disk, and were closely spaced. Most specimens occur in bedding-parallel orientation, although a few specimens are preserved vertically cross-cutting the laminations in the rock. There is good evidence that the pedal disk was partly buried and that it anchored specimens to the fine-grained substrate, and that the polyps were arranged in clusters of two to five individuals similar to extant anemones.

A. kunmingensis is found only near Ercaicun in the Haikou area. Associated trilobites confirm its placement in the Cambrian *Eoredlichia-Wutingaspis* Biozone.

Key references

Hou *et al.* 2005; Zhang Zhi-fei & Holmer 2014.

The Cambrian Fossils of Chengjiang, China: The Flowering of Early Animal Life, Second Edition. Hou Xian-guang, David J. Siveter, Derek J. Siveter, Richard J. Aldridge, Cong Pei-yun, Sarah E. Gabbott, Ma Xiao-ya, Mark A. Purnell, Mark Williams.

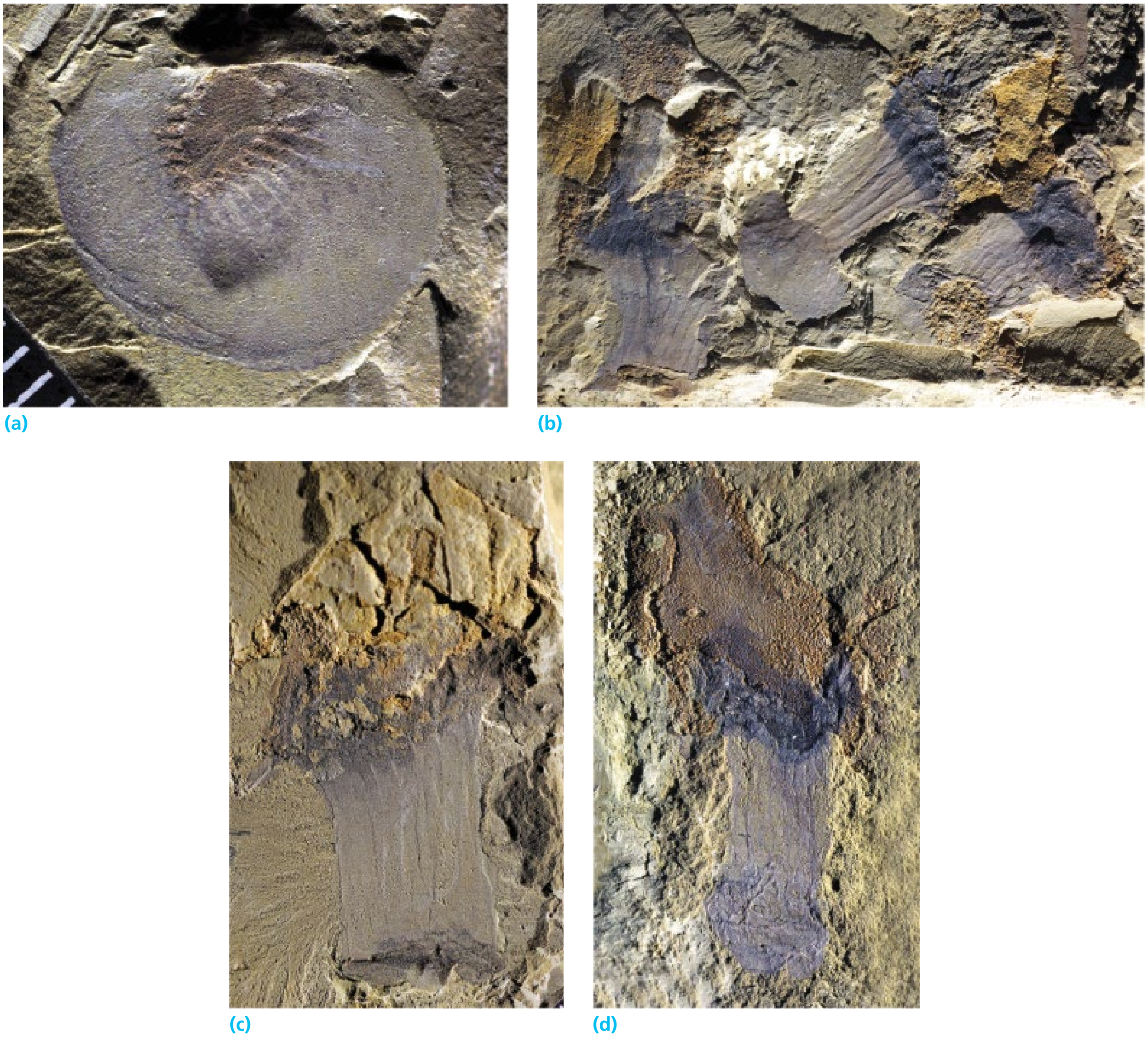


Figure 11.1 ***Archisaccophyllia kunmingensis.*** (a) YKLP 10165, ×5.7; Ercaicun, Haikou, Kunming. (b) YKLP 10382-10384, ×2.1; Ercaicun, Haikou, Kunming. (c) YKLP 10379, ×2.7; Ercaicun, Haikou, Kunming. (d) YKLP 13828, ×3.6; Ercaicun, Haikou, Kunming.

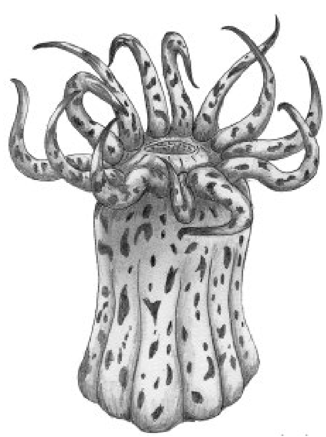


Figure 11.2 Reconstruction of ***Archisaccophyllia kunmingensis.***

Genus *Xianguangia* Chen & Erdtmann, 1991

Xianguangia sinica Chen & Erdtmann, 1991

There are tens of specimens of this species, which are dominantly preserved laterally collapsed, although specimens preserved in dorsoventral aspect do occur; all have very low relief. The tissues were completely soft in life and likely collapsed very soon after death.

The animal was conical, about 6 cm high and 3 cm across, and preserved flattened. There is a smooth pedical disk, about 9 mm high and 2.1 cm wide, which is clearly separated from the column by a 2 mm thick constriction. The column tapers from the base upward, and extending from the top of the column are about 16 tentacular structures, which are all approximately the same size and clearly were flexible. The tentacles, which taper to a point, are assumed to have surrounded a centrally positioned orifice although that site is obscured by the tentacles. The column wall may have been thin so as to allow the internal septa partitions to be seen, of which there appear to be about 16.

On the basis of external morphology this species has been allied with the sea anemones (Chen Jun-yuan & Erdtmann 1991). The number of projections on the body wall is thought to correspond to internal compartments (16) within the body of a typical modern sea anemone.

Xianguangia sinica is known only from the lower Cambrian of Yunnan Province.

Key references

Chen Jun-yuan & Erdtmann 1991; Hou *et al*. 2004a; Chen Jun-yuan 2004.

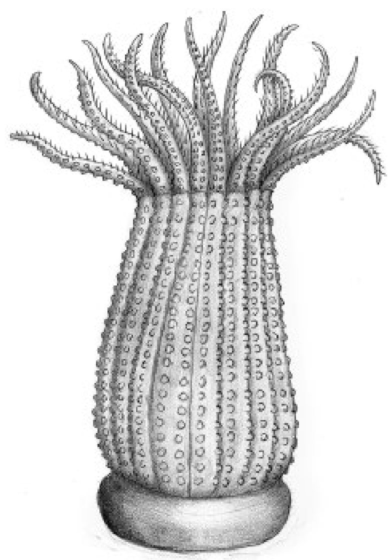
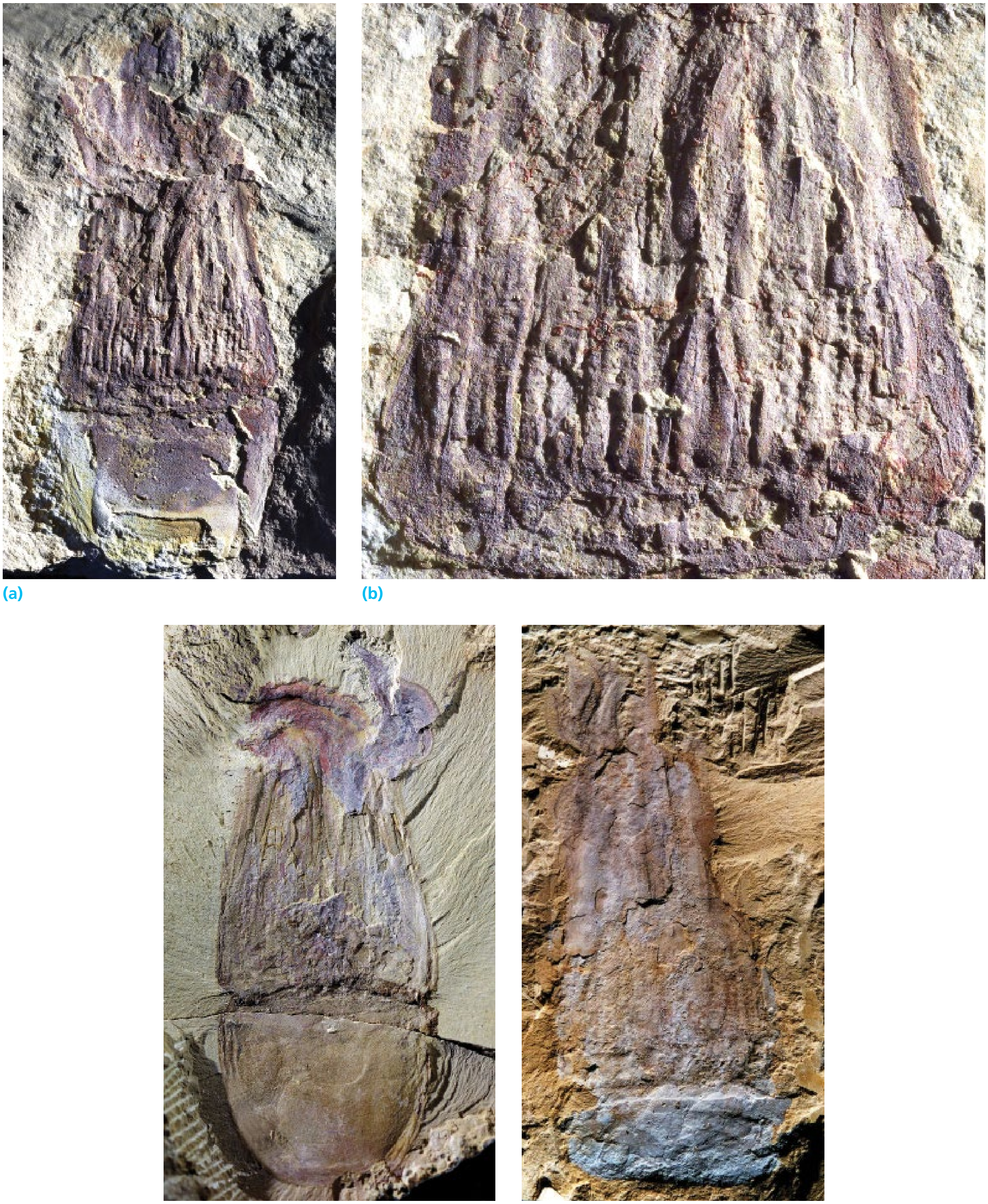


Figure 11.3 Reconstruction of ***Xianguangia sinica*** (modified from Hou *et al*. 2004a).

Figure 11.4 ***Xianguangia sinica***. **(a)**, **(b)** YKLP 13829, ×2.1, ×5.9; Mafang, Haikou, Kunming. **(c)** YKLP 13830, ×2.7; Ercaicun, Haikou, Kunming. **(d)** NIGPAS 108506a, ×2.1; Maotianshan, Chengjiang.



(a) (b) (c) (d)

12 Entoprocta

Extant members of the phylum Entoprocta are small, sessile, benthic animals. They are goblet-shaped, either solitary or colonial, and use their crown of ciliated tentacles for suspension feeding. Entoprocts are monophyletic, and widely agreed to sit within Spiralia. Their relationship with other spiralians, including the Trochozoa, however, remains unclear. Their fossil record consists of only two species, one Jurassic occurrence and one Cambrian record from the Chengjiang biota.

Genus *Cotyledion* Luo & Hu *in* Luo, Hu, Chen, Zhang & Tao, 1999

Cotyledion tylodes Luo & Hu *in* Luo, Hu, Chen, Zhang & Tao, 1999

Cotyledion tylodes is one of a number of taxa of enigmatic goblet-shaped organisms in the Chengjiang biota. Specimens of this species were originally considered, with reservation, as Echinodermata (Chen Jun-yuan *et al.* 1996), or referred to Problematica (Luo *et al.* 1999). Subsequent studies based on larger collections have reached rather different conclusions regarding the affinities of *C. tylodes*, which is now known from more than 400 specimens from several localities.

C. tylodes is an erect, goblet-shaped animal with a body comprising a stalked calyx ranging between 4.3 mm and 4.2 cm in length. The calyx is cup-shaped or conical with an open central cavity the upper rim of which is encircled by slender tentacles. Specimens preserve evidence of at least nine tentacles but there may have been as many as 34. The stalk is cylindrical or slightly tapered in shape, and varies in length; it is terminated by a knob-shaped holdfast, which in many specimens is attached to a hard skeletal fragment (e.g., trilobite segment). The body wall is completely covered by oval plates or sclerites, which may have been biomineralized in life, forming a scleritome. Internally, the calyx contains a U-shaped structure, preserved as dark traces. Crucially for the phylogenetic hypothesis that *C. tylodes* is an entoproct, this is interpreted as an alimentary canal with a narrow anterior esophagus, enlarged stomach, and curved narrow intestine connecting a mouth and an anal opening, both of which are associated with the ring of tentacles (Zhang Zhi-fei *et al.* 2013).

Early interpretations of the affinity of *Cotyledion* were hampered by the lack of material, hence the rather equivocal assignments to Echinodermata (Chen Jun-yuan *et al.* 1996) and Problematica (Luo *et al.* 1999). Lophophorate affinities were suggested (Chen Liang-zhong *et al.* 2002; Zhang Xing-liang *et al.* 2001) but that interpretation was considered to be based on taphonomic artifacts, and a stem-cnidarian affinity was thought to be more likely (Clausen *et al.* 2010). More recently it has been argued that the holdfast, stalk, and calyx – with tentacles surrounding a mouth and anus linked by a U-shaped gut – represent a combination of features seen only in entoprocts (Zhang Zhi-fei *et al.* 2013). *Cotyledion* differs in several respects from extant entoprocts (larger size, more extensive body cavity, external sclerites), and its exact phylogenetic placement remains equivocal, but the balance of evidence has been taken to indicate that it is a stem entoproct. *Cambrotentacus sanwuia* Zhang & Shu *in* Zhang *et al.*, 2001 probably represents the same species as *C. tylodes*.

Cotyledion has been interpreted as a solitary, sessile, benthic animal and a presumed suspension feeder (Zhang Zhi-fei *et al.* 2013). Multiple specimens gregariously attached to hard skeletal remains of other animals are not uncommon, and there is evidence that the tentacles had a degree of retractability.

Cotyledion tylodes is known only from the Chengjiang biota, but occurs at several localities – Ercai, Mafang, Jianshan, and Erjie – near Haikou Town, Yunnan Province.

Key references

Clausen *et al.* 2010; Zhang Zhi-fei *et al.* 2013.

The Cambrian Fossils of Chengjiang, China: The Flowering of Early Animal Life, Second Edition. Hou Xian-guang, David J. Siveter, Derek J. Siveter, Richard J. Aldridge, Cong Pei-yun, Sarah E. Gabbott, Ma Xiao-ya, Mark A. Purnell, Mark Williams.

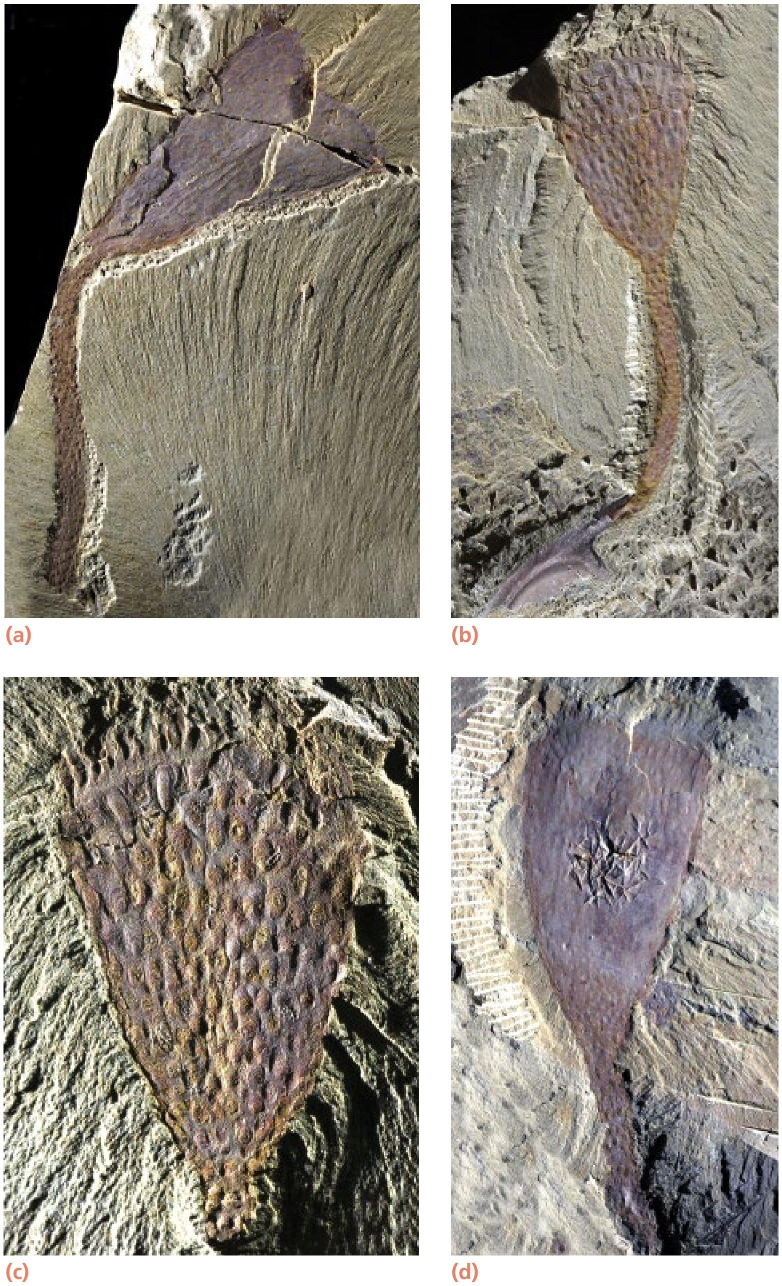


Figure 12.1 ***Cotyledion tylodes***. **(a)** YKLP 11045, ×1.5; Ercaicun, Haikou, Kunming. **(b)** YKLP 13832a, ×1.7; Erjie, Jinning. **(c)** YKLP 13833, ×3.6; Erjie, Jinning. **(d)** YKLP 13834, ×1.3; Erjie, Jinning.

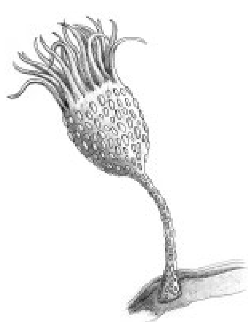


Figure 12.2 Reconstruction of ***Cotyledion tylodes***.

13 Phoronida

Phoronida is a phylum of marine benthic animals that are commonly known as horseshoe worms. Diversity is low, with only 10 extant species known. The body of adult phoronids can be divided into two regions: a conspicuous crown of tentacles (the lophophore) arranged in a horseshoe shape around the mouth; and a slender trunk with a bulbous swelling at the posterior end (the ampulla) anchoring the animal inside its chitinous tube, which supports and protects the soft body. Well-developed muscles running the length of the body enable the animal to withdraw entirely into its tube. When the lophophore is extended at the top of the body, cilia on the tentacles draw food particles to the mouth. The intestine is U-shaped, so food moves down through the descending part of the gut to the stomach, which is in the ampulla. Solid wastes are then moved up through the ascending part of the gut and out through the anus, which is outside and slightly below the lophophore.

Traditionally, phoronids were grouped with brachiopods and bryozoans into the clade Lophophorata, as they all feed using lophophores. However, numerous molecular studies failed to find support for Lophophorata as a monophyletic clade (Kocot *et al.* 2010; Edgecombe *et al.* 2011b) and resolved Phoronida as the sister group to Brachiopoda. Despite this, more recent molecular phylogenies have renewed support for the traditional view (Nesnidal *et al.* 2013; Laumer *et al.* 2015) that the Lophophorata hypothesis might be correct and Bryozoa becomes the sister group to Phoronida, with this clade sister to Brachiopoda.

There are no indisputable body fossils of phoronids (Taylor, P.D. *et al.* 2010). The earliest putative fossil record is *Iotuba chengjiangensis* (Chen Jun-yuan & Zhou 1997) from the Chengjiang biota. The Chengjiang species *Archisaccophyllia kunmingensis* Hou *et al*., 2005, generally considered to be a cnidarian, has also been interpreted as a stem phoronid (Zhang Zhi-fei & Holmer 2014). Various trace fossils from different geological periods have also been suggested to have been made by phoronids.

Genus *Iotuba* Chen & Zhou, 1997

Iotuba chengjiangensis Chen & Zhou, 1997

Iotuba chengjiangensis is relatively rare, known from fewer than 10 specimens. The specimens are compressed on the rock and preserved in a pinkish color. Slight relief is seen around the sediment-filled intestine and the body surface ornament. The body is preserved either relatively straight or in a U-shaped curve.

This is a relatively large worm, and a complete specimen can reach 24 cm long. The elongate body is cylindrical, slightly tapered toward the anterior end, which is armed by a circle of long setae or tentacles. The body surface is covered with fine, dense spines and indistinct annulations. In the initial descriptions (Chen Jun-yuan & Zhou 1997; Chen Jun-yuan 2004), it is suggested that the trunk tube has only one opening anteriorly, with a U-shaped digestive tract recurved at the posterior end of the trunk. However, later researchers considered that the U-shaped intestine is an artifact caused by the curvature of the trunk (Huang 2005; Ma *et al.* 2010). Therefore, the digestive tract is actually straight, with the mouth and anal openings situated at the anterior and posterior ends of the body respectively. A muscular pharynx is observed at the anterior part of the trunk (Chen Jun-yuan 2004; Huang 2005).

The Cambrian Fossils of Chengjiang, China: The Flowering of Early Animal Life, Second Edition. Hou Xian-guang, David J. Siveter, Derek J. Siveter, Richard J. Aldridge, Cong Pei-yun, Sarah E. Gabbott, Ma Xiao-ya, Mark A. Purnell, Mark Williams.

I. chengjiangensis is the only known species of the genus *Iotuba*. A new genus and species erected later, namely *Eophoronis chengjiangensis* Chen, 2004, is considered to be a junior synonym (Huang 2005; Ma *et al.* 2010). The animal was originally put into the Phoronida based on its U-shaped digestive tract and a circular crown of tentacles at the anterior end of the body (Chen Jun-yuan & Zhou 1997; Chen Jun-yuan 2004). However, later studies discounted the presence of a U-shaped digestive tract in this animal, and the circular crown of tentacles was also thought to differ from the horseshoe-shaped tentacle crown of extant Phoronida (Huang 2005; Ma *et al.* 2010). Consequently it was suggested that this animal had closer affinity with priapulids and in particular with the living tentacular priapulid *Maccabeus* (Huang 2005). Nevertheless, because it lacks some diagnostic features of priapulids, the affinity of the species remains problematic.

Due to the controversy regarding the morphology and affinity of *I. chengjiangensis*, its mode of life is unclear. The sediment infill in some parts of the digestive tract indicates that the animal might have burrowed in the sea bottom and engaged at least partially in deposit feeding.

I. chengjiangensis is unknown outside the Chengjiang biota.

Key references

Chen Jun-yuan & Zhou 1997; Chen Jun-yuan 2004; Huang 2005; Ma *et al.* 2010.

Figure 13.1 ***Iotuba chengjiangensis***. (a) ELRCC 53002a, ×3.0; Maotianshan, Chengjiang. (b) (c) ELRCC 53001b, ×1.5, ×4.0; Maotianshan, Chengjiang.

14 Brachiopoda

Brachiopods are benthic marine animals with a shell consisting of two valves, termed dorsal and ventral; the ventral valve is usually the slightly larger of the pair. Attachment to the sea floor is often by means of a fleshy stalk or pedicle that extends from the posterior end of the shell. Brachiopods gain their food from suspended organic matter in the water using a delicate filtering organ termed the lophophore. All the brachiopods from the Chengjiang biota are relatively primitive, lacking hinge structures (except *Longtancunella chengjiangensis*) to operate the valves, which are held together in these forms by internal muscle systems. Some of them, such as *Yuganotheca elegans*, probably represent stem brachiopods. At least two major groups are represented in the Chengjiang biota: the Linguliformea, in which the shell is chitinophosphatic and soft parts are known from an increasing number of species; and the Rhynchonelliformea, which have calcareous shells and articulated structures (e.g., the short strophic hinge line of *Longtancunella*) but for which examples with soft-part preservation are scarce (e.g., see Zhang Zhi-fei *et al*. 2007b, 2011b). The enigmatic genus *Heliomedusa* was considered to be a representative of another major group of brachiopods, the Craniiformea, but recently it was re-evaluated as a stem brachiopod.

The Cambrian Fossils of Chengjiang, China: The Flowering of Early Animal Life, Second Edition. Hou Xian-guang, David J. Siveter, Derek J. Siveter, Richard J. Aldridge, Cong Pei-yun, Sarah E. Gabbott, Ma Xiao-ya, Mark A. Purnell, Mark Williams.

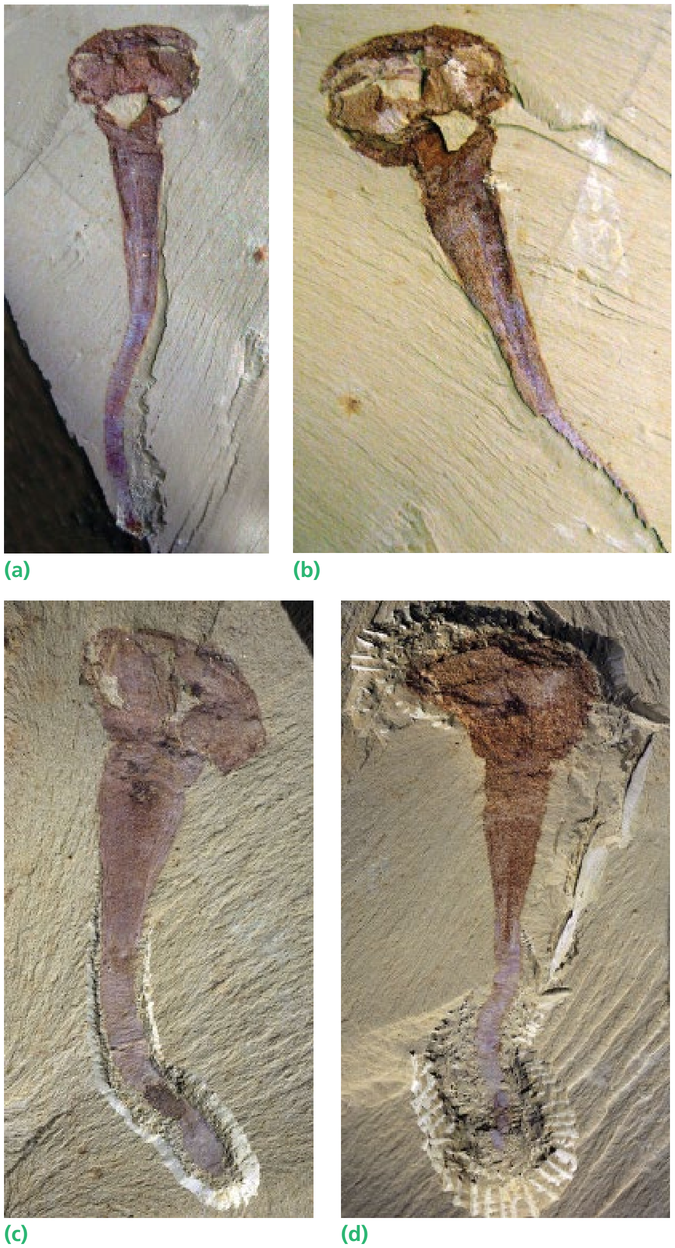


Figure 14.1 ***Yuganotheca elegans***. **(a)** YKLP 13835a, ×1.4; Ercaicun, Haikou, Kunming. **(b)** YKLP 13835b, ×2.0; Ercaicun, Haikou, Kunming. **(c)** YKLP 13837, ×2.2; Ercaicun, Haikou, Kunming. **(d)** YKLP 13838, ×2.3; Ercaicun, Haikou, Kunming.

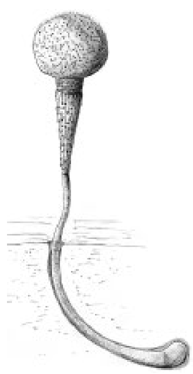


Figure 14.2 Reconstruction of ***Yuganotheca elegans***, with only one valve shown (modified from Zhang Zhi-fei *et al.* 2014).

Genus *Yuganotheca* Zhang, Li & Holmer *in* Zhang *et al.*, 2014

Yuganotheca elegans Zhang, Li & Holmer *in* Zhang *et al.*, 2014

Yuganotheca elegans is known from hundreds of specimens, typically as mass accumulations. The part of the animal containing the valves is invariably preserved as a mold of reddish-brown color covered by siliceous grains that are possibly a result of agglutination (Zhang Zhi-fei *et al.* 2014). The pedicle normally occurs as a flattened grayish impression. The lophophores are preserved in a few specimens.

The pair of valves are connected by a short, soft-bodied median collar to an elongate cone-shaped tube from which protrudes a soft pedicle. The valves are subcircular to oval in outline, strongly convex, and up to 1.4 cm long and about 1.7 cm wide. They are commonly strongly deformed and were probably at best poorly mineralized. Delicate setae are preserved projecting from the margin of the valves. The curled terminal part of each lophophore bears eight fine tentacles. The median collar connects to the umbo of the ventral valve and shows annulations, suggesting that this region was possibly flexible and contractible. The conical tube is up to 2.1 cm long, shows longitudinal growth increments, and has a distinctive edge, suggesting some degree of rigidity and biomineralization. The narrow pedicle is up to 3 cm long and has a terminal bulb. Annulations are apparent along its length and a supposed coelomic canal is observed in some specimens. A possible U-shaped gut occurs in the region of the median collar and conical tube.

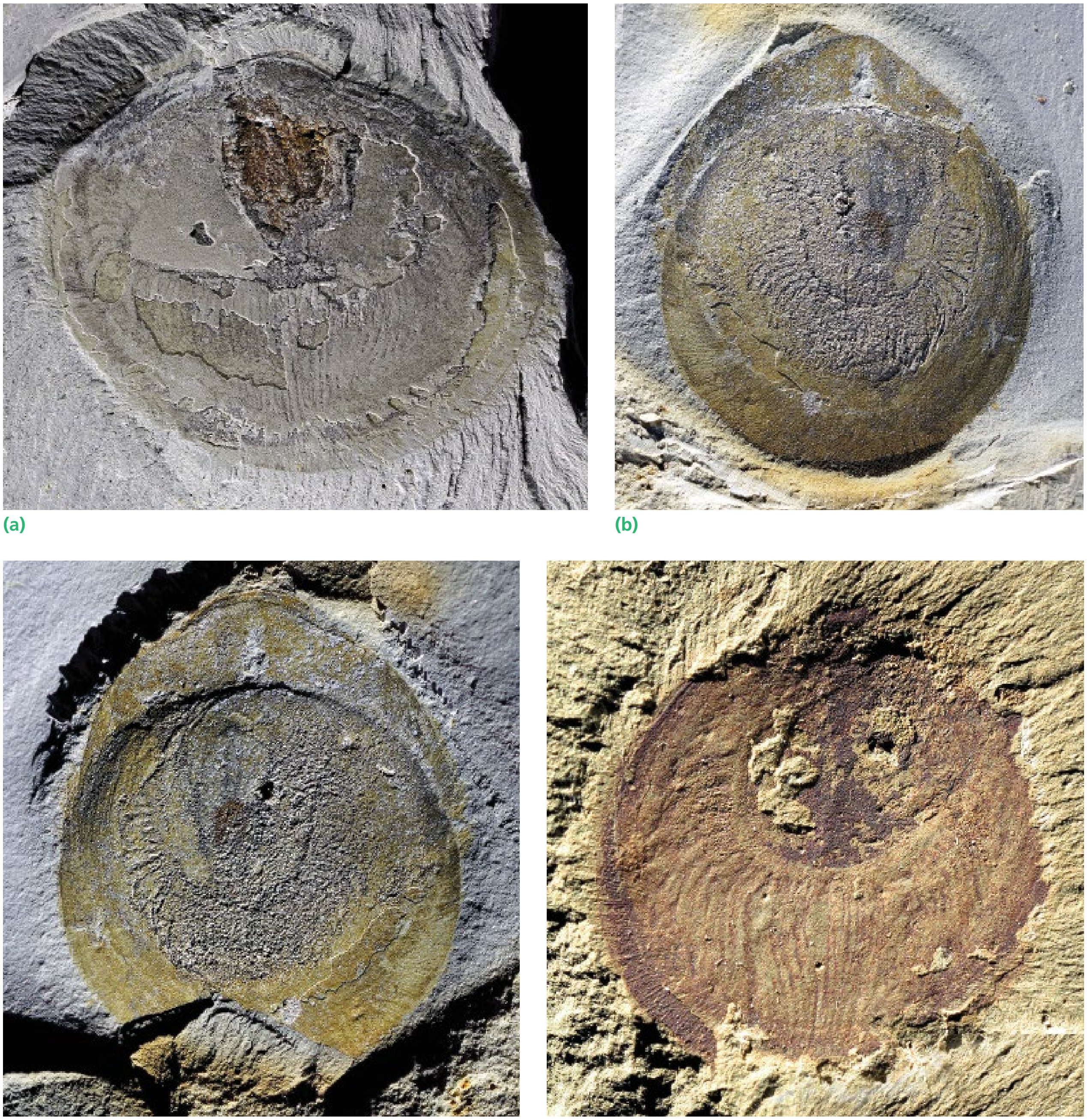
Y. elegans not only has characters typical of brachiopods, such as a pair of bisymmetrical valves and a pedicle with a coelomic cavity, but also it displays some features recalling living phoronids, such as agglutination, a tubular structure, and a U-shaped gut. *Y. elegans* has been, therefore, interpreted as a stem group brachiopod, representing an evolutionary transition from phoronids to brachiopods (Zhang Zhi-fei *et al.* 2014).

The long pedicle and its terminal bulb for attachment indicate that *Y. elegans* was probably a semi-infaunal sessile animal. The marginal setae and the morphology of the lophophore suggest that *Y. elegans* fed by filtering organic matter in the sea water. *Y. elegans* is known from localities in Haikou, Jinning, Annin, and the Chengjiang area.

Key reference

Zhang Zhi-fei *et al.* 2014.

Figure 14.3 ***Heliomedusa orienta*. (a)** YKLP 13839, ×4.0; Ercaicun, Haikou, Kunming. **(b)** YKLP 13840, ×3.8; Ercaicun, Haikou, Kunming. **(c)** YKLP 13841, ×4.1; Ercaicun, Haikou, Kunming. **(d)** RCCBYU 10204, ×4.2; Mafang, Haikou, Kunming.



(a) (b) (c) (d)

Genus *Heliomedusa* Sun & Hou, 1987

Heliomedusa orienta Sun & Hou, 1987

This ovate brachiopod is one of the commonest animals in the Chengjiang biota. The specimens are preserved as red-stained composite molds and casts, with internal features strongly displayed. The specimens show considerable compaction with associated deformation, although some of the original convexity of the valves may remain. Preserved soft tissues reported from specimens of *Heliomedusa* include sensory setae, often apparent around the margin, the lophophore, mantle canals, and probable traces of the nerves.

Both valves are convex, from 0.3 to 2.2 cm in length and generally slightly broader than long; the posterior margin is straight or very slightly curved. The shell is thin and appears to have been only weakly biomineralized. The ventral valve shows a beak-like umbo. The apex of the dorsal valve lies to the posterior of the center of the shell, while the ventral apex is at the posterior margin, where it is commonly preserved flattened to form a concave circular cicatrix, or attachment scar. Muscle scars are often evident, with an elevated main middle scar flanked by pairs of anterolateral and posterolateral scars. The surfaces of the valves clearly show growth lines and fine radial ridges. Dense, short, fine setae extend along almost the entire margin of both valves; a few of these setae are distinctively coarser and longer than their neighbors. The lophophore is well preserved in many specimens, with two arms freely curving posteriorly along the lateral body wall. Both arms bear a series of long, slender tentacles, each of which bears two rows of fine lateral cilia. No sign of a pedicle has been observed.

Although it was originally described as a jellyfish (Sun & Hou 1987a) *Heliomedusa* is now accepted to be a brachiopod. However, its position within the Brachiopoda is quite controversial. Jin and Wang (1992) considered that *Heliomedusa* was a craniopsid (Craniiformea). That interpretation was widely followed (Hou *et al.* 1999, 2004a; Popov & Holmer 2000; Zhang Xi-guang *et al.* 2003) until Chen Jun-

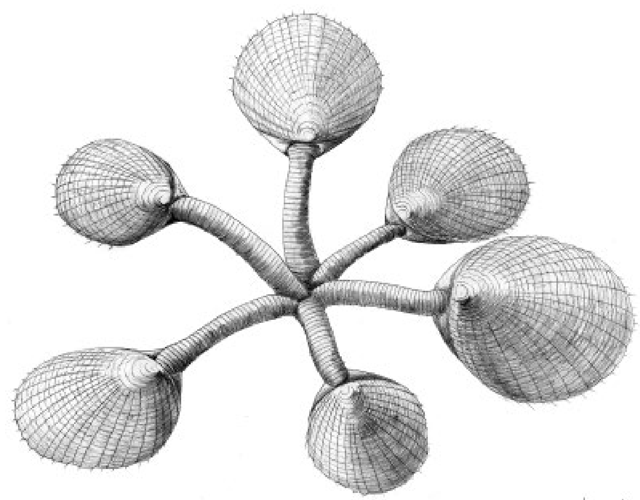


Figure 14.4 Reconstruction of ***Longtancunella chengjiangensis***.

Figure 14.5 ***Longtancunella chengjiangensis***. **(a)** RCCBYU 10292, ×2.9; Mafang, Haikou, Kunming. **(b)** NIGPAS 11545a, ×3.6; Maotianshan, Chengjiang.

(a)

(b)

yuan *et al.* (2007a) reinterpreted *Heliomedusa* as a discinid, a group of Linguliformea. Others have argued that *Heliomedusa* might be a stem brachiopod (Zhang Zhi-fei *et al.* 2009).

Heliomedusa lacks a pedicle, and the fine setae that occur around much of its margin suggest that this species did not burrow but lay on the surface of the sediment, as an epifaunal suspension feeder (Chen Jun-yuan & Zhou 1997; Zhang Zhi-fei *et al.* 2009). The cicatrix sometimes apparent at the ventral apex indicates that some or all individuals may have been attached to a hard substrate.

This species has a widespread distribution. It occurs at many Chengjiang localities in Yunnan Province.

Key references:

Sun & Hou 1987a; Jin & Wang 1992; Hou *et al.* 1999, 2004a; Chen Jun-yuan *et al.* 2007a; Zhang Zhi-fei *et al.* 2009.

Genus *Longtancunella* Hou, Bergström, Wang, Feng & Chen, 1999

Longtancunella chengjiangensis Hou, Bergström, Wang, Feng & Chen, 1999

This brachiopod mostly occurs as clusters conjoined by the pedicles, although isolated individuals do occur. It is generally found anchored by its pedicle to other animals, such as fragments of trilobites and the shells of other brachiopods. Both the shell and the pedicle are normally preserved as darkened flat impressions. Some features show slight relief, particularly the pedicle.

Both valves are of similar size, thin, slightly convex, and subcircular in outline. Their maximum length is 2.1 cm and maximum width is about 1.9 cm. A short strophic hinge line has been recognized in one specimen. The original

Figure 14.6 ***Diandongia pista*****. (a)** RCCBYU 10291, ×8.9; Mafang, Haikou, Kunming. **(b)** RCCBYU 10289, ×8.4; Mafang, Haikou, Kunming. **(c)** YKLP 13845, ×5.1; Mafang, Haikou, Kunming.

(a)

(b)

(c)

shell material is not preserved and neither ornament nor growth lines are apparent. Sparse, delicate setae are evident along the mantle margin, extending 1–2 mm beyond the edge of the shell. In some cases, the remnants of a pair of lophophoral arms are preserved. The remains of the mantle canal might be represented by grooves on the shell. The pedicle protrudes from a hole located in the umbo region of ventral valve. It is robust, less than 1 cm long and tapered. Some pedicles are clearly annulated.

Longtancunella has long been regarded as a lingulid brachiopod (Hou *et al.* 1999; Zhang Zhi-fei *et al.* 2007c), but Zhang Zhi-fei *et al.* (2011a) considered it to be an early representative of the rhynchonelliforms, possibly belonging to the Class Chileata.

The apparent gregarious association of individuals indicates that *Longtancunella* was probably an epifaunal suspension feeder, with the stout pedicle holding the animal clear of the muddy seabed.

Longtancunella is a rare component of the Chengjiang biota. It has been found in the Haikou, Jinning, and Chengjiang areas.

Key references

Hou *et al.* 1999, 2004a; Zhang Zhi-fei *et al.* 2007c, 2011a.

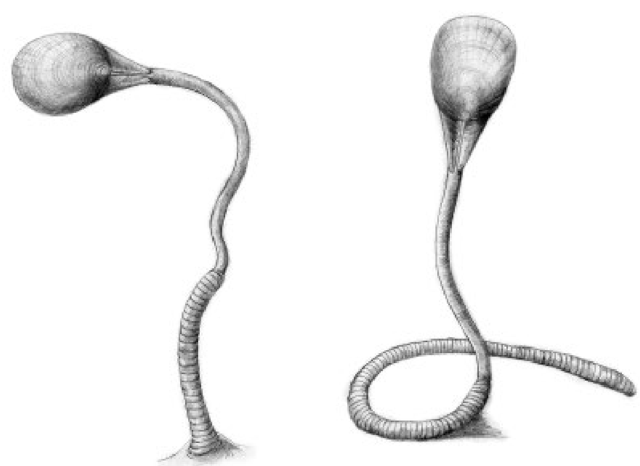
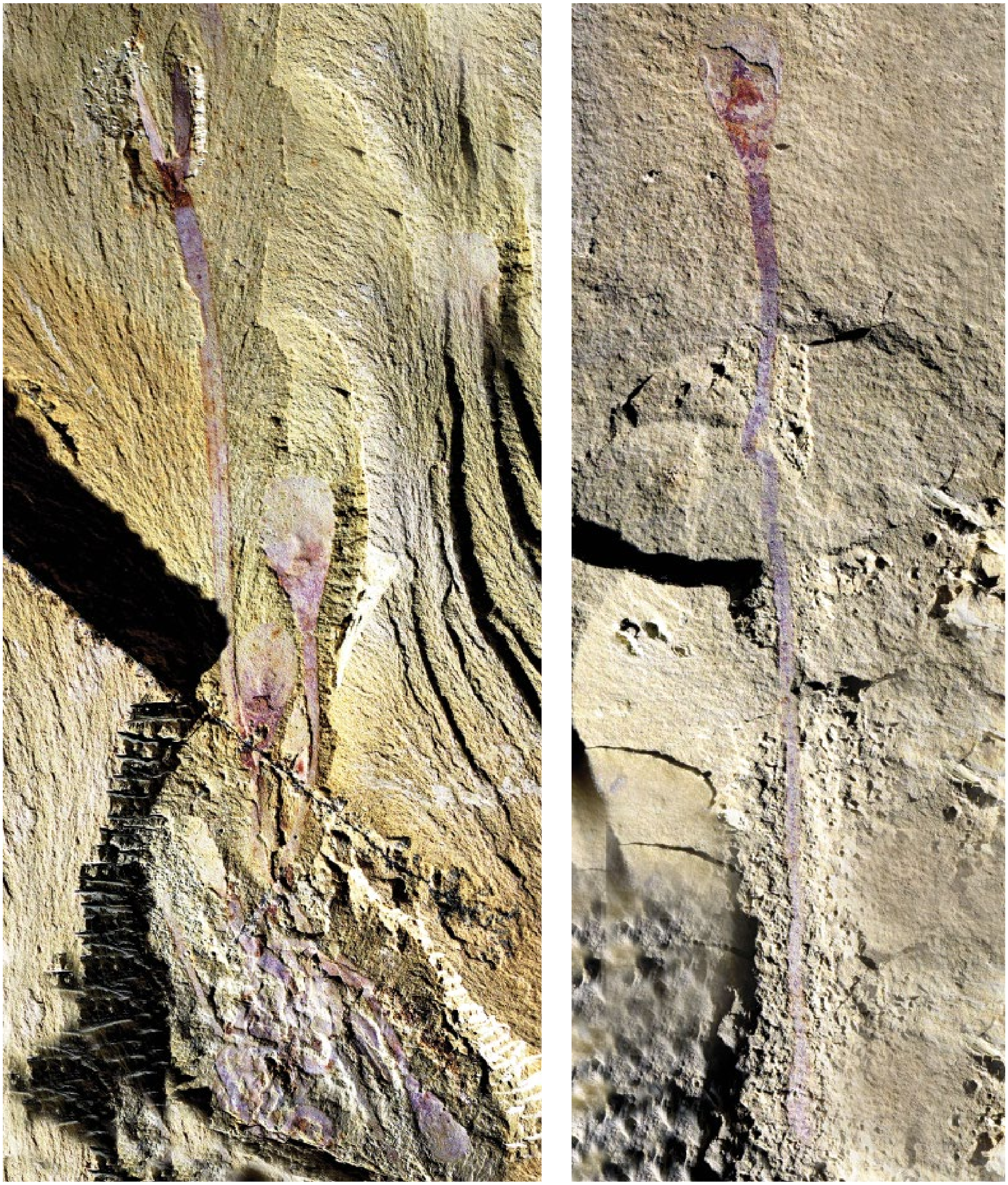


Figure 14.7 Reconstruction of ***Lingulellotreta malongensis***.

Figure 14.8 ***Lingulellotreta malongensis***. **(a)** YKLP 13846, ×3.7; Mafang, Haikou, Kunming. **(b)** YKLP 13847, ×5.7; Ercaicun, Haikou, Kunming.



(a) (b)

Genus *Diandongia* Rong, 1974

Diandongia pista Rong, 1974

This is a common brachiopod of the Chengjiang biota. Specimens are usually found preserved in three dimensions, but the valves are sometimes a little compressed and cracked. The pedicle is preserved in only a very few cases.

The valves are ovoid in outline, normally with width greater than length and with the ventral valve slightly the larger of the two. The size of the valves ranges from about 2 × 3 mm to 10 × 12 mm. The profile is biconvex, with the ventral valve more curved toward the umbo. Both valves clearly display concentric growth lines, and some specimens show weak costae toward the anterior margin. A fine reticulate ornament is particularly well developed near the umbo. Internally on the ventral valve there is a visceral platform that does not extend as far as the valve mid-length. The pedicle is thin, slender, and some 0.7 mm wide and about 1.6 cm long. No internal features have been recognized in the pedicle.

Diandongia pista was erected as a lingulate brachiopod (Rong 1974), an assignment that is widely accepted (Luo *et al.* 1999; Hou *et al.* 1999, 2004a; Zhang Zhi-fei *et al.* 2003, 2010, 2011c).

Diandongia was inferred to be epifaunal, with the pedicle anchored to another benthic organism or cemented to some other type of substrate (Zhang Zhi-fei *et al.* 2003). Its shell is also a host for the attachment of epibiont animals (Zhang Zhi-fei *et al.* 2010). *Diandongia* also apparently had the ability to self-heal damage to the shell (Zhang Zhi-fei *et al.* 2011c).

This species is relatively abundant in the Chengjiang and Haikou areas. It also occurs elsewhere in the lower Cambrian strata of South China.

Key references

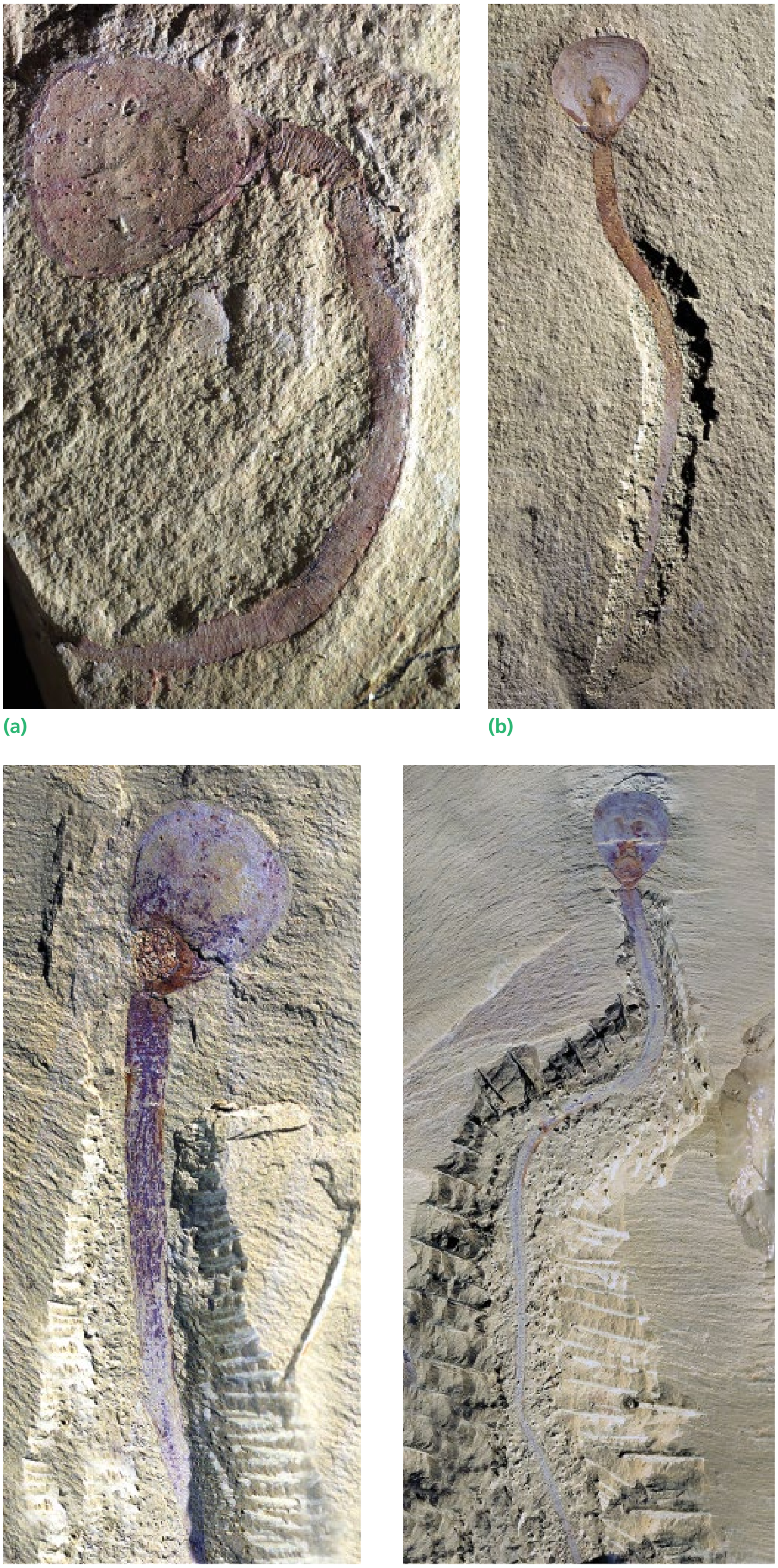
Rong 1974; Luo *et al.* 1999; Zhang Zhi-fei *et al.* 2003, 2010, 2011c; Hou *et al.* 2004a.

Genus *Lingulellotreta* Koneva *in* Gorjansky & Koneva, 1983

Lingulellotreta malongensis (Rong, 1974)

Lingulellotreta malongensis is a common constituent of the Chengjiang biota. A remarkable feature is the spectacularly long pedicle, which is preserved in its entirety in many individuals. Both the shell and the pedicle are preserved as

Figure 14.9 ***Lingulella chengjiangensis***. **(a)** RCCBYU 10294, ×3.9; Ercaicun, Haikou, Kunming. **(b)** YKLP 13849, ×1.8; Ercaicun, Haikou, Kunming. **(c)** YKLP 13850, ×4.2; Ercaicun, Haikou, Kunming. **(d)** YKLP 13851, ×2.9; Xiaolantian, Chengjiang.



(a) (b) (c) (d)

15 Annelida

This large phylum of worms numbers over 14,000 species. Annelida are found worldwide, in terrestrial, freshwater, and marine habitats (Rouse & Pleijel 2007). The basic annelid body form consists of three regions: an anterior head, an elongated trunk, and a post-segmental pygidium. Most annelids are also known as segmented worms, as the trunk consists of repeated units called segments, which are often separated by septa internally and appear as ring-like annulations externally. However, the segments are poorly defined or absent in other annelids, such as in Echiura (spoon worms) and Sipuncula (peanut worms). In addition to segmentation, another distinctive feature of annelids is the chitinous cuticular structures called chaetae, which show a huge amount of variation.

Traditionally, Annelida contains three classes: Polychaeta (e.g., bristle worms), Oligochaeta (e.g., earthworms), and Hirudinea (e.g., leeches). It is now recognized that Oligochaeta and Hirudinea form a clade, Clitellata, which appear to resolve inside Polychaeta. Polychaeta may therefore be synonymous with Annelida. Increasing evidence from both morphological and molecular data suggests that the previously recognized phyla Echiura and Sipuncula should be placed within Annelida, although their relationships with other annelid lineages are still unresolved.

Sipunculans are a small group of marine burrowing worms, with only a few hundred living species. The body is divided into a retractable elongated anterior introvert and an expanded unsegmented trunk that somewhat resembles a peanut. The mouth is located at the anterior end of the introvert and is characterized by the presence of ciliated tentacles. The intestine forms a twisted loop, with the anus emerging on the side of the anterior part of the trunk. The phylogenetic position of this group of animals has been troublesome, and until recently it was considered to be an independent phylum that is closely associated with either annelids or mollusks. The latest molecular studies have increasingly suggested that Sipuncula should be part of Annelida (Rouse & Pleijel 2007; Dordel *et al.* 2010; Dunn *et al.* 2014). This is also supported by new evidence that the rudimentary neural segmentation similar to that of annelids occurs in the early larval stage of sipunculans, even if these traits are absent in the adults (Wanninger *et al.* 2009).

As annelids are predominantly soft-bodied organisms, their presence in the fossil record is relatively sparse. The majority of annelid fossils consist of the remains of jaws of polychaetes and their mineralized tubes, but some exceptionally preserved annelid body fossils have been reported from various Lagerstätten. The oldest widely accepted fossil annelids come from the early Cambrian Sirius Passet and Guanshan biotas and the middle Cambrian Burgess Shale (Parry *et al.* 2015). Despite the great biodiversity present in the Chengjiang biota, finds of possible annelids are extremely rare. Here we introduce one possible polychaete and one sipunculan species from the Chengjiang biota. If these taxonomic interpretations are correct, they represent the earliest records of annelid fossils.

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Genus *Cambrosipunculus* Huang, Chen, Vannier & Salinas, 2004

Cambrosipunculus tentaculatus Huang, Chen, Vannier & Salinas, 2004

This is an extremely rare species, known only from one complete specimen and one nearly complete specimen. Both specimens are flattened, except for some slight relief around the mud-filled intestine and the ornamentation of the proboscis. The body is twisted and preserved in a light brown to rusty color.

The complete specimen is 3.7 cm long and 4 mm wide. The elongate body is divided into a narrower introvert and an unsegmented trunk, in the ratio of 4:6. The introvert is slightly tapered anteriorly. The anterior part of the introvert is armed with two types of hooks: a distal ring of large hooks and some smaller ones scattered further back. The tip of the introvert is crowned with more than 10 short tentacles. The introvert appears to be retractable at the anterior region. There is no clear boundary between the introvert and the trunk. The trunk is cylindrical and tapers slightly toward the posterior end. Some annulations and fine papillae are observed on the trunk surface. The digestive tract forms a U-shaped loop at the posterior end of the trunk and runs anteriorly to the anus, which is located near the introvert-trunk junction. Both the descending and ascending portions of the gut are rather straight and close to each other.

C. tentaculatus is the type species of *Cambrosipunculus*. In the original description another (but unnamed) species, *Cambrosipunculus* sp., is reported, which shows a more twisted body and a volcano-like structure at the anus region (Huang *et al.* 2004a). *Cambrosipunculus* shows striking similarity to the only other known Chengjiang sipunculan, namely *Archaeogolfingia caudata* Huang *et al.*, 2004. It is suggested that *Cambrosipunculus* differs from *Archaeogolfingia* in the absence of a caudal appendage and in having a less wavy intestine (Huang *et al.* 2004a; Chen Jun-yuan 2004). However, most diagnostic differences between these three Chengjiang sipunculan species may be the result of taphonomic factors, and their taxonomic relationships require further investigation. Both *Cambrosipunculus* and *Archaeogolfingia* show a strong resemblance to modern sipunculans, especially the Family Golfingiidae (Huang *et al.* 2004a).

The U-shaped gut with an anteriorly placed anus suggests that the Cambrian sipunculans were sedentary organisms that lived in burrows. The partly dark and partly mud-filled intestine and the presence of tiny hooks in the anterior part of the introvert suggest that these animals might have used the introvert to scrape or capture food from the sediment surface like many modern sipunculans (Huang *et al.* 2004a).

Both *Cambrosipunculus* and *Archaeogolfingia* are only recorded from the lower Cambrian Chengjiang biota, Yunnan Province.

Key references

Huang *et al.* 2004a; Chen Jun-yuan 2004.

Figure 15.1 ***Cambrosipunculus tentaculatus***, ELRCC SK 69002a, ×5.9; Shankou village, Kunming.

Genus *Maotianchaeta* Chen, 2004

Maotianchaeta fuxianella Chen, 2004

This is one of the rarest species in the Chengjiang biota. Only one specimen has been discovered so far, consisting of part and counterpart. The specimen is flattened on the rock surface and preserved in a pinkish color, while the attachment areas of the supposed parapodia to the trunk are preserved as dark brown spots. The body is curved and twisted.

The single specimen is nearly complete and is 5.4 cm long and 6 mm wide. Some slender tentacle-like structures are seen protruding out of the trunk at regular intervals, which are interpreted as parapodia (Chen Jun-yuan & Zhou 1997; Chen Jun-yuan 2004). According to the spacing of the parapodia, it is estimated that there are 50 pairs of parapodia along the body. Each parapod has a wide proximal base and tapers distally. Chaeta-like structures are observed at the distal end of the parapodia (Chen Jun-yuan 2004). The dark-brown spots at the attachment areas of the parapodia are interpreted as sclerites (Chen Jun-yuan & Zhou 1997).

Maotianchaeta fuxianella is monospecific. Based on the parapod-like structures, the animal is considered to be a polychaete (Chen Jun-yuan & Zhou 1997; Chen Jun-yuan 2004). However, due to a lack of specimens and detailed description, the affinities of this animal remain problematic.

Little is known about the lifestyle of *M. fuxianella*. No trace of the intestine is preserved to indicate the possible diet. The supposed parapodia were presumably for locomotion.

M. fuxianella is only known from the lower Cambrian Chengjiang biota, Yunnan Province.

Key references

Chen Jun-yuan & Zhou 1997; Chen Jun-yuan 2004.

Figure 15.2 ***Maotianchaeta fuxianella***. ELRCC 54001b, ×7.4; Maotianshan, Chengjiang.

16 Trochozoa of Uncertain Affinity

Of the well-known phyla that are accommodated within Trochozoa, only brachiopods are common in the Chengjiang biota. The mollusks, which constitute one of the most diverse invertebrate phyla today, common in marine, freshwater, and terrestrial ecosystems, are almost unknown from the biota. *Helcionella yunnanesis* Zhang & Babcock, 2002, present as a few external mold specimens, is generally accepted to be a helcionellid, and thus some sort of conchiferan, although to which of the mollusk crown groups it is most closely related is an unresolved question.

The Chengjiang contains a number of taxa for which there is general agreement that they belong within Trochozoa, but to which of the extant phyla they are most closely related is matter of debate. The Hyolitha and the genus *Nectocaris* have each been compared to mollusks, with varying degrees of disagreement. On the basis of current evidence neither group can be comfortably accommodated within the total group Mollusca. Similarly, *Wiwaxia* shares some anatomical features with mollusks, but has other characters suggesting annelid affinities. That Hyolitha, *Nectocaris*, and *Wiwaxia* are treated together here should not be taken to imply that they constitute a clade.

The Hyolitha is an extinct group of bilaterian animals, which range in age from Cambrian to Permian. Two morphologically distinct subgroups are known: Orthothecida and Hyolithida. Hyolithida are generally considered to be monophyletic, but it is unclear whether Orthothecida are a clade, and although a close relationship with Hyolithida is considered likely by many authors (e.g., Devaere *et al.* 2014) uncertainty remains (e.g., Martí Mus & Bergström 2005). All Chengjiang hyoliths are assigned to Hyolithida. They are known almost exclusively from the hard parts of the skeleton, which in hyolithids are characterized by a conical shell with a protruding ventral shelf (ligula), an external operculum, and a pair of curved spines known as helens; these different skeletal elements were held together by soft tissues (Martí Mus & Bergström 2005).

Because they are known from little more than fossilized remains of their hard parts, many aspects of hyolithids remain enigmatic, including their affinities. They are widely considered to be trochozoans, and based on a number of shared characteristics a close relationship with mollusks has been proposed (e.g., Devaere *et al.* 2014; Martí Mus 2014). Aspects of their ecology are similarly unconstrained. Hyolithids are generally considered to be relatively sedentary (in the absence of evidence that they had any means of active propulsion) and to have lived on the sea floor. Their occurrence in shales is taken to indicate a preference for muddy substrates. What they ate is uncertain, but surface detritivory and/or deposit feeding is consistent with what is known of their anatomy and from comparison of gut morphology with sipunculans (Marek & Yochelson 1976; Devaere *et al.* 2014).

Cambrian hyoliths are known, for example, from Siberia, North America, and many European countries (Malinky & Berg-Madsen 1999). Hyoliths are relatively common fossils of the Chengjiang biota, with a recent overview of the community ranking one species (*Ambrolinevitus ventricosus*) among the 20 most abundant species in the Chengjiang biota (Zhao Fang-chen *et al.* 2010). Seven species have been described or simply recorded, several of which are difficult to evaluate based on the published information.

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Genus *Ambrolinevitus* Syssoiev, 1958

Ambrolinevitus maximus Jiang, 1982

Although rarely associated with the soft-bodied biota, the shells of this hyolithid are more abundant at other horizons. They are preserved flattened, essentially into two dimensions, with little relief.

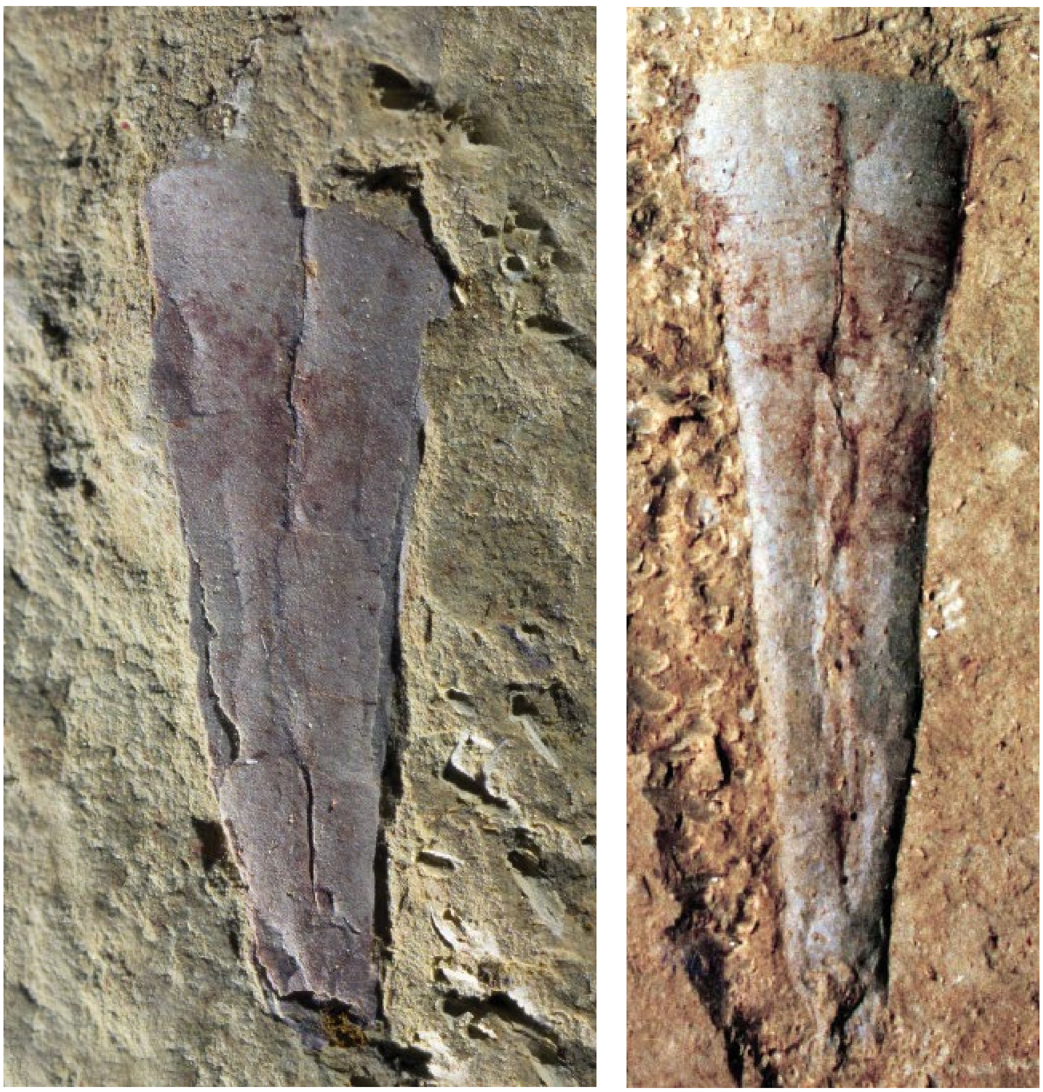
The shell is elongate, cone-shaped, and has straight sides. It has a maximum length of 1.6 cm and its maximum width at the aperture is 6 mm; the apex is somewhat obtuse. The shell has a narrow longitudinal groove centered along its length, which probably represents a post-mortem collapse feature, and narrow, dense growth lines, some 19–22 per millimeter, parallel to the apertural margin.

Some closely packed and in some cases subparallel aligned bedding plane assemblages of *Ambrolinevitus* material in the Chengjiang biota have been interpreted as possible gut or coprolite contents (Chen Jun-yuan & Zhou 1997).

A. maximus is unknown outside the Chengjiang biota.

Key references

Jiang 1982; Chen Jun-yuan *et al.* 1996; Chen Jun-yuan & Zhou 1997; Hou *et al.* 1999.



(a) (b)

Figure 16.1 ***Ambrolinevitus maximus***. **(a)** YKLP 13853, ×9.7 ; Ma'anshan, Chengjiang. **(b)** RCCBYU 10240, ×6.5; Xiaolantian, Chengjiang.

Ambrolinevitus ventricosus Qian, 1978

This small hyolithid species is among the most abundant taxa in the Chengjiang biota. It is not uncommon to find tens of specimens crowded together, in some cases showing a subparallel orientation possibly indicating paleocurrent alignment. The moldic shells, originally composed of calcium carbonate, are preserved flattened with some slight relief. Soft parts are unknown.

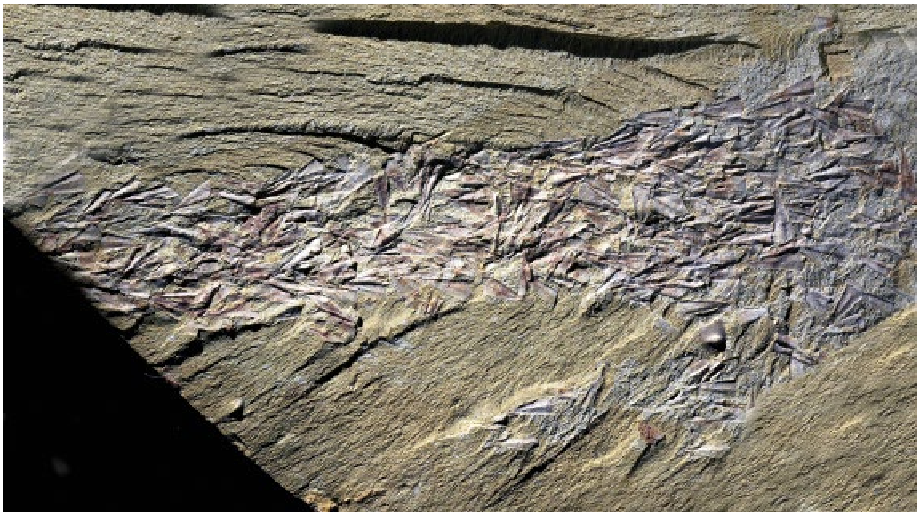
The cone-shaped shell has straight sides, a sharply pointed apex, and is relatively small. The largest specimens are only about 5 mm long and 1.5 mm wide at the apertural end. The angle of divergence of the shell is approximately 20°. The external part of the shell has narrow, dense growth lines, 18–20 per millimeter, and a central longitudinal groove flanked each side by a longitudinal ridge.

A. ventricosus has been recorded only from the lower Cambrian of Yunnan Province.

Key references

Qian 1978; Hou *et al*. 1999.

Figure 16.2 ***Ambrolinevitus ventricosus***. **(a)**, **(b)**, **(c)** RCCBYU 10241, ×1.7, ×6.3, ×8.9; Ma'anshan, Chengjiang.



(a)

(b)

(c)

Genus *Burithes* Missarzhevsky, 1969

Burithes yunnanensis Hou, Bergström, Wang, Feng & Chen, 1999

Burithes yunnanensis is known from hundreds of shells. They are normally preserved flattened yet retaining an overall cone-shape and, in some cases, weak relief. Rare specimens bearing partial remains of the soft tissues await description. This species has the largest shell of all the Chengjiang hyolithids. It attains a length of up to 3.5 cm and is up to 1.5 cm wide at the apertural end. The apical angle of the shell is about 25°. The shell surface has weak growth lines parallel to the apertural margin, but lacks any form of longitudinal ornament.

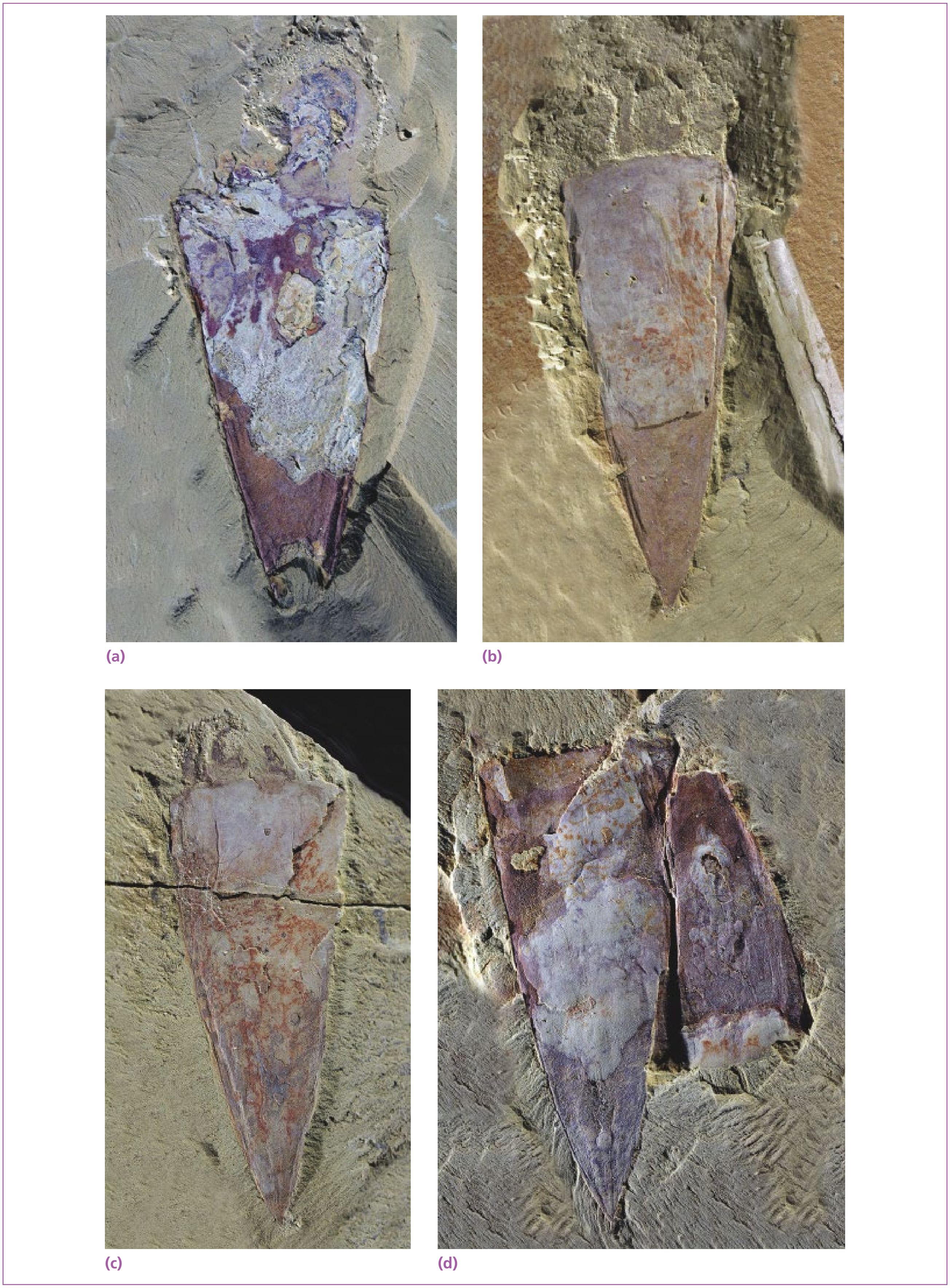
The Chengjiang hyolithid *Glossolites magnus* is closely similar to *B. yunnanensis* and may represent the same species.

All known occurrences of *B. yunnanensis* are from the lower Cambrian of Yunnan Province.

Key reference

Hou *et al*. 1999.

Figure 16.3 ***Burithes yunnanensis*.** **(a)** YKLP 13854, ×2.8; Mafang, Haikou, Kunming. **(b)** YKLP 13855, ×2.9; Mafang, Haikou, Kunming. **(c)** YKLP 13856, ×3.2; Mafang, Haikou, Kunming. **(d)** YKLP 13857, ×3.2; Mafang, Haikou, Kunming.


(a)
(b)
(c)
(d)

Genus *Linevitus* Syssoiev, 1958

Linevitus opimus Yu, 1974

This relatively rare hyolithid species is known from the remains of its thin, mineralized shells, which typically are preserved flattened but retain slight relief.

The elongate, conical shell is up to 1.5 cm wide at its apertural end and up to 3.0 cm long, tapering gradually to a sharp apex. The apical angle of the shell is approximately 33°. The dorsal side of the shell shows fine growth lines, parallel to the margin of the aperture. The ventral side seems to be only slightly convex and has a central longitudinal groove that tapers from aperture to apex.

Linevitus opimus is known from a few specimens associated with the soft-bodied elements of the Chengjiang biota. It may be more common at other horizons locally.

Key references

Yu 1974; Hou *et al.* 1999.

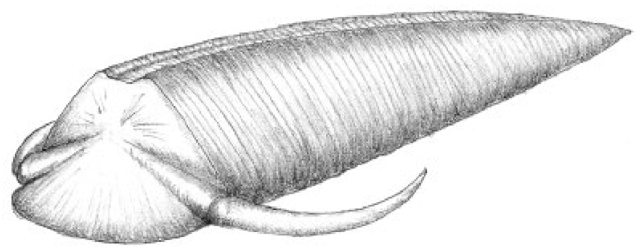
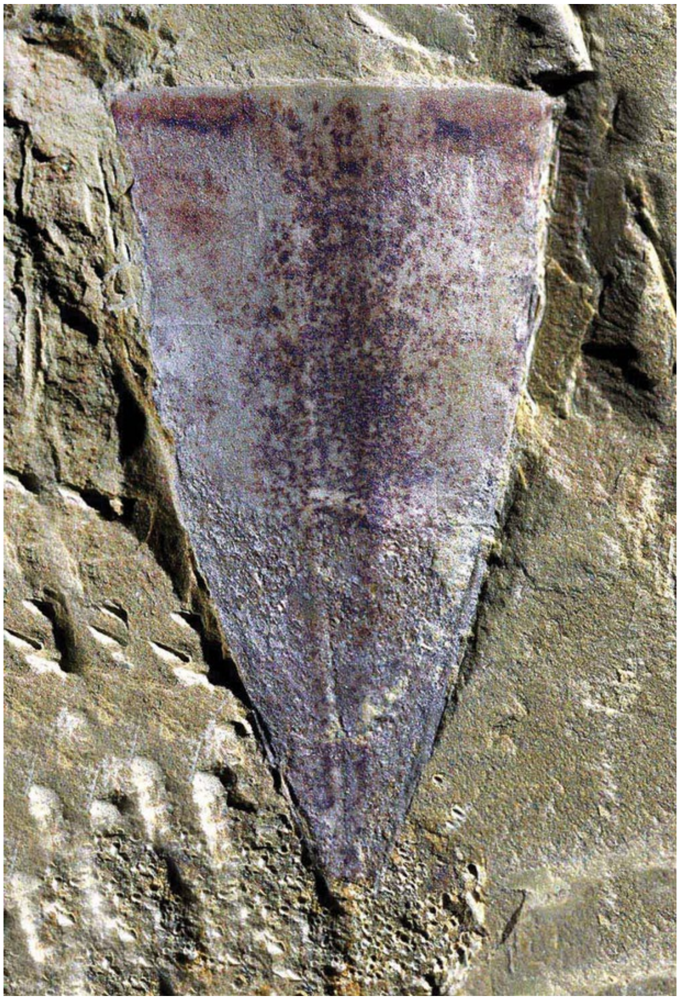


Figure 16.4 Reconstruction of a generalized hyolithid, with some characteristics of ***Linevitus*** (modified from Hou *et al.* 2004a).

Figure 16.5 ***Linevitus opimus***. RCCBYU 10239, ×8.2; Maotianshan, Chengjiang.



Genus *Nectocaris* Conway Morris, 1976

Nectocaris pteryx Conway Morris, 1976

Known from a few tens of specimens, this species was first described from the Chengjiang biota under the name *Petalilium latus* Luo *et al*. 1999. Subsequent work suggested that the Chengjiang species was synonymous with *Vetustovermis planus* from the Cambrian Emu Bay Shale Lagerstätte of Australia (Chen Jun-yuan *et al*. 2005) and also with *Nectocaris pteryx* Conway Morris, 1976 from the Burgess Shale (Smith, M.R. 2013). Because of the differences in age, species level synonymy between *N. pteryx* (middle Cambrian) and *P. latus* (lower Cambrian) might be considered tentative (Smith, M.R. 2013) but morphological criteria that might distinguish between them are lacking.

The body of *N. pteryx* comprises a distinct trunk and head. Most of the Chengjiang specimens are 5–6 cm in length, but a few are larger, up to 10 cm. The trunk is dorsoventrally flattened, torpedo-shaped, lacking segmentation or biomineralized components, and flanked laterally on each side by fins with fine superficial striations. The small head bears paired eyes on short stalks (preserved as carbon-rich films, and presumably pigmented in life), and two flexible anterior tentacles. A short, proximally narrowing conical tube, or so-called funnel, occurs near the boundary between head and trunk. The preservation of the fossils indicates an internal axial space or cavity of some sort, and numerous transversely orientated internal structures, paired across the axis of the trunk, up to 50 in number. Two different types of transverse structures have been described. The interpretation of these structures, on the one hand as gills within a cavity, on the other as organs associated with the alimentary tract, depends on the anatomical model and phylogenetic hypothesis of the interpreter. Some rather vague structures posterior of the mouth have been tentatively interpreted as a radula or beaks (Smith, M.R. 2013), but these have not been described in Chengjiang material.

N. pteryx has been interpreted as an organism of unknown affinity (Conway Morris 1976), an annelid worm (Glaessner 1979), a chordate (Simonetta 1988), an arthropod (Luo *et al.* 1999), and as a mollusk-like organism with affinities outside the Mollusca (Chen Jun-yuan *et al.* 2005). Recently, discussion has focused on possible cephalopod affinities (Smith, M.R. & Caron 2010; Smith, M.R. 2013) or not (Runnegar 2011; Vinther 2015). The argument rests largely on the proposed homologies of the axial space and transverse structures of the trunk, and the funnel. According to the cephalopod model, these body parts are gills within a mantle cavity, and a cephalopod funnel. Alternatively, the axial space and transverse structures are interpreted as features of the alimentary tract, and the funnel as a foregut structure or proboscis of some sort (Mazurek & Zaton 2011; Runnegar 2011). According to this hypothesis *Nectocaris* lacks any clear derived characters of cephalopods; that its body is generally reminiscent of a cephalopod is a result of convergence. Critics of the cephalopod hypothesis also point out that this interpretation of *Nectocaris* contradicts other compelling evidence for the pattern and timing of evolution and character acquisition in cephalopods (Kröger *et al*. 2011; Runnegar 2011), and it is possible that the cephalopod interpretations of anatomy are too strongly colored by the overall resemblance and consequent choice of cephalopods as comparative model (Donoghue & Purnell 2009).

Whatever its affinities, aspects of the anatomy of *Nectocaris* – such as the dorsoventrally flattened body with lateral fins, paired eyes, and anterior tentacles – suggest of a degree of ecological convergence with coleoid cephalopods. It seems likely that it was an active nektonic animal, although a somewhat more gastropod-like reconstruction has been proposed (Chen Jun-yuan *et al*. 2005).

If synonymy of the three species of *Nectocaris* is accepted, *N. pteryx* is known from Australia, Canada, and the Chengjiang Lagerstätte. If they are distinct species, *N. latus* is restricted to the Chengjiang biota, with occurrences at Haikou, Shankou village, Mafang, and Anning in Yunnan Province.

Key references

Luo *et al*. 1999; Chen Jun-yuan *et al*. 2005; Runnegar 2011; Smith, M.R. 2013.

Figure 16.6 ***Nectocaris pteryx***. **(a)**, **(b)** YKLP 13858, ×1.7, ×3.0; Mafang, Haikou, Kunming. **(c)** RCCBYU 10365, ×1.3; Mafang, Haikou, Kunming.


(a) **(b)**

(c)

Genus *Wiwaxia* Walcott, 1911

Wiwaxia papilio Zhang, Smith & Shu, 2015

Only recently reported from the Chengjiang biota, *Wiwaxia* is now known from a handful of associated sclerites and articulated specimens. All the articulated specimens are small (less than 8 mm in body length) and might be juveniles (Zhang Zhi-fei *et al*. 2015), but sclerites of up to 8 mm long are known (Zhao Fang-chen *et al*. 2014c), indicating that the biota also contained larger, presumably adult individuals.

The ovoid body of *Wiwaxia* is covered on its dorsal surface by nine overlapping, transverse rows of posteriorly directed sclerites, preserved as carbonaceous remains. The ventral surface is unarmored, presumed to be a muscular foot. The characteristic sclerites have a narrow root that widens into a flat blade, incorporating a series of narrow internal chambers aligned with the long axis. The shape of the sclerites varies consistently within each row: the sclerites on the ventrolateral margin are sickle-shaped, while others are rounded, and about half as wide as they are long; adult specimens can also have elongate spiny dorsal sclerites, but these are not present on the small Chengjiang specimens. The anteriormost row is formed of sclerites arranged as a pair of bilaterally symmetrical rosettes. Toward the anterior of the ventral surface is a series of curved triangular carbonaceous structures, arranged in two or three rows. These are interpreted as a toothed feeding apparatus, analogous or possibly homologous with the radula of mollusks.

The affinities of *Wiwaxia* have been the subject of considerable debate (see Eibye-Jacobson 2004; Smith, M.R. 2014). Hypotheses range from the original suggestion that it was a polychaete (Walcott 1911b), through a variety of taxa now accommodated within Trochozoa – including stem annelid, crown group polychaete, and stem or primitive crown group mollusk (e.g., Conway Morris & Peel 1995; Scheltema & Ivanov 2002; Butterfield 2003; Caron *et al*. 2006). Much of the debate has focused on annelid and mollusk affinities, based on the annelid-like construction of *Wiwaxia*'s sclerite covering, and the mollusk-like mouthparts and foot. The most recent evaluation (Zhang Zhi-fei *et al*. 2015) concludes that these conflicting characters could be reconciled in one of three ways: *Wiwaxia* as stem annelid, as stem mollusk, or in the stem of the mollusk + annelid clade. At present, the precise affinities of *Wiwaxia* within Trochozoa cannot be resolved beyond this.

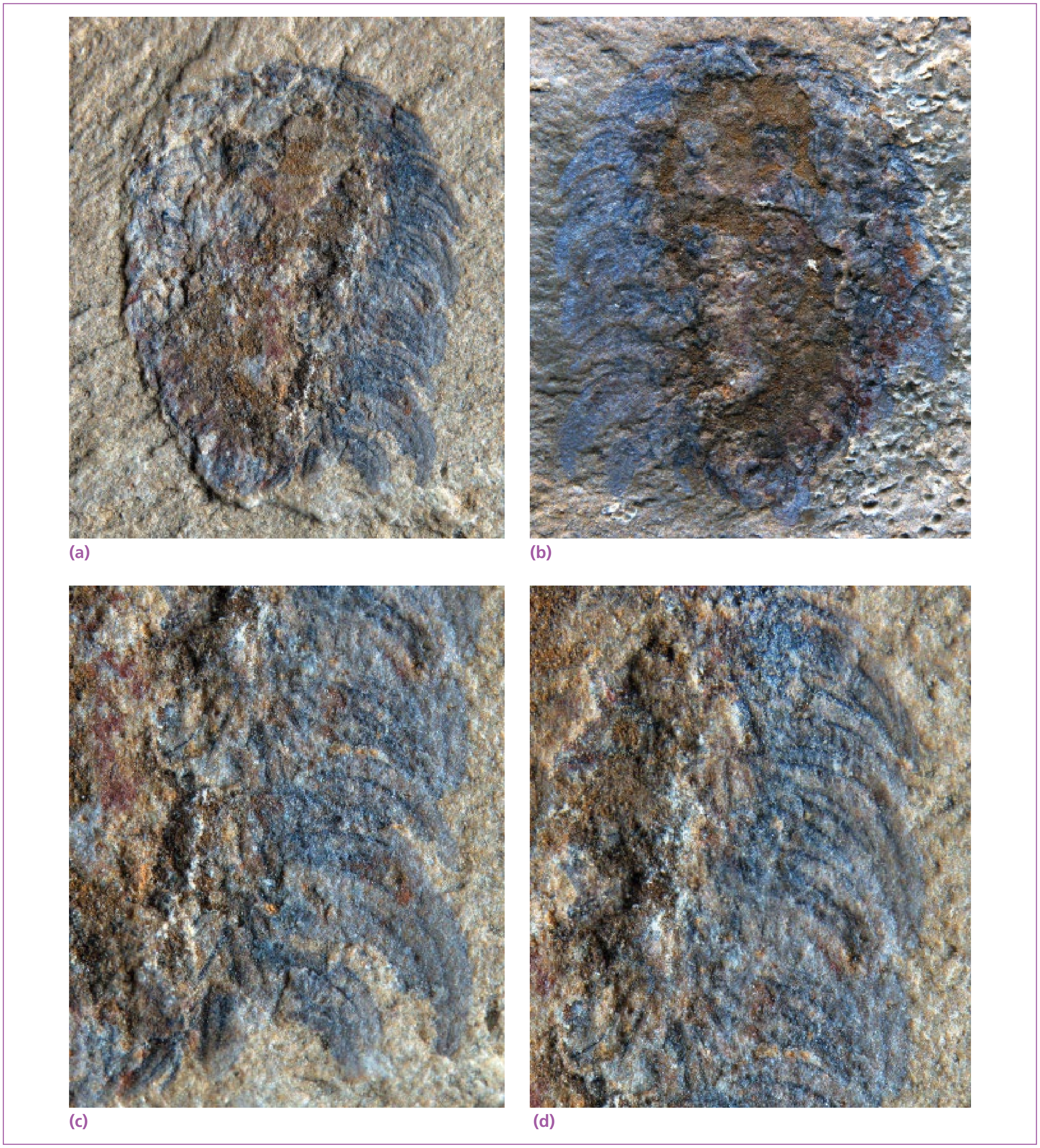
Compared to its affinities, very little has been written about the ecology of *Wiwaxia*. It was clearly a benthic animal, and consideration of the functional morphology of the radula-like mouthparts suggests that it was a deposit feeder (Smith, M.R. 2012).

Wiwaxia sclerites are found in multiple Cambrian Lagerstätten, yet in the Chengjiang biota they are rare, until recently considered to be absent. The few known specimens come from localities near Haikou Town (Jianshan, Mafang, and Ercaicun) in Yunnan Province.

Key references

Zhao Fang-chen *et al*. 2014c; Zhang Zhi-fei *et al*. 2015.

Figure 16.7 ***Wiwaxia papilio***. **(a)**, **(c)**, **(d)** YKLP 13859a, ×15.5, ×32.7, ×32.7; Ercaicun, Haikou, Kunming. **(b)** YKLP 13859b, ×15.9; Ercaicun, Haikou, Kunming.



17 Priapulida and Relatives

At the present day Priapulida is a small phylum of marine benthic worms with only 19 known extant species. However, this group of animals and their relatives were once dominant members of the benthic fauna in Cambrian marine communities. Adult priapulids have a cylindrical body that can be divided into at least two regions: an anterior invaginable introvert covered by longitudinal rows of scalids, and an unsegmented trunk with annulated cuticle. In phylogenetic analyses Priapulida shares a close affinity with two other vermiform phyla: Kinorhyncha and Loricifera. Although the interrelationships between these three phyla are not yet fully resolved, they form a monophyletic clade known as Scalidophora, which is supported by several common morphological characters, for example, scalids covering the introvert. In some phylogenetic analyses, Scalidophora and Nematoida (including Nematomorpha and Nematoda) form a monophyletic clade called Cycloneuralia, which is often supported by morphologists, as they share a non-segmented body terminating in an eversible mouth in front of a circumoral, ring-shaped brain. However, other molecular analyses suggest that Scalidophora and Nematoida are paraphyletic, with Nematoida more closely allied to Panarthropoda.

The majority of worms described from the Chengjiang biota have been assigned to the Priapulida, but the exact phylogenetic position of some Chengjiang vermiform taxa and their interrelationships have proven to be problematic. Some taxa with elongated bodies (e.g., *Mafangscolex*, *Maotianshania*, and *Cricocosmia*) were placed into Nematomorpha (Hou & Bergström 1994; Hou *et al.* 2004a), but recent phylogenetic analyses have resolved them as stem nematomorphs, stem scalidophorans, or stem priapulids (Harvey *et al.* 2010; Wills *et al.* 2012; Ma *et al.* 2014a), so their exact affiliations remain uncertain. Most taxa included within this chapter appear to be stem scalidophorans or stem priapulids, with the exception of *Eximipriapulus* and *Xiaoheiqingella*, which are placed within the priapulid crown group. It was also suggested that the Chengjiang genus *Sicyophorus* might be closely related to Loricifera, based on its ovoid trunk with longitudinal plates. In addition to the species treated in this chapter there are also several other Chengjiang taxa that have been suggested to be priapulids and relatives, such as *Tabelliscolex hexagonus* Han *et al.*, 2003, *Paratubiluchus bicaudatus* Han *et al.*, 2004, *Laojieella thecata* Han *et al.*, 2006, *Omnidens amplus* Hou *et al.*, 2006, and *Tabelliscolex chengjiangensis* Han *et al.*, 2007.

Genus *Mafangscolex* Hu, 2005

Mafangscolex sinensis (Hou & Sun, 1988)

Mafangscolex sinensis is relatively common in the Chengjiang biota, and a few hundreds of specimens are known. It occurs as flattened body fossils, typically curved or coiled. Biomineralized elements are embedded within the soft tissue. Specimens are preserved in a variety of colors, ranging from light to dark gray, and sometimes more reddish.

This worm is relatively large, about 8–10 cm long and 2 mm wide. The elongate body is composed of a proboscis and a trunk. The proboscis can be subdivided into an introvert, collar, and everted pharynx. The introvert is slightly narrower than the trunk, with the anterior third bearing 13–15 longitudinal rows of hook-like scalids, with at least seven scalids in each row. The collar is smooth and short.

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Two sections can be identified in the elongate pharynx: an anterior section armed with long, strong spines; and a posterior section armed with small spicules (Huang 2005). The elongate and slender trunk has about five annuli per millimeter along its entire length. Each annulus is covered by four transverse rows of tiny circular, plate-like sclerites, each with a single small node in the center. The size of the sclerites is much larger in the outer two rows than the inner two rows: the diameter of the former is approximately 45 microns while the latter is about 10 microns, but intermediate sizes are also found. A pair of strong hooks is present at the posterior end of the trunk. The gut is narrow, straight, and often preserved along the ventral side of the body as a black flat band extending throughout.

Mafangscolex is monospecific. The animal was originally assigned to the genus *Palaeoscolex* (Hou & Sun 1988), and later reassigned to a new genus, *Mafangscolex* Hu, 2005. *Mafangscolex* lacks the diagnostic cuticular ornamentation of *Palaeoscolex* (Hu 2005; Harvey *et al.* 2010; García-Bellido *et al.* 2013). Along with other palaeoscolecid worms, recent phylogenetic analyses have resolved this animal as either a stem cycloneuralian or a stem priapulid (Harvey *et al.* 2010). It also appears to share a close relationship with *Cricocosmia*.

The dark, flat gut without sediment infilling suggests that *M. sinensis* was non-deposit feeding, but possibly led an epifaunal and predatory lifestyle. However, the recent discovery of a dozen specimens preserved within their tube-like burrows suggests infaunal behavior (Huang *et al.* 2014).

M. sinensis is unknown outside the Chengjiang biota, Yunnan Province.

Key references

Hou & Sun 1988; Hu 2005; Huang 2005; Harvey *et al.* 2010; García-Bellido *et al.* 2013; Huang *et al.* 2014.

Figure 17.1 ***Mafangscolex sinensis*****.** **(a)** RCCBYU 10222, ×2.6; Ma'anshan, Chengjiang. **(b), (c), (d)** YKLP 13861, ×1.4, ×6.4, ×11.1; Mafang, Haikou, Kunming.

Genus *Maotianshania* Sun & Hou, 1987

Maotianshania cylindrica Sun & Hou, 1987

Maotianshania cylindrica is a relatively abundant palaeoscolecid worm from the Chengjiang biota and is known from thousands of specimens. Most specimens are flattened and preserved in a light-brown to rusty color. The specimens are typically preserved in the shape of a number six, with the front half of the body being relatively straight to gently curved, while the posterior half of the body tends to be coiled.

The individuals are on average about 2.5 cm long and 2 mm wide. The relatively elongate body can be divided into an anterior proboscis and a trunk. The proboscis is composed of an introvert with scalids, a smooth collar, and an everted pharynx with neatly arranged pharyngeal teeth (Sun & Hou 1987b; Hou & Bergström 1994; Huang 2005; Hu 2005). The posterior part of the introvert is devoid of scalids and is as wide as the trunk, but it can be distinguished from the latter due to the lack of annuli. The elongate trunk has well-marked, relatively wide annuli (3–4 per millimeter). The surface of the trunk is uniformly covered by tiny sclerites, which are nearly equal in size, ranging from 15 to 20 μm in diameter. The shape of individual sclerites is irregular, and four nodes are present at the convex upper surface of each (Hu 2005). The posterior end of the trunk is bluntly rounded, lacking annuli and terminating in a pair of strong, curved hooks. The alimentary canal is straight, comparatively narrow, and largely preserved as a flattened black film, but sediment infill is frequently observed in the posterior part of the gut.

M. cylindrica is the type and only species of *Maotianshania*. It shares many similarities with other Chengjiang palaeoscolecid worms, but the lack of large paired sclerites along the trunk (as seen in *Cricocosmia* and *Tabelliscolex*) makes the species most closely resemble *Mafangscolex sinensis* (Hou & Sun, 1988). *Maotianshania* differs from *Mafangscolex* in its relatively smaller size, wider annuli, uniformly distributed small sclerites, and the presence of four small nodes on each sclerite. Along with other Cambrian palaeoscolecid worms, *M. cylindrica* has been placed close to either nematomorphs (Hou & Bergström 1994) or priapulids (Sun & Hou 1987b; Conway Morris 1997; Huang 2005). Recent phylogenetic analyses (Harvey *et al.* 2010; Wills *et al.* 2012; Ma *et al.* 2014a) resolve the taxon as either a stem scalidophoran or a stem priapulid.

The dark, flat gut with frequent sediment infill indicates that *M. cylindrica* was probably both a deposit feeder and a carnivore. Its burrowing behavior remains poorly understood.

M. cylindrica is known only from the lower Cambrian of Yunnan Province. It occurs in many Chengjiang fossil sites.

Key references

Sun & Hou 1987; Hou & Bergström 1994; Conway Morris 1997; Huang 2005; Hu 2005; Harvey *et al.* 2010; Wills *et al.* 2012; Ma *et al.* 2014a.

Figure 17.2 ***Maotianshania cylindrica***. **(a)**, **(b)** YKLP 13860, ×2.6, ×7.0; Maotianshan, Chengjiang. **(c)**, **(d)** YKLP 13864, ×3.6, ×21.1; Maotianshan, Chengjiang.

Genus *Cricocosmia* Hou & Sun, 1988

Cricocosmia jinningensis Hou & Sun, 1988

This worm is one of the most abundant species in the Chengjiang community, with tens of thousands of specimens collected. Most specimens are preserved in a reddish to rusty color, and in a variety of attitudes: curled, curved, twisted, or straight. The body is always flattened, but in some cases the sclerites are preserved in slight relief.

An average individual is about 5 cm long and 2 mm wide. The elongate, slender body can be divided into an anterior proboscis and a trunk. The proboscis can be subdivided into an introvert, collar, everted pharynx, and digestive tract (Huang 2005). The introvert has the same width as the trunk, with a slight taper toward the anterior, and is covered by elongate, slightly curved spines. The collar is short, smooth, and cone-shaped. The pharynx is elongate and can be completely everted. Three sections of the pharynx are recognized based on the constriction between each section and the difference in pharyngeal teeth morphology and arrangement. In some specimens, a smooth, expanded structure is seen anterior to the fully everted pharynx, which is interpreted as the protruding part of the digestive tract (Huang 2005). The elongate trunk is distinctly annulated and tapers slightly toward the posterior end. The anterior-most part of the trunk has narrow annuli (about 40 per centimeter), but without any ornament. The main body of the trunk has relatively wider annuli (20–24 per centimeter), each of which bears one pair of lateral sclerites. Each sclerite has a subcircular base with a reticulate surface and a central curved spine (Hou & Bergström 1994; Huang 2005; Han *et al.* 2007). Two additional longitudinal rows of tiny spines are observed on the ventral side of the trunk (Han *et al.* 2007). A pair of curved hooks is situated at the posterior termination of the body. The gut is straight, flat, and stands out as a black band extending from the proboscis to the posterior end of the trunk.

Cricocosmia is monospecific. It shares some morphological similarities with many other Cambrian palaeoscolecid worms, a group that has usually been referred to either the Phylum Priapulida or the Phylum Nematomorpha (Hou & Bergström 1994; Huang 2005). Recent phylogenetic analyses have consistently resolved *Cricocosmia* as the sister taxon of *Tabelliscolex*, and together they are placed either as stem scalidophorans or, more likely, as stem priapulids (Harvey *et al.* 2010; Wills *et al.* 2012; Ma *et al.* 2014a).

As with other Cambrian palaeoscolecids, *C. jinningensis* was probably an infaunal species, living within the subsurface of the marine sediment. The dark, flat gut is seldom preserved infilled with mud, which indicates that the animal was more likely to be a predator than a deposit feeder.

C. jinningensis is known only from the lower Cambrian of Yunnan Province, but a possible *Cricocosmia* has also been reported from the middle Cambrian Kaili biota of Guizhou Province, China (Zhao Yuan-long *et al.* 1999a).

Key references

Hou & Sun 1988; Hou & Bergström 1994; Huang 2005; Han *et al.* 2007; Harvey *et al.* 2010; Wills *et al.* 2012; Ma *et al.* 2014a.

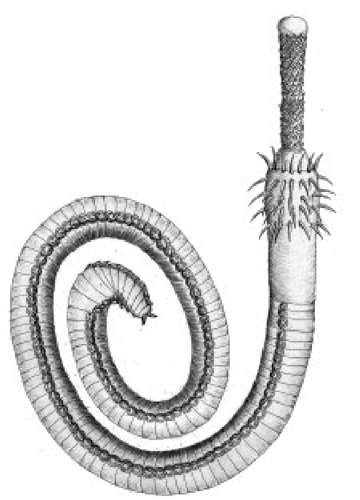
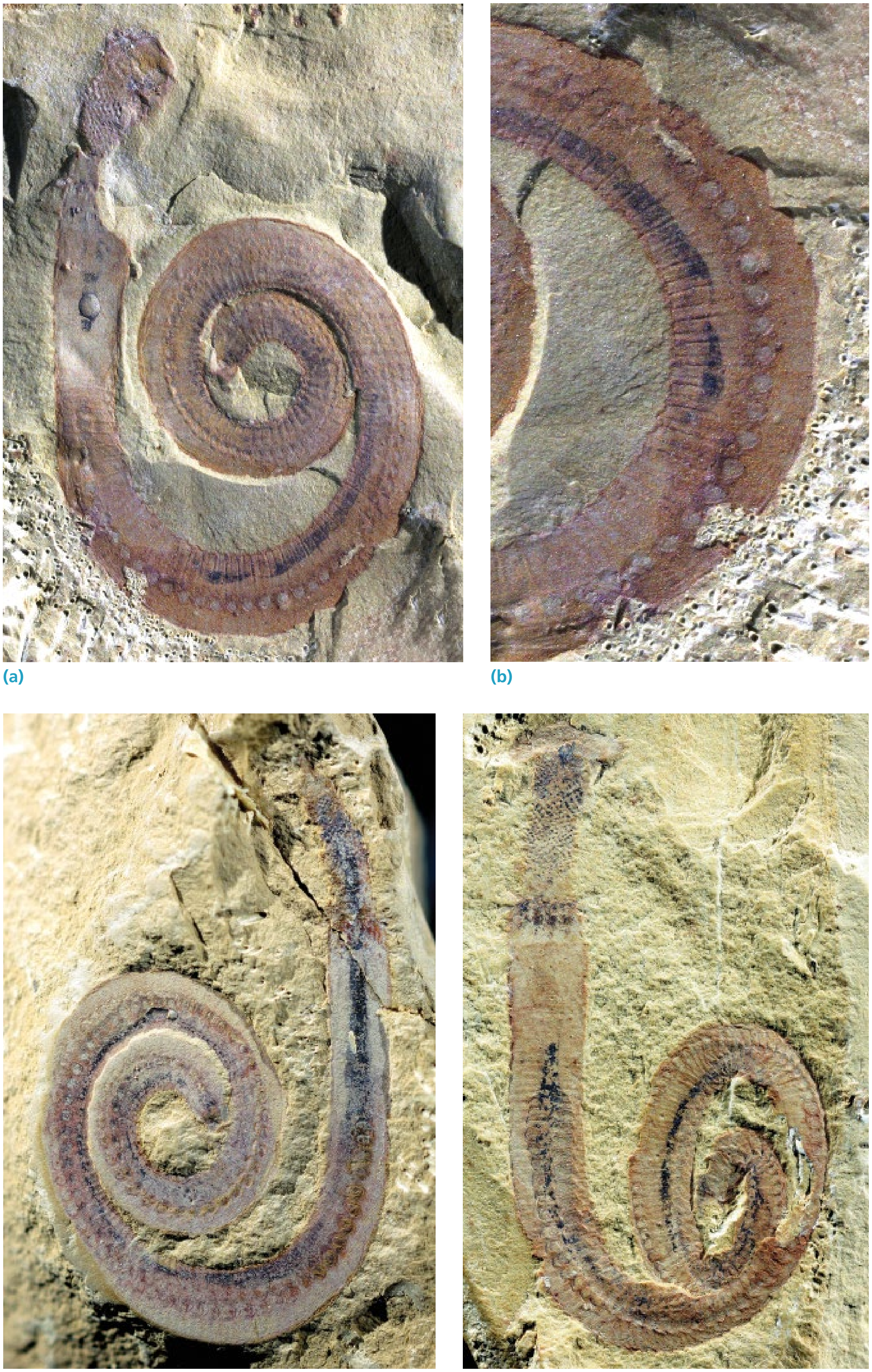


Figure 17.3 Reconstruction of ***Cricocosmia jinningensis*** (modified from Hou *et al.* 2004a, with proboscis based on Huang 2005).

Figure 17.4 ***Cricocosmia jinningensis***. **(a)**, **(b)** YKLP 13865, ×4.7, ×7.9; Mafang, Haikou, Kunming. **(c)** YKLP 13866, ×4.3; Mafang, Haikou, Kunming. **(d)** YKLP 13867, ×5.4; Mafang, Haikou, Kunming.



(a) (b) (c) (d)

Genus *Paraselkirkia* Hou, Bergström, Wang, Feng & Chen, 1999

Paraselkirkia sinica (Luo & Hu *in* Luo, Hu, Chen, Zhang & Tao, 1999)

Paraselkirkia sinica is unusual among Chengjiang priapulid worms, because the animal is typically comprised of an outer rigid tube into which the soft parts can be withdrawn completely. Hundreds of specimens are known, but in the majority only the more decay-resistant tubes remain. Both the soft parts and the tube are flattened and preserved in a light-brown color.

Specimens with a fully everted proboscis can reach 1.3 cm long, with a proboscis over 3 mm in length and a tube about 1 cm long. The proboscis is divisible into several parts (stages), each characterized by spines of a particular size, morphology, and array, or by a lack of them. The detailed morphology and interpretation of these proboscis parts is somewhat controversial (Luo *et al.* 1999; Hou *et al.* 1999; Huang 2005), and requires further investigation. The tube is narrow, elongate, and tapers posteriorly. Its wide end is flat and circular, with a diameter less than 2 mm; its narrower end terminates in a blunt point. The surface of the tube bears fine, regularly spaced annulations. The soft trunk of the worm is concealed inside the tube, but the trace of the gut is often still evident through the tube. The gut is dark, flat, and straight and extends from the mouth opening to the posterior end of the tube, where an anal opening presumably exists.

Paraselkirkia is monospecific. *P. sinica* was originally described under the name *Selkirkia sinica* Luo & Hu, 1999, which is judged to be conspecific with the Chengjiang species *Paraselkirkia jinningensis* Hou *et al.* 1999. *P. sinica* shows striking similarities to the Burgess Shale priapulid *Selkirkia columbia* Conway Morris, 1977. However, some differences are recognized between *Paraselkirkia* and *Selkirkia*, including the size and shape of their tubes and their proboscis morphology (Luo *et al.* 1999). In phylogenetic analysis *P. sinica* has always been resolved as the sister taxon of *S. columbia*, and together they have been resolved as either close to the living priapulid group Tubiluchidae (Wills *et al.* 2012) or as stem scalidophorans (Ma *et al.* 2014a).

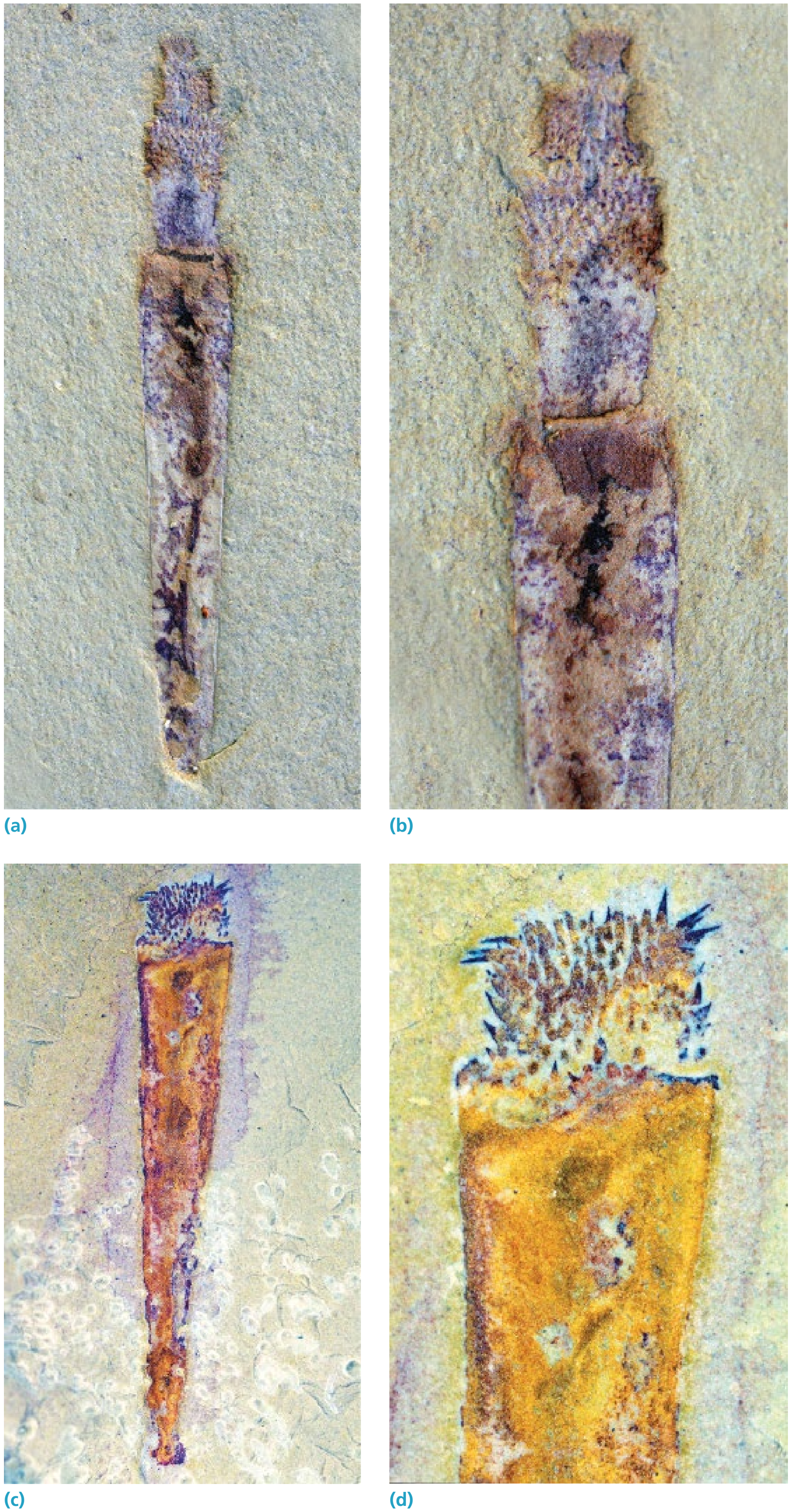
P. sinica is likely to have led a similar lifestyle to that of *Selkirkia*, which has been suggested to be a burrower, living in a tube vertically embedded into the sediment (Briggs *et al.* 1994). However, the stiff trunk tube is likely to restrict burrowing activities, so alternatively these animals might have lived on the sea bottom surface, moving their body by using their proboscis and searching for prey or feeding on dead animals (Maas *et al.* 2007).

P. sinica has been recorded only from the lower Cambrian Chengjiang biota of Yunnan Province.

Key references

Conway Morris 1977a; Briggs *et al.* 1994; Hou *et al.* 1999; Luo *et al.* 1999; Huang 2005; Maas *et al.* 2007; Wills *et al.* 2012; Ma *et al.* 2014a.

Figure 17.5 ***Paraselkirkia sinica***. **(a)**, **(b)** YKLP 13868, ×10.4, ×16.8; Jianshan, Haikou, Kunming. **(c)**, **(d)** RCCBYU 10238, ×8.5, ×21.2; Ercaicun, Haikou, Kunming.


(a)
(b)
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Genus *Corynetis* Luo & Hu *in* Luo, Hu, Chen, Zhang & Tao, 1999

Corynetis brevis Luo & Hu, 1999

Corynetis brevis is relatively rare and only known from about 100 specimens. It occurs as compressed fossils in a rusty color against the yellow rock matrix. Slight relief can be observed along the sediment infill inside the gut, and on the body surface ornament. The body is preserved as either straight or curved.

The size and shape of the specimens vary due to the different attitude of individual animals when they were fossilized. The average body length is about 3 cm. The body is divided into an anterior proboscis, trunk, and a short eversible caudal projection. The proboscis consists of an introvert, collar, and an everted pharynx. The introvert is smooth and narrow, terminating anteriorly with a circle of long spines. The unarmed collar is long and tapers anteriorly. The everted pharynx is long and lined with spinose or cuspidate pharyngeal teeth (Luo *et al.* 1999; Chen Jun-yuan 2004; Huang *et al.* 2004b; Huang 2005). Immediately posterior to the introvert is the trunk, which gradually increases in diameter toward its middle and posterior regions. The trunk surface is clearly marked by annuli that bear tiny setae, which appear to be long and thick at the anterior part of the trunk, small and irregular in the middle part, and arranged in distinct transverse rows in the posterior part. There is an eversible caudal projection at the posterior end of the body. The gut is straight and extends throughout the body.

C. brevis is the only known species of the genus *Corynetis*. It shows striking similarities with *Anningvermis multispinosus* Huang *et al.*, 2004, but the difference between them is likely to be the result of the body shape changing when the animal was moving. As there is a lack of diagnostic characters by which to separate these two taxa, it has been suggested that they should be regarded as synonymous (Ma *et al.* 2010). This is supported by the fact that *Corynetis* and *Anningvermis* are consistently resolved as sister to each other in phylogenetic analyses (Wills *et al.* 2012; Ma *et al.* 2014a). *C. brevis* has been placed as a stem cycloneuralian, a stem scalidophoran, or a stem priapulid in phylogenetic trees (Harvey *et al.* 2010; Wills *et al.* 2012; Ma *et al.* 2014a), and it also appears to have a close affinity with the Burgess Shale species *Louisella pedunculata*.

It has been suggested that *C. brevis* was an active mud burrower and a predator of meiobenthic animals such as the small arthropod *Ercaia minuscula* (Huang *et al.* 2004b). It appears that the animal dwelt in the burrow with only the anterior proboscis outside the sediment, and the circle of elongate spines at the base of the collar helped to detect prey and trigger the capture response.

Corynetis is only known from the Chengjiang biota.

Key references

Luo *et al.* 1999; Huang *et al.* 2004b; Chen Jun-yuan 2004; Huang 2005; Ma *et al.* 2010, 2014a; Wills *et al.* 2012.

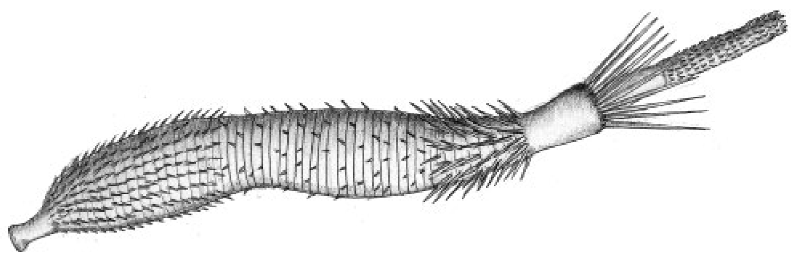
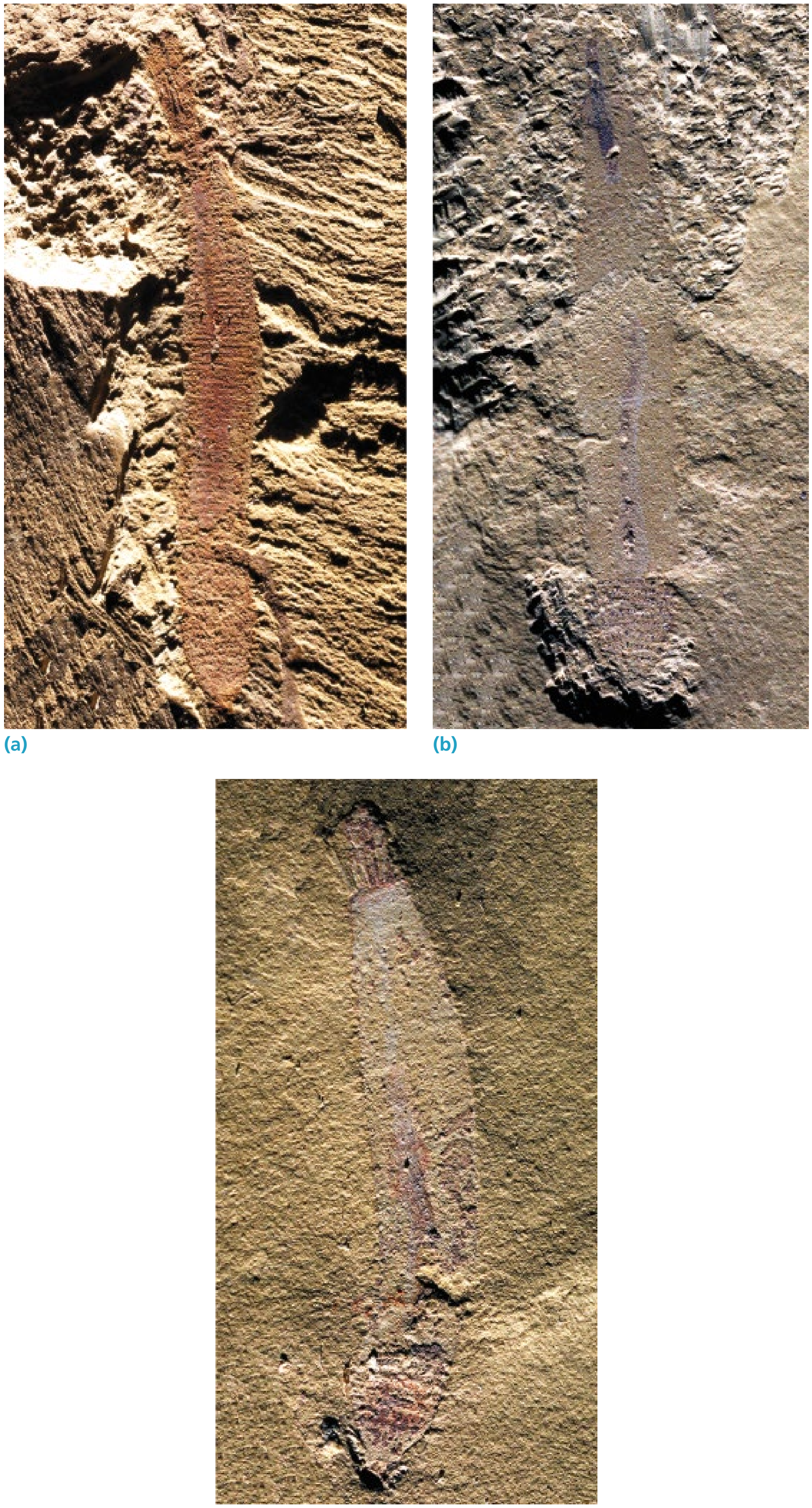


Figure 17.6 Reconstruction of ***Corynetis brevis*** (modified from Huang *et al.* 2004b).

Figure 17.7 ***Corynetis brevis***. **(a)** YKLP 13870, *circa* ×5.5; Mafang, Haikou, Kunming. **(b)** YKLP 13871, *circa* ×5.5; Xiaolantian, Chengjiang. **(c)** YKLP 13872, ×5.3; Ercaicun, Haikou, Kunming.



(a) (b) (c)

Genus *Sicyophorus* Luo & Hu *in* Luo, Hu, Chen, Zhang & Tao, 1999

Sicyophorus rarus Luo & Hu *in* Luo, Hu, Chen, Zhang & Tao, 1999

This is a relatively common priapulid-like worm, known from over a thousand specimens. In many cases the material consists of compressed, complete individuals, and the posterior half of the body is often better preserved with an apparently rigid outline. Detailed structures can be detected by subtle differences in color and relief.

The size of the animal is generally about 1 cm long. The overall body shape is reminiscent of a dumb-bell, with a subequally expanded introvert and posterior trunk connected by a constricted neck region. The introvert bears spine-like scalids arranged in about 20 longitudinal rows and 14 circlets. The narrower anterior part of the proboscis is protrusive and appears to bear a regular array of tiny spines. The trunk cuticle is apparently more rigid than the introvert, and is covered in a series of 13–15 longitudinal plates divided by dark ridges. The distinct gut is heavily coiled and filled with sediment, almost entirely occupying the ovoid trunk.

The monotypic *Sicyophorus* was originally described as having an uncertain taxonomic affinity, but *Protopriapulites haikouensis* Hou *et al.*, 1999, a junior synonym, was assigned to the Priapulida based on the arrangement of scalids on the introvert (Hou *et al.* 1999, 2004a). The distinct trunk plates show some resemblance to the loricate larvae of extant priapulids, but the specimens are much larger than any known priapulid larvae and are considered to be adults (Huang 2005; Maas *et al.* 2007). The species was also suggested to be a loriciferan, based on its constricted neck and ovoid trunk with longitudinal plates (Huang 2005), but it lacks some crucial characteristics of this group. Recent phylogenetic analyses resolved this species as either a stem scalidophoran or a stem priapulid (Ma *et al.* 2014a).

Like most priapulid-like worms, *S. rarus* was probably a burrower, but progress was most likely driven by peristaltic movements of the introvert, as the trunk appears to be inflexible. The coiled shape and sediment infilling of the gut indicate that the animal was a deposit feeder, perhaps digesting organic material from the sediment.

Sicyophorus is known from various localities of the Chengjiang biota, and has also been reported from slightly younger Kaili biota.

Key references

Luo *et al.* 1999; Hou *et al.* 1999, 2004a; Huang 2005; Maas *et al.* 2007; Ma *et al.* 2014a.

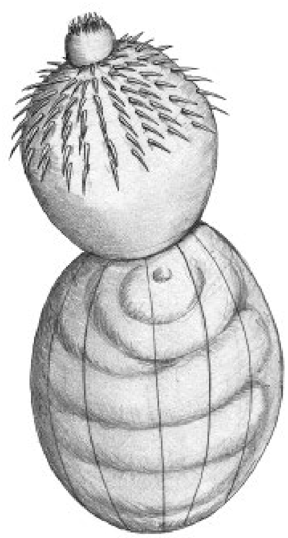
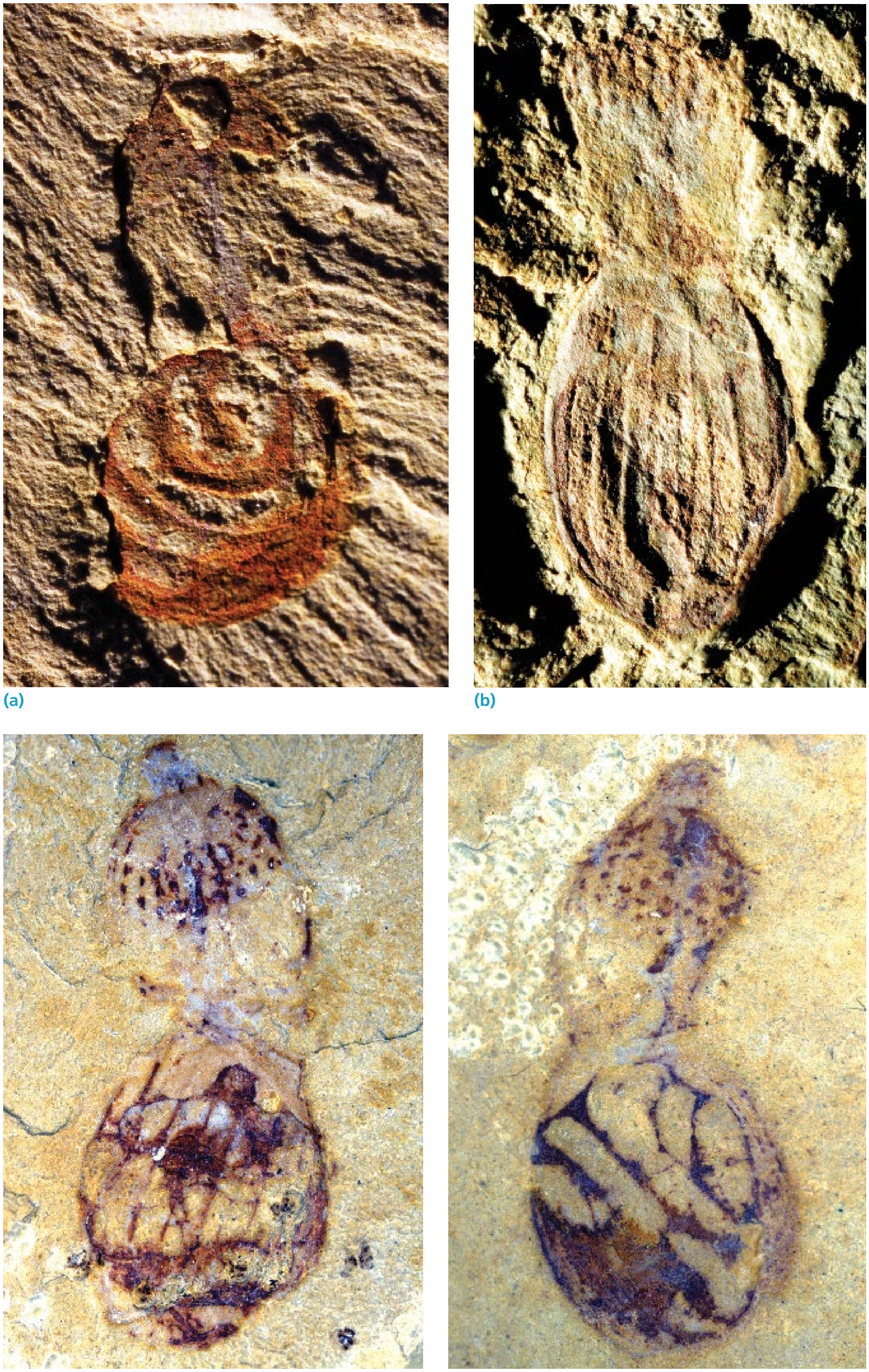


Figure 17.8 Reconstruction of ***Sicyophorus rarus*** showing internal coiled gut.

Figure 17.9 ***Sicyophorus rarus***. **(a)** YKLP 13873, ×15.0; Mafang, Haikou, Kunming. **(b)** YKLP 13874, ×12.3; Mafang, Haikou, Kunming. **(c)** RCCBYU 10231, ×11.5; Mafang, Haikou, Kunming. **(d)** RCCBYU 10232, ×11.6; Mafang, Haikou, Kunming.



(a) (b) (c) (d)

Genus *Palaeopriapulites* Hou, Bergström, Wang, Feng & Chen, 1999

Palaeopriapulites parvus Hou, Bergström, Wang, Feng & Chen, 1999

This is one of the rarest priapulid-like worms, known from approximately 10 specimens. The specimens appear flattened against the typically yellow background of the rock.

Individuals are about 10 mm long. The body is divided into the approximately equal-sized ovoid introvert and the trunk, which are connected by a narrower distinct neck region. Spine-like scalids cover the anterior half of the introvert and are arranged in about 20 longitudinal rows. The protruding, anterior part of the proboscis is much narrower than the introvert. The trunk appears to be encased in a kind of thick cuticle and displays a number of fine longitudinal striations that are possibly the result of taphonomic compression. The intestine is typically narrow, straight, and flat and often preserved in a dark color. In some specimens the gut is curved near the posterior end of the trunk, where numerous hooks are observed (Hou *et al.* 2004a).

Palaeopriapulites parvus is the only known species of the genus. It shares striking similarities with *Sicyophorus rara* Luo & Hu, 1999, and has been suggested to be a possible synonym of the latter species (Chen Liang-zhong *et al.* 2002; Huang 2005). However, *P. parvus* is distinctly different from *Sicyophorus* in its lack of a heavily coiled gut filling the trunk region (Hou *et al.* 2004a) and its lack of rigid loricate-like plates covering the trunk. Recent phylogenetic analyses resolved this species as a sister taxon to *Sicyophorus*, and together they are placed basal to crown scalidophorans or to crown priapulids (Ma *et al.* 2014a).

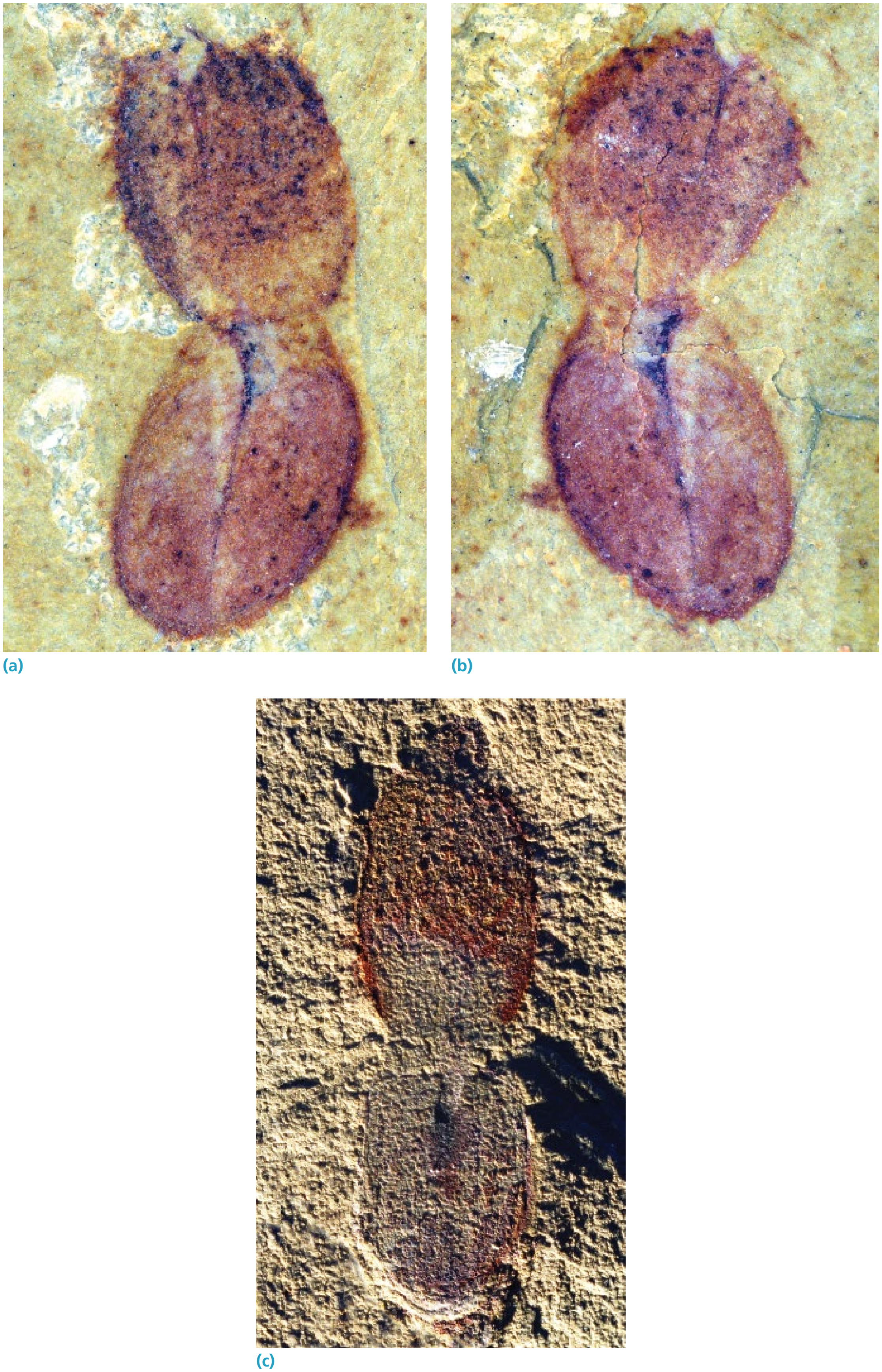
P. parvus is presumed to have had a burrowing lifestyle. The difference in gut morphology from *Sicyophorus* and the lack of sediment infilling indicate that this animal occupied a slightly different ecological niche. The dark flat gut suggests that this animal might be more of a carnivore.

Palaeopriapulites is principally known from the Chengjiang biota. It has also been reported from the slightly younger Cambrian Kaili biota.

Key references

Hou *et al*. 1999, 2004a; Chen Liang-zhong *et al.* 2002; Huang 2005; Ma *et al.* 2014a.

Figure 17.10 ***Palaeopriapulites parvus***. **(a)** NIGPAS 115446a, ×9.3; Maotianshan, Chengjiang. **(b)** NIGPAS 115446b, ×9.3; Maotianshan, Chengjiang. **(c)** YKLP 13875, *circa* ×9.5; Mafang, Haikou, Kunming.



Genus *Eximipriapulus* Ma, Aldridge, Siveter, Siveter, Hou & Edgecombe, 2014

Eximipriapulus globocaudatus Ma, Aldridge, Siveter, Siveter, Hou & Edgecombe, 2014

The name of this species alludes to its exquisite preservation, of both external structures and internal anatomy. It is relatively rare, with only some 12 specimens known.

Presumed mature specimens are about 1.4 cm long and 3 mm wide, but the size and shape of specimens varies, depending on the nature of their activity at the moment of death and preservation. Specimens consist of three parts: an anterior proboscis, a stout trunk, and a distinctly expanded posterior region. The proboscis itself is subdivided into four parts from anterior to posterior: a partially eversible pharynx lined with pharyngeal teeth; a smooth collar and non-retractable collar; a completely invaginable bulbous introvert covered by long spine-like scalids arranged in approximately 30 longitudinal rows and nine circlets; and a narrower neck region bearing conical to triangular scalids arranged in approximately 30 longitudinal rows and 13 circlets. The unsegmented trunk is stout, cylindrical, and slightly tapered toward both ends, with annulations each about 0.1 mm wide. Different types of cuticular ornament are present on the trunk surface, including spinules along the annuli and larger setae scattered around the mid-trunk region. The posterior region of the body is distinctively expanded and globular, with a smooth surface. Several specialized regions of the alimentary canal are recognized: a mouth opening leading to a muscular pharynx, and thence to an esophagus, a wide midgut, a hindgut with a round muscular structure, and a terminal anus. A putative juvenile specimen is also recognized in the original description.

The monotypic *Eximipriapulus* shows similarities to some Cambrian priapulid-like worms, such as *Ottoia* (Conway Morris 1977a) and *Xiaoheiqingella* (Chen Liangzhong *et al.* 2002), all of which have a bulbous introvert covered by scalids and a stout body shape. However, *E. globocaudatus* differs from those genera by having a distinct neck region with scalids of a second type, and a distinctly expanded posterior region. Based on phylogenetic analysis, this species appears to be one of the few Cambrian taxa embedded within the priapulid crown group and positioned basal to the extant clade that includes the families Maccabeidae, Halicryptidae and Priapulidae.

The morphological and anatomical details preserved in this material allow direct comparison with extant priapulids, including the different stages of the proboscis and their movement, inference of a spacious body cavity, and the details of the complex alimentary canal. The species is considered to be an active burrower using a double-anchor strategy, and was both a deposit-feeder and a carnivore (Ma *et al.* 2014a).

Eximipriapulus is unknown outside the Chengjiang biota.

Key reference

Ma *et al.* 2014a.

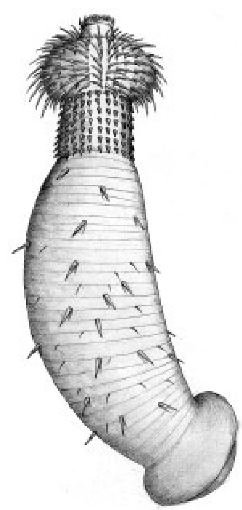
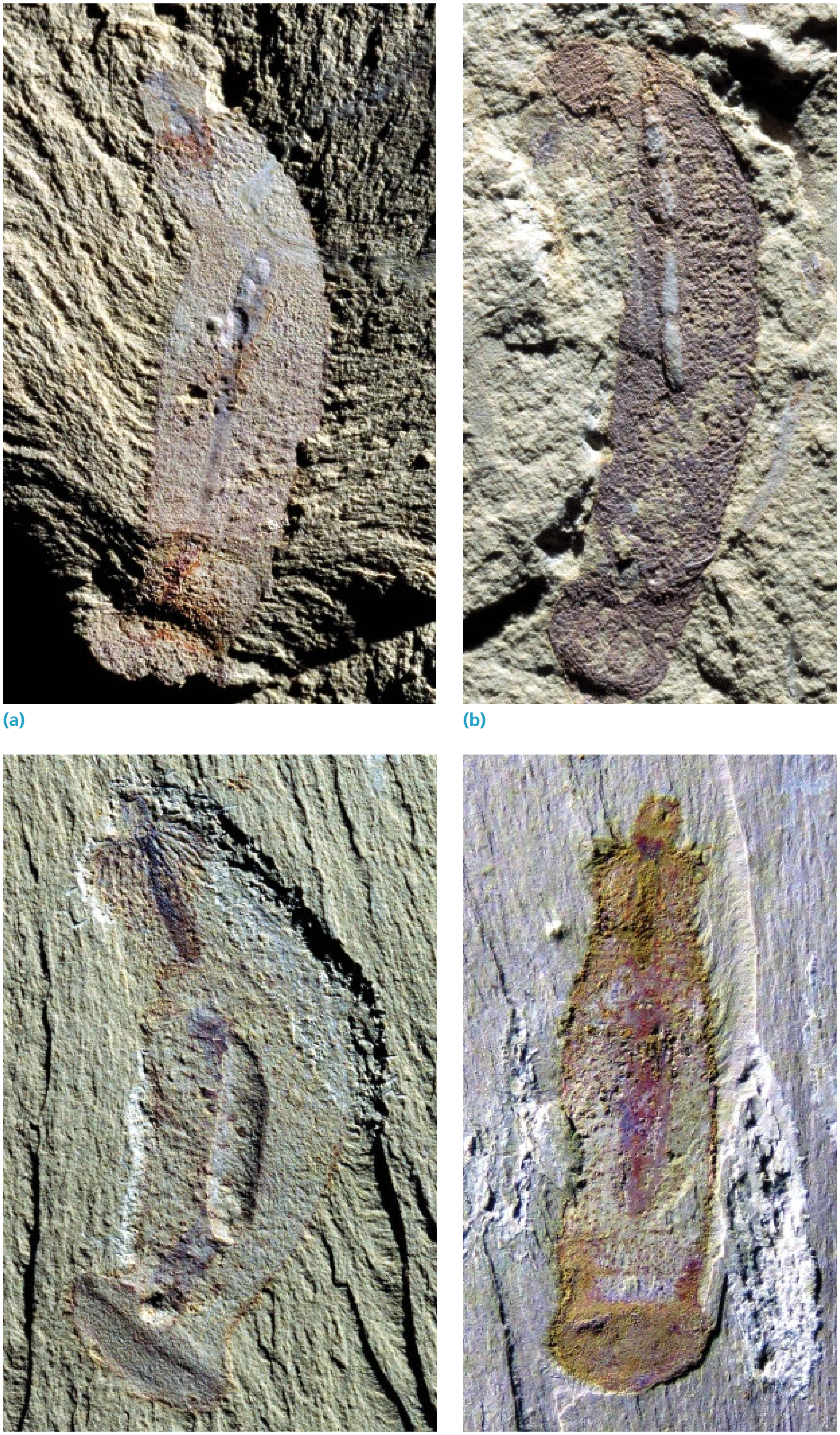


Figure 17.11 Reconstruction of ***Eximipriapulus globocaudatus*** (after Ma *et al.* 2014a).

Figure 17.12 ***Eximipriapulus globocaudatus***. **(a)** YKLP 11327b, ×8.3; Mafang, Haikou, Kunming. **(b)** YKLP 11332a, ×7.7; Mafang, Haikou, Kunming. **(c)** YKLP 11326a, ×8.2; Mafang, Haikou, Kunming. **(d)** YKLP 13876, *circa* ×8.0; Ercaicun, Haikou, Kunming.



(a) (b) (c) (d)

Genus *Xiaoheiqingella* Hu *in* Chen, Luo, Hu, Yin, Jiang, Wu, Li & Chen, 2002

Xiaoheiqingella peculiaris Hu *in* Chen, Luo, Hu, Yin, Jiang, Wu, Li & Chen, 2002

Xiaoheiqingella peculiaris is a rare species, known from only about 70 specimens. They are preserved as flattened fossils in a light- to dark-brown color, with slight relief around the introvert scalids and some parts of the gut. The body is often preserved curved or twisted.

This species, one of the smallest priapulid worms from the Chengjiang biota, is less than 1.5 cm long and 4 mm wide. The body is divisible into four sections: an anterior proboscis, neck, trunk, and a pair of long caudal appendages (Huang *et al.* 2004c; Han *et al.* 2004). The proboscis is divided into the introvert, collar, and everted pharynx. The introvert is subspherical. The anterior half of the introvert bears 25 longitudinal ridges armed with scalids, while only a few additional scalids are scattered at the posterior half of the introvert. A circle of elongate spines is observed at the anterior end of the introvert (Huang *et al.* 2004c). The collar is smooth and short and tapers anteriorly. The pharynx is infrequently preserved as a short protrusion at the anteriormost end of the proboscis during eversion. A few specimens show spine-like pharyngeal teeth arranged pentagonally. The neck appears as a constriction marking a sharp boundary between the introvert and the trunk. The cylindrical trunk is finely annulated. The posterior pre-anal region of the trunk can be expanded and displays about 14 rings of papillae. One or a pair of caudal appendages is attached at the posterior end of the trunk (Huang *et al.* 2004c, 2006; Han *et al.* 2004; Han & Hu 2006). The caudal appendages are weakly annulated and appear to be expandable and contractile (Han *et al.* 2004). The gut is narrow, often slightly twisted or coiled at the anterior part of the trunk, and has sediment infill. It extends from the anterior end of the proboscis to the posterior end of the trunk.

X. peculiaris is the only known species of *Xiaoheiqingella*. *Yunnanpriapulus halteroformis* Huang *et al.*, 2004 is considered to be a junior synonym of *X. peculiaris*. The morphological difference between the two taxa is likely to be the result of the body shape changing when the animal was moving (Han *et al.* 2004; Han & Hu 2006; Ma *et al.* 2010). This synonymy is also supported by phylogenetic analyses, in which *X. peculiaris* and *Y. halteroformis* are consistently resolved as sister taxa (Harvey *et al.* 2010; Wills *et al.* 2012; Ma *et al.* 2014a). *Xiaoheiqingella* shows many features known from living priapulids and it has been placed within the Recent family Priapulidea (Huang *et al.* 2004c). Phylogenetic analyses resolve *Xiaoheiqingella* as a crown priapulid, closely allied to a crown-group clade composed of Priapulidae, Maccabeidae, and Halicryptidae (Harvey *et al.* 2010; Wills *et al.* 2012; Ma *et al.* 2014a).

The specimens of *X. peculiaris* are often preserved at an angle of about 30–40° to bedding in the rocks, indicating that they were burrowing and might even be able to burrow vertically (Han *et al.* 2004). The black organic remains inside the gut suggest a carnivorous lifestyle, but the twisted gut with sediment infill also indicates occasional mud eating.

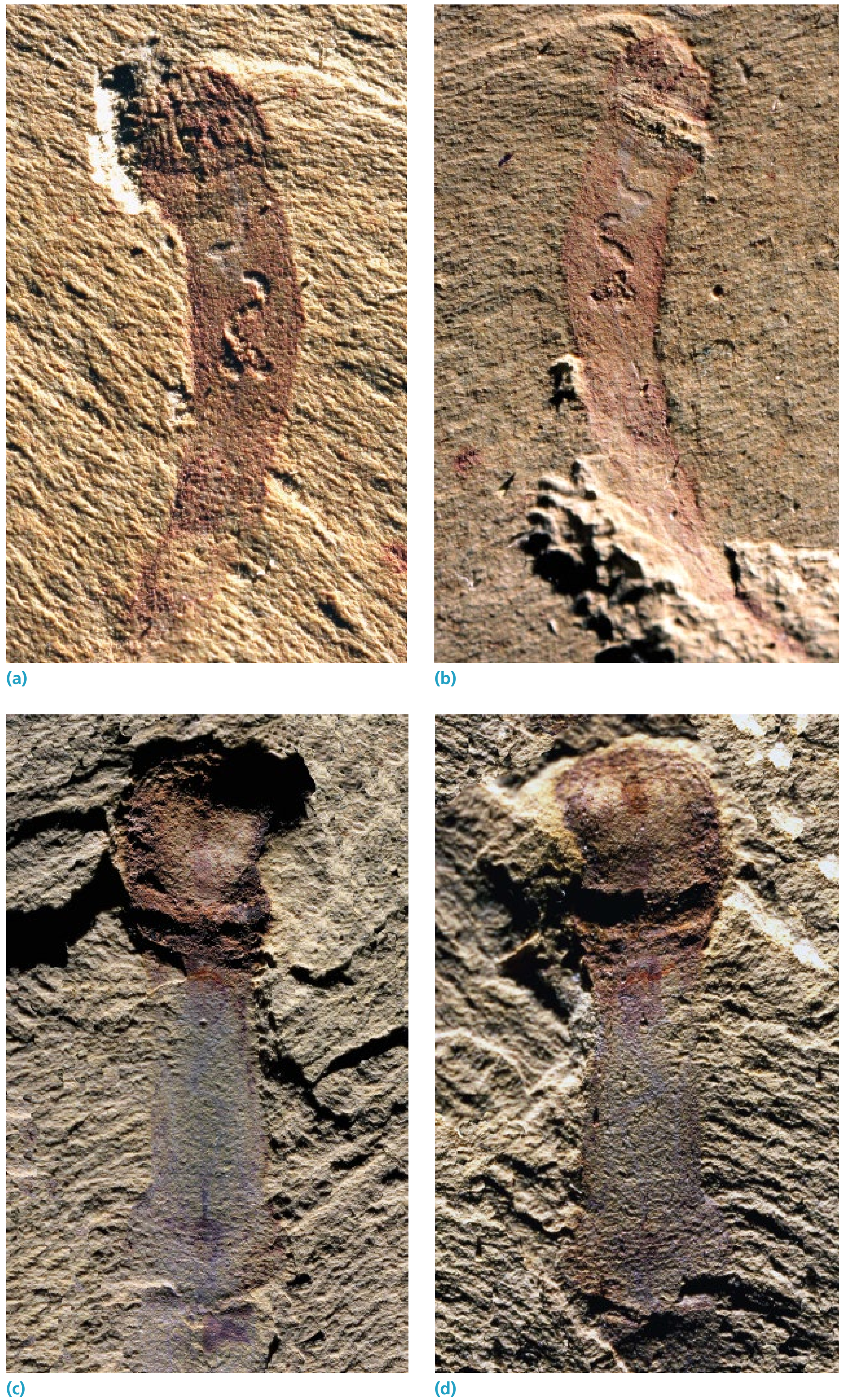
Xiaoheiqingella is only recorded from the Chengjiang biota.

Key references

Chen Liang-zhong *et al.* 2002; Huang *et al.* 2004c, 2006; Han *et al.* 2004; Han & Hu 2006; Ma *et al.* 2010, 2014a; Harvey *et al.* 2010; Wills *et al.* 2012.

Figure 17.13 Reconstruction of ***Xiaoheiqingella peculiaris*** (modified from Huang *et al.* 2004c and Han *et al.* 2004).

Figure 17.14 ***Xiaoheiqingella peculiaris***. **(a)** YKLP 13877a, ×12.5; Maotianshan, Chengjiang. **(b)** YKLP 13877b, ×12.5; Maotianshan, Chengjiang. **(c)** YKLP 13878a, ×11.0; Mafang, Haikou, Kunming. **(d)** YKLP 13878b, ×11.0; Mafang, Haikou, Kunming.



Genus *Omnidens* Hou, Bergström & Yang, 2006

Omnidens amplus Hou, Bergström & Yang, 2006

This species is only known from elements of the mouth of about 20 specimens. The hard sclerites of the mouth are preserved in marked relief.

The largest mouth sclerite is 4.7 cm long, and the animal is estimated to be over 1 m long (Hou *et al.* 2006b). The mouth at the presumed anterior end of the body consists of three types of sclerites: (1) Approximately 12 radiating rows of pectinate sclerites (5–6 spines of subequal length) decreasing in size from the outside, each row with at least six sclerites. The sclerites alternate in position to form spirals rather than rings and are interpreted as pharyngeal teeth (Hou *et al.* 2006b). (2) Outside the pharyngeal teeth, there is a circle of approximately 14–16 large, cone-shaped plates, each with a raised spinose structure at the distal tip. They are preserved as a continuous series of pharyngeal teeth, all oriented in the same direction. The large plates possibly closed the mouth when the pharyngeal teeth are withdrawn. (3) Posterior to the large plates, there are numerous button-shaped sclerites with a few nodes or low cusps, each sclerite surrounded by smooth cuticle. These structures are interpreted as scalids on an introvert.

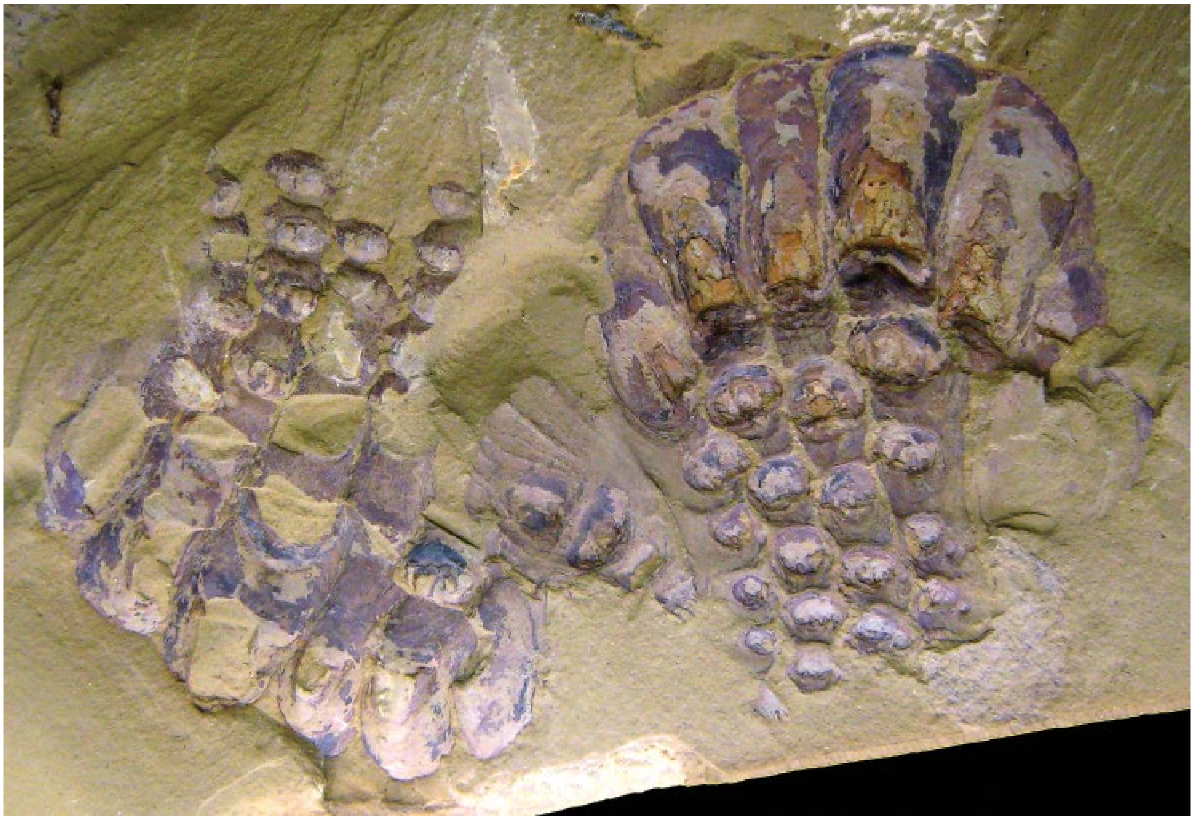
Omnidens amplus is the only known species of *Omnidens*. The specimens were initially interpreted as the mouth of an exceptionally large anomalocaridid (Chen Jun-yuan *et al.* 1994; Chen Jun-yuan & Zhou 1997). However, Hou *et al.* (2006b) noted distinct differences between *O. amplus* and anomalocaridid mouthparts and interpreted the material as the mouth of a giant priapulid-like animal. The exact affinities of *O. amplus* can only be resolved with the discovery of more complete specimens.

The formidable mouth elements indicate that *O. amplus* was likely to be a predator. The species is known only from the Chengjiang biota.

Key references

Chen Jun-yuan *et al.* 1994; Chen Jun-yuan & Zhou 1997; Hou *et al.* 2006b.

Figure 17.15 ***Omnidens amplus***. **(a)** YKLP 10153a and 10154a, ×2.0; Mafang, Haikou, Kunming. **(b)** YKLP 10153b and 10154b, ×2.0; Mafang, Haikou, Kunming.



(a)

(b)

Genus *Acosmia* Chen & Zhou, 1997

Acosmia maotiania Chen & Zhou, 1997

This is a rare worm in the Chengjiang community, with fewer than 10 specimens known. They are typically flattened and preserved in a light-brown color. Some parts of the gut are preserved in slight relief with sediment infilling.

This worm is relatively large, up to 10 cm long and 8 mm wide. The cylindrical body is subdivided by a constriction into an anterior proboscis and a posterior trunk. The barrel-shaped proboscis terminates anteriorly with a broad mouth opening, which is armed with an array of hooks. The trunk is annulated and ornamented with papillae and fine spines. These ornamentations are relatively obscure and appear to be more evident in the anterior and posterior parts of the body. The alimentary canal of the animal is pronounced, with a strong muscular pharynx located immediately behind the mouth opening, which is preserved in a darker color. The gut is wide and straight, with a striated surface, and often infilled with sediment.

Acosmia maotiania is the only known species of *Acosmia*. Chen Jun-yuan and Zhou (1997) considered it to be the largest and rarest priapulid in the Chengjiang biota. However, as it lacks some diagnostic features of priapulids, a more thorough investigation regarding its affinities is required.

The specimens are often preserved either tightly curved, or with the mouth opening parallel to the bedding plane, suggesting that the animal might have lived in a U-shaped burrow. The widely observed sediment infill in the gut indicates a deposit-feeding lifestyle.

A. maotiania is known only from the Chengjiang biota, Yunnan Province.

Key reference

Chen Jun-yuan & Zhou 1997.

Figure 17.16 ***Acosmia maotiania***. **(a)** RCCBYU 10234, ×4.4; Maotianshan, Chengjiang. **(b)** RCCBYU 10235, ×4.5; Maotianshan, Chengjiang. **(c)** RCCBYU 10236, ×2.9; Maotianshan, Chengjiang.

(a)

(b)

(c)

Genus *Archotuba* Hou, Bergström, Wang, Feng & Chen, 1999

Archotuba elongata (Luo & Hu *in* Luo, Hu, Chen, Zhang & Tao, 1999)

This species is relatively common with hundreds of known specimens, which are essentially the remains of the tubes of the animal. All of the specimens are preserved as compressed fossils, in a whitish color, sometimes with rusty patches. No proboscis or other soft parts of the animal have been discovered.

The tube is shaped like an elongated cone. Large individuals can reach 5 cm in length and 6 mm in diameter for the wide opening, with a sharply pointed posterior end. The surface of the tube is smooth and lacks ornamentation, but a few specimens show sparsely distributed annulations. Parts of the intestine can be seen through the tube as a dark longitudinal structure running down the midline of the fossil.

Archotuba is monospecific. *A. elongata* was originally reported as *Selkirkia*? *elongata* Luo & Hu, 1999. Chengjiang material recorded under the name *Cambrorhytium* sp. nov. of Chen & Zhou, 1997 and the species *Archotuba conoidalis* Hou *et al.*, 1999 are considered to be the same species as *A. elongata*. *A elongata* shows similarities to the other Cambrian tube-dwelling genera *Selkirkia* and *Paraselkirkia* in having a conical tube with annulations and a straight intestine. However, due to a lack of detailed information about its proboscis or other soft-part anatomy, the taxonomic and phylogenetic position of *A. elongata* remains problematic. It was originally assigned to Priapulida (Luo *et al.* 1999; Hou *et al.* 1999), but others have suggested that it might be related to cnidarians (Chen Jun-yuan & Zhou 1997; Chen Jun-yuan 2004; Huang 2005).

The animal possibly had a sessile life, as the tube is often found attached to the shell of other benthic organisms, such as brachiopods and hyolithids. Sometimes several of these tubes are found together with their apices emanating from the same area of substrate and the tubes oriented subparallel to each other. The dark gut may imply a carnivorous diet. A sedentary lifestyle would be very different from the active burrowing of priapulids. At the same time there are no tentacles observed to support the cnidarian interpretation.

A. elongata has only been recorded from the Cambrian Chengjiang biota, Yunnan Province.

Key references

Chen Jun-yuan & Zhou 1997; Luo *et al.* 1999; Hou *et al.* 1999; Chen Jun-yuan 2004; Huang 2005.

Figure 17.17 ***Archotuba elongata***. **(a)** NIGPAS 115452, ×1.7; Ma'anshan, Chengjiang. **(b)** NIGPAS 115450a, ×2.4; Ma'anshan, Chengjiang. **(c)** NIGPAS 115453, ×5.0; Maotianshan, Chengjiang.


(a)


(b)


(c)

18 Lobopodians

Lobopodia is the commonly used informal term for a group of animals popularly characterized as worms with legs. The term was coined (Snodgrass 1938) to describe soft, unsegmented, and uniramous appendages, as seen in living velvet worms – the onychophorans (claw bearers). After the discovery of *Aysheaia* from the middle Cambrian Burgess Shale (Walcott 1911b; Whittington 1978), that genus together with Onychophora and Tardigrada were grouped into the Phylum Lobopodia (Simonetta & Delle Cave 1981). Dzik & Krumbiegel (1989) followed this systematic arrangement and put marine onychophoran-like fossils into the Class Xenusia, which is included in the phylum Lobopodia. However, with increasing input of new fossil evidence phylogenetic analyses show that fossil lobopodians do not form a monophyletic clade, but represent three panarthropod clades (Edgecombe & Legg 2014; Ma *et al.* 2014c; Smith, M.R. & Ortega-Hernández 2014).

Most fossil lobopodians are known from marine deposits around the world, primarily from Cambrian Lagerstätten, but some species are also reported from the Ordovician, Silurian, and Carboniferous. Cambrian lobopodians exhibit a high level of morphological diversity, but in general they share a worm-like annulated body bearing numerous pairs of unjointed legs with terminal claws. Some Cambrian forms are also armed with isolated, toughened sclerites or spines in the trunk region. These unusual character combinations make Cambrian lobopodians particularly relevant for understanding the origin and early evolution of panarthropods. However, resolving the phylogenetic relationships between these extinct groups and their extant proxies has been historically problematic, as the lobopodian part of the phylogenetic tree has been unstable and analyses have shown considerable topological conflict (Edgecombe & Legg 2014). Hence, the exact affinities of Cambrian lobopodians remain uncertain.

More than 30 lobopodian species are reported from the stratigraphic record, including 10 named genera from the Cambrian Chengjiang biota, making it the richest source of fossil lobopodians. This chapter includes most of the well-known Chengjiang lobopodians. The two lobopodian taxa *Jianshanopodia decora* Liu *et al.*, 2006 and *Megadictyon haikouensis* Luo & Hu *in* Luo *et al.*, 1999 (see also Liu Jian-ni *et al.* 2007) were established on incomplete specimens and their nature is uncertain.

Genus *Paucipodia* Chen, Zhou & Ramsköld, 1995

Paucipodia inermis Chen, Zhou & Ramsköld, 1995

Paucipodia inermis is a relatively large lobopodian with comparatively minimal external anatomical features. About 25 specimens have been reported so far. Specimens are preserved in a light-brown to pinkish color and strongly flattened against the yellow matrix, except for the occasional relief of the sediment-filled parts of the gut or the leg attachment areas. The animals are compressed dorsoventrally or laterally, and preserved straight or curled up.

The species is comparatively featureless, with a sleek and well-defined body margin. One complete specimen reaches 12.5 cm in length and is 4.9 mm wide. The body is elongate, tapered toward both ends, and bears nine pairs of appendages ventrolaterally. The legs, each of which has two terminal claws, become shorter toward both ends of the animal. The trunk extends beyond the legs at both ends, without a distinct boundary between the trunk, head, and tail sections of the body. The head is much more slender than the tail and displays interesting structural details, including pharyngeal teeth arranged around the mouth opening, and a pair of swellings interpreted as

The Cambrian Fossils of Chengjiang, China: The Flowering of Early Animal Life, Second Edition. Hou Xian-guang, David J. Siveter, Derek J. Siveter, Richard J. Aldridge, Cong Pei-yun, Sarah E. Gabbott, Ma Xiao-ya, Mark A. Purnell, Mark Williams.

pre-esophageal, dorsally expanded brain lobes (Hou *et al.* 2004c). The body surface shows very fine annulations, and circular muscle fibers can be seen in some specimens. The alimentary canal is straight with occasional sediment infilling. A pair of violet-colored bands with repeated paired structures are observed beside the alimentary canal, which were interpreted as paired ventral nerve cords with segmental ganglia (Hou *et al.* 2004c).

P. inermis is monotypic. *Paucipodia haikouensis* Luo & Hu *in* Chen *et al*., 2002 is regarded as the same species (Hou *et al*. 2004c). The distinct lack of dorsal sclerites, surface papillae, or any other cuticular ornament gives *P. inermis* a markedly different appearance from other Cambrian lobopodians. Phylogenetic analyses resolve *Paucipodia* as one of the most basal lobopodian species, appearing closely related to *Diania* (e.g., Ma *et al.* 2014c). Both taxa share a relatively large body size, tapering toward both ends (one end being narrower than the other), and lacking clear division between the leg-bearing trunk and the head.

In the Chengjiang several specimens of *P. inermis* are preserved entombed aongside *Eldonia,* indicating a close ecological association between the two. *P. inermis* may have fed on living or dead *Eldonia*. Further evidence for this lifestyle is the occurrence of terminal claws on the limbs of *P. inermis*, which suggests that it was better adapted for climbing (e.g., on carcasses) rather than walking (Hou *et al.* 2004c).

This species is only known from the Chengjiang biota.

Key references

Chen Jun-yuan *et al.* 1995c; Hou *et al.* 2004c; Ma *et al.* 2014c.

Figure 18.1 ***Paucipodia inermis*.** **(a)** RCCBYU 10185, ×2.4; Mafang, Haikou, Kunming. **(b)** RCCBYU 10183, ×1.6; Mafang, Haikou, Kunming. **(c)** RCCBYU 10184, ×1.1; Mafang, Haikou, Kunming.

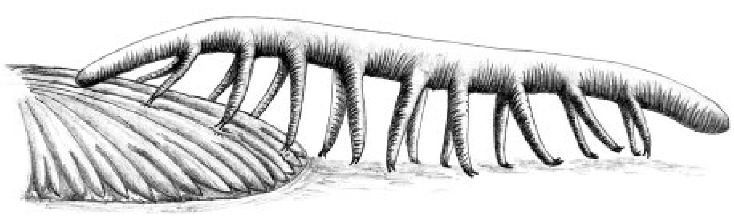


Figure 18.2 Reconstruction of ***Paucipodia inermis*** (after Hou *et al.* 2004a) crawling on *Eldonia.*

Genus *Diania* Liu, Steiner, Dunlop, Keupp, Shu, Ou, Han, Zhang & Zhang, 2011

Diania cactiformis Liu, Steiner, Dunlop, Keupp, Shu, Ou, Han, Zhang & Zhang, 2011

Diania cactiformis is a relatively rare species, known from approximately 40 specimens, but only four of which are complete. All known specimens are compressed dorsoventrally, with cuticular ornamentation often preserved in strong relief and a rusty color.

Complete specimens reach up to 6 cm long. A vermiform body bears 10 pairs of appendages along the trunk. Compared with other Cambrian lobopodian animals, the appendages of *D. cactiformis* are distinctly wider and more robust, with the maximum width greater than the trunk. The legs are uniquely covered by four longitudinal rows of strong rigid spines that are closely arranged with one following another. The attachment areas of these spines are often preserved as circular impressions. The legs are annulated, with seven fine annulations at the proximal end where spines are lacking, and around 15 wider annulations distally corresponding to the spine attachment points. All appendages gradually taper toward their distal ends, which lack terminal claws, but bear non-specialized spines at the tip of the appendages. The relatively slender trunk tapers toward both ends and extends beyond the appendages at both ends. The trunk surface carries fine annulations, about 4–5 per millimeter, with papillae arranged along the annulations. At the junction where the paired appendages are attached, the trunk stem is slightly expanded into a circular structure with possible thickened epidermis to support the robust lobopods. One end of the trunk is long and slender; the other end is wider and tapers sharply toward the tip. Both ends lack distinct head features such as a mouth, antennae, and eyes, and therefore its anteroposterior orientation remains uncertain. No internal anatomical structures are known.

D. cactiformis was initially interpreted as possessing arthropod-like, sclerotized, and articulated appendages, and the species was suggested to be the sister taxon of euarthropods (Liu Jian-ni *et al.* 2011). However, other authors have opined that the preservation of certain features is more likely the result of a taphonomic artifact and that there is no unequivocal evidence of sclerotization, segmentation, or articulation in the appendages (Ma *et al.* 2014c). As it proved impossible (Legg *et al.* 2011; Mounce & Wills 2011) to replicate the original phylogenetic results of Liu Jian-ni *et al.* (2011), the phylogenetic position of *D. cactiformis* became obscure. Subsequent phylogenetic analysis resolved the species as basal to most Cambrian lobopodians, far removed from euarthropods (Ma *et al.* 2014c), and of relatively close affinity to another Chengjiang lobopodian, *Paucipodia inermis*.

The mode of life of *D. cactiformis* is difficult to envisage due to its unusual appearance. The spines along the appendages were likely to be defensive. Also, unlike other Cambrian lobopodians, the appendages are much more laterally attached to the trunk and there are no specialized terminal claws. Therefore, the animal seems poorly adapted for walking or climbing, and instead perhaps crawled on the sea floor. No clear gut structure or associated sediment has been observed in any specimen, and it has been suggested that *D. cactiformis* may have fed on carrion (Ma *et al.* 2014c).

This species is only known from the Chengjiang biota, from several localities.

Key references

Liu Jian-ni *et al.* 2011; Legg *et al.* 2011; Mounce & Wills 2011; Ma *et al.* 2014c.

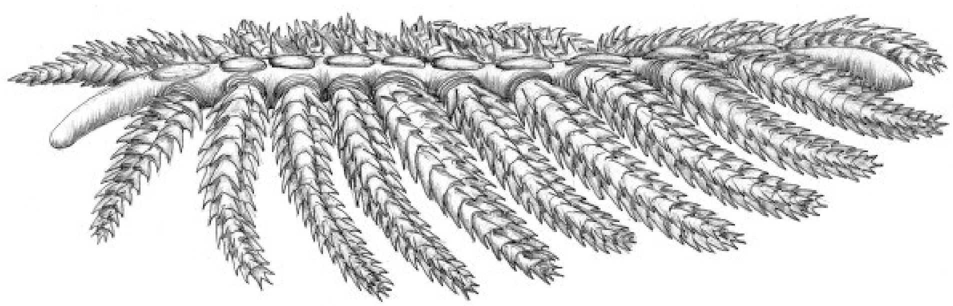
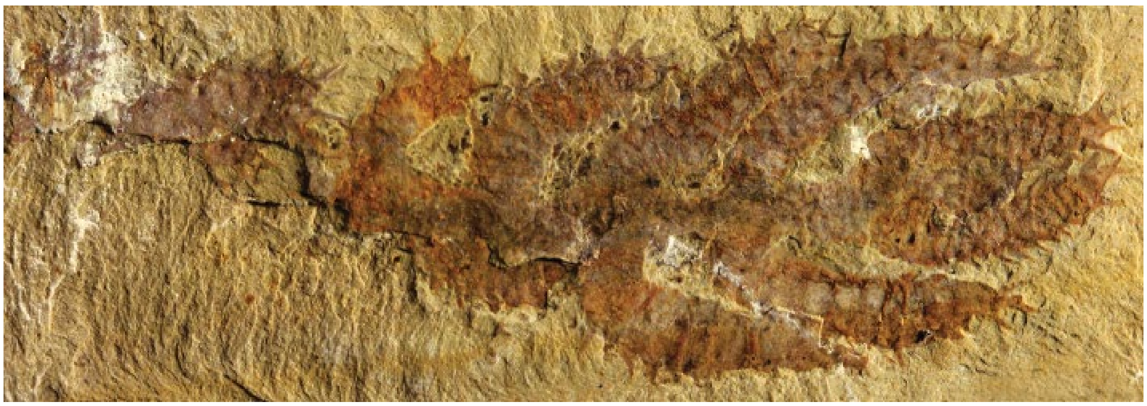


Figure 18.3 Reconstruction of ***Diania cactiformis*** (after Ma *et al.* 2014c).

Figure 18.4 ***Diania cactiformis***. **(a)** YKLP 11314a, ×3.2; Jianshan, Haikou, Kunming. **(b), (c)** YKLP 11314b, ×3.6, ×9.5; Jianshan, Haikou, Kunming. **(d)** YKLP 11318, ×4.7; Ercaicun, Haikou, Kunming.

(a)



(b)

(c)

(d)

Genus *Microdictyon* Bengtson, Matthews & Missarzhevsky, 1981

Microdictyon sinicum Chen, Hou & Lu, 1989

Microdictyon sinicum is known from over one hundred specimens. The soft parts of the body are flattened and preserved in a pinkish color, while the sclerites tend to be strongly mineralized and preserved in dark-brown, three-dimensional relief.

Specimens vary in size from 1–8 cm long. The body is cylindrical and clearly tapers toward one end that is extended, narrow, and limbless and is suggested to be the anterior end (Ramsköld 1992; Chen Jun-yuan *et al.* 1995d; Ramsköld & Chen 1998). However, the antero-posterior orientation of the animal has been controversial, as the short end terminating with a small projection and a pair of curling legs has also been suggested to be the head (Hou & Bergström 1995; Bergström & Hou 2001). There are nine pairs of trunk sclerites, which vary in both size and shape on a single specimen. The sclerites tend to be smaller and round toward the extended limbless end, but much larger and ovoid toward the short end. The surface of each sclerite has hexagonal, cylindrical perforations and spiky nodes. The trunk margin is clear, smooth, and dorsally humped above each trunk sclerite. The surface of the trunk between the sclerites is annulated. There are 10 pairs of legs; each pair splays ventrally beneath a pair of trunk sclerites, except for two pairs corresponding with the last sclerite at the short end. All legs are annulated and have a central canal and two terminal claws.

The genus *Microdictyon* was established based on isolated, phosphatic net-like sclerites from the lower Cambrian of South Kazakhstan (Bengtson *et al.* 1981). *Microdictyon* sclerites are now known to be globally widespread. The enigmatic nature of these sclerites was only elucidated by the discovery of complete body fossils of *Microdictyon sinicum*, showing that these sclerites formed part of a lobopodian. Recent phylogenetic analyses show that *Microdictyon* is closely related to *Paucipodia* and *Diania* (Ma *et al.* 2014c; Smith, M.R. & Ortega-Hernández 2014), all of which have an elongated, narrow, limbless end suggested to be the head. More distantly, *Microdictyon* also shares some similarities with *Cardiodictyon* and *Hallucigenia* based on its segmentally arranged trunk sclerties.

A cluster of small to medium-sized *M. sinicum* specimens are found compressed on *Eldonia* specimens (Chen Jun-yuan *et al.* 1995e), suggesting a life association. Thus, for those who consider that *Eldonia* had a medusoid-like lifestyle *M. sinicum* has been interpreted as pseudopelagic, living attached to the supposed floating bodies of *Eldonia*. However, the lifestyle of *Eldonia* is controversial. For example, it has been pointed out that *Eldonia* might be benthic, and *M. sinicum* should at least be to some degree a carrion-feeder, using its claws to get a firm hold on the prey or carcass (Bergström & Hou 2001).

More than a dozen species of *Microdictyon* have been reported from lower and middle Cambrian strata, occurring in Australia, China, England, Greenland, Kazakhstan, Mexico, and various localities in northwestern Europe and North America, Russia and Turkey (Topper *et al.* 2011). All records except *M. sinicum* are based on sclerites alone. *M. sinicum* is known only from the Chengjiang biota, Yunnan Province.

Key references

Bengtson *et al.* 1981; Chen Jun-yuan *et al.* 1989a, 1995d; Ramsköld 1992; Hou & Bergström 1995; Ramsköld & Chen 1998; Bergström & Hou 2001; Topper *et al.* 2011; Ma *et al.* 2014c; Smith, M.R. & Ortega-Hernández 2014.

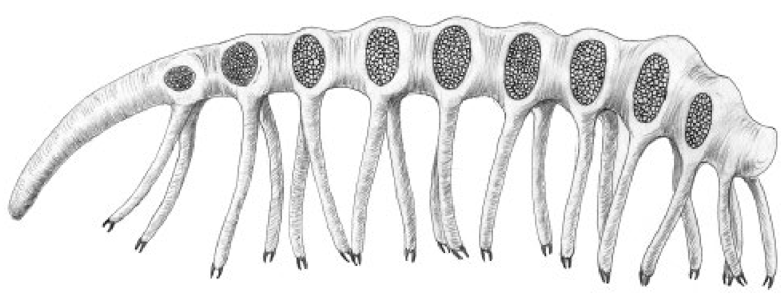
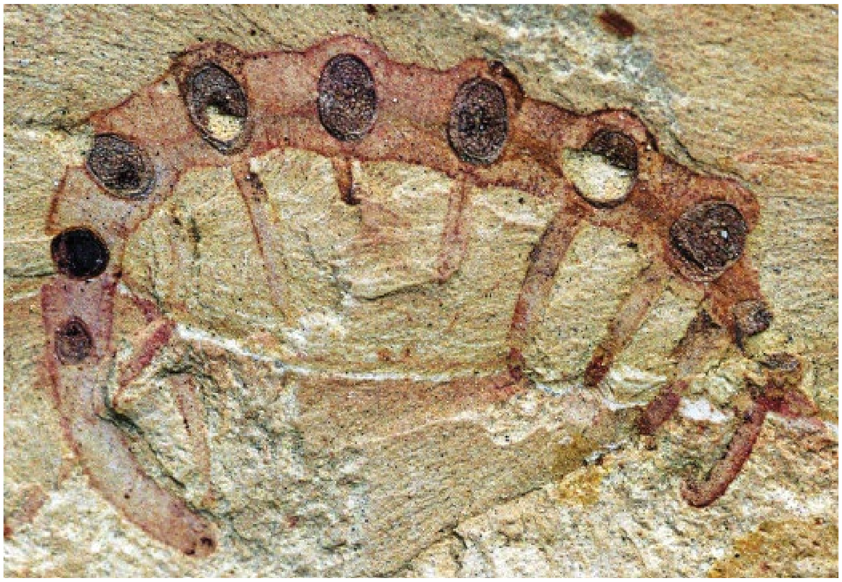


Figure 18.5 Reconstruction of ***Microdictyon sinicum*** (modified from Hou *et al.* 2004a).

Figure 18.6 ***Microdictyon sinicum***. **(a)** NIGPAS 115297, ×6.8; Maotianshan, Chengjiang. **(b)** RCCBYU 10249, ×4.7; Maotianshan, Chengjiang. **(c)** NIGPAS, ×5.5; Maotianshan, Chengjiang.



(a)

(b)

(c)

Genus *Onychodictyon* Hou, Ramsköld & Bergström, 1991

Onychodictyon ferox Hou, Ramsköld & Bergström, 1991

This is a relatively common Chengjiang lobopodian. At least 250 specimens are known. The specimens of *Onychodictyon ferox* are typically preserved in a strong rusty or brown color, with strong relief and mineralization around the sclerites.

O. ferox is seemingly sturdier than most other Cambrian lobopodians; a complete specimen can reach 7 cm long and 5 mm wide. The body is divided into a head region and an elongated trunk. The features of the head region have been controversial with regard to its shape, mouth structure, and the existence of antennae and a sclerotized head shield (Hou *et al.* 1991; Ramsköld & Hou 1991; Hou & Bergström 1995; Ramsköld & Chen 1998). The latest study shows that the head region is composed of an anterior-most bulbous proboscis, an arcuate sclerite, and a region bearing a pair of lateral eyes and feather-like antenniform appendages (Ou *et al.* 2012b). There are 10 pairs of oval-shaped sclerites arranged along the trunk, each of which is finely reticulate and has a sharp central spine. Beneath each pair of sclerites there is a pair of walking legs, with two additional pairs of legs located in front of the first pair of sclerites and at the posterior end of the body. Each of these legs is annulated, bearing longitudinal rows of papillae and a pair of large, curved, strongly sclerotized claws. The two most anterior pairs of legs appear to be somewhat shorter than the others. The trunk is strongly annulated except for the sclerite-bearing region. The key distinguishing feature of this animal is the longitudinal rows of long, finger-like papillae covering the whole body. The alimentary canal is straight, flat, and dark, extending from a terminal mouth at the proboscis to the posterior end, with a bulbous pharynx located behind the head region (Ou *et al.* 2012b).

O. ferox is the type species of *Onychodictyon*. A congeneric species, *Onychodictyon gracilis*, was erected by Liu Jian-ni *et al.* (2008), but the supposed morphological difference between the two species may be a taphonomic artifact. The phylogenetic position of *Onychodictyon* has been less stable in recent analyses (Ma *et al.* 2014c; Smith, M.R. & Ortega-Hernández 2014; Yang Jie *et al.* 2015). It has been placed close to the lobopodians *Aysheaia*, *Diania*, and *Paucipodia*; resolved as a stem tardigrade; or put into the cluster with the lobopodians *Hallucigenia* and *Luolishania*.

Onychodictyon has the strongest claws of any lobopodian, which are clearly well adapted for a grasping or attaching function. Together with the fact that the dark, flat gut lacks sediment infilling, this lobopodian could be interpreted to have led a predatory life style.

O. ferox is unknown outside of the Chengjiang biota of Yunnan Province. However, some isolated phosphatic sclerites of *Onychodictyon* have been reported from the lower Cambrian of North Greenland (Topper *et al.* 2013).

Key references

Hou *et al.* 1991; Ramsköld & Hou 1991; Hou & Bergström 1995; Ramsköld & Chen 1998; Liu Jian-ni *et al.* 2008; Ou *et al.* 2012b; Topper *et al.* 2013; Ma *et al.* 2014c; Smith, M.R. & Ortega-Hernández 2014; Yang Jie *et al.* 2015.

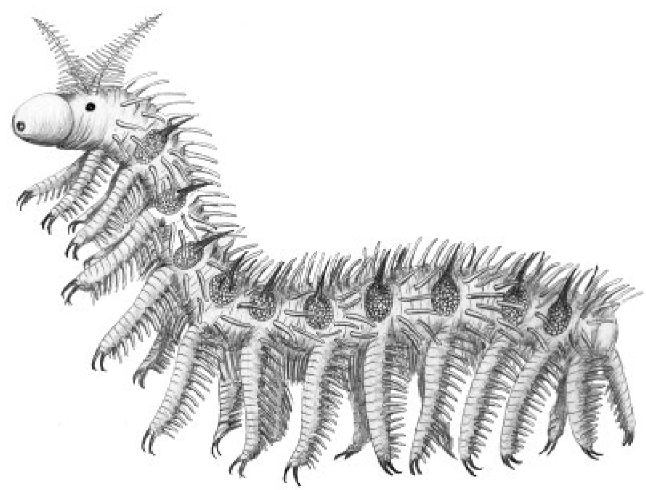


Figure 18.7 Reconstruction of ***Onychodictyon ferox*** (modified from Hou *et al.* 2004a, with head based on Ou *et al.* 2012b).

Figure 18.8 ***Onychodictyon ferox***. **(a), (b)** YKLP 13880, ×2.2, ×5.0; Ercaicun, Haikou, Kunming. **(c)** YKLP 13879, ×3.6; Mafang, Haikou, Kunming.

(a)

(b)

(c)

Genus *Cardiodictyon* Hou, Ramsköld & Bergström, 1991

Cardiodictyon catenulum Hou, Ramsköld & Bergström, 1991

This lobopodian species is relatively common, with over 200 specimens recorded. Most specimens are flattened, but often show some slight relief around the sclerites and head shield. The animals are often preserved in a curled or curved posture.

The animal is relatively slender with a high number of segments, and a complete specimen can reach 3 cm in length and 1 mm wide. A distinct head region is elongated, expanded, and covered by a pair of elliptical sclerites (Hou & Bergström 1995; Bergström & Hou 2001). A pair of eyes occurs on the head (Liu Jian-ni & Dunlop 2014). The trunk is long, slender, and tapers slightly toward both ends. It has been suggested that the number of trunk segments varies and that they are marked by 21–25 saddle-like sclerites that straddle the trunk (Hou *et al.* 1991; Hou & Bergström 1995), but others consider that there are a fixed number of 25 segments (Liu Jian-ni & Dunlop 2014). Beneath each pair of trunk sclerites, there is a pair of ventral legs, each of which bears fine annulations and possibly four terminal claws. Approximately two more pairs of legs (Hou & Bergström 1995; Ramsköld & Chen 1998) are situated in front of the first pair of trunk sclerites and beneath the head, which appears to be bent forward and may have differed functionally from the other legs. The posterior trunk terminates bluntly behind the last pair of legs. The alimentary canal is straight, thin, flat, and preserved in black.

C. catenulum represents the only known species of *Cardiodictyon*. Recent phylogenetic analyses (Ma *et al.* 2014c; Smith, M.R. & Ortega-Hernández 2014) show that the animal shares close affinities with *Hallucigenia* and *Luolishania*, all of which have an expanded head region covered by a pair of large head sclerites, a pair of lateral eyes, and specialized anterior appendages.

Little is known about the mode of life of *C. catenulum*, but it is suggested that the animal led a benthic life in common with most other Cambrian lobopodians. The dark and flat gut, without sediment infilling, indicates that *C. catenulum* was more likely to have been a carnivore or omnivore, and its specialized anterior appendages might have been used for feeding.

This species is unknown outside the lower Cambrian of Yunnan Province.

Key references

Hou *et al.* 1991; Ramsköld 1992; Hou & Bergström 1995; Ramsköld & Chen 1998; Bergström & Hou 2001; Liu Jian-ni & Dunlop 2014; Ma *et al.* 2014c, Smith, M.R. & Ortega-Hernández 2014.

Figure 18.9 ***Cardiodictyon catenulum***. **(a)** YKLP 13883, ×4.8; Mafang, Haikou, Kunming. **(b)** NIGPAS 115293a, ×9.7; Maotianshan, Chengjiang. **(c)** RCCBYU 10245, ×5.6; Mafang, Haikou, Kunming.

(a) (b) (c)

Genus *Hallucigenia* Conway Morris, 1977

Hallucigenia fortis Hou & Bergström, 1995

This is one of the most celebrated Cambrian lobopodians, known from around 20 specimens. Most specimens are laterally flattened on fine-grained mudstone, with slight relief around the dorsal spine attachment areas.

The length of a complete specimen is estimated to be about 2.2 cm. A distinctly expanded head is ellipsoidal in shape, separated from the trunk by a sharp constriction and covered by a pair of thin sclerites (Hou & Bergström 1995). However, the latter finding has not been universally accepted (Ramsköld & Chen 1998). A pair of lateral eyes is situated dorsolaterally on the head, each of which is suggested to consist of two to three visual units (Ma *et al.* 2012a). The trunk is cylindrical with smooth margins and carries seven pairs of long, thorn-shaped spines dorsolaterally, each corresponding to a pair of slender, annulated, and flexible legs situated ventrally. Another two pairs of even longer and slender legs are present in front of the first pair of spines, and one more pair of legs is also observed behind the last pair of spines. Each leg may have two terminal claws. Fine annulations are observed on the surface of some parts of the trunk and legs. The trunk tapers posteriorly, with a tail behind the last pair of legs. Short sections of the gut are preserved in some specimens.

The genus *Hallucigenia* includes two other species. *H. sparsa* Conway Morris, 1977, from the Cambrian Burgess Shale of British Columbia, was originally described (Walcott 1911b) as a species of the polycheate genus *Canadia*, but later Conway Morris (1977b) recognized the singular morphology of this species, establishing a new genus with *H. sparsa* as the type species. However, the animal was reconstructed upside down, so its lobopodian identity was not recognized until 1991 by Ramsköld & Hou. Owing to a lack of evidence of clear head structures, the anterior-posterior orientation of *H. sparsa* has been a subject of debate. M.R. Smith and Caron (2015) redescribed *H. sparsa* and revealed a new set of head features, including a pair of dorsal eyes, a lamellae-like mouthpart, and a foregut lined by pharyngeal teeth. *H. fortis* differs distinctly from *H. sparsa* as the former has an expanded and ellipsoidal head, while the latter has an elongated and slender head. *H. hongmeia* Steiner *et al.*, 2012 was reported from the Cambrian Guanshan biota, Yunnan Province, China, but precise comparison with the two other species of *Hallucigenia* is difficult because the head and the most anterior part of the trunk of *H. hongmeia* are missing (Steiner *et al.* 2012). The phylogenetic relationships of the three *Hallucigenia* species are not yet fully resolved (Smith, M.R. & Ortega-Hernández 2014), but they all appear to share close affinities with the Chengjiang lobopodians *Luolishania* and *Cardiodictyon*.

H. fortis might have led an epibenthic, crawling mode of life. The first two pairs of appendages are morphologically differentiated and might have performed a sensory function, while the posterior pairs are undifferentiated legs for locomotion.

H. fortis is only known from the Chengjiang biota in Yunnan Province, but the genus is also reported from the Burgess Shale, Canada, and the Guanshan biota, China. It may also be present in the Cambrian Kaili biota, Guizhou Province, China (Zhao Yuan-long *et al.* 1999b).

Key references

Conway Morris 1977b; Ramsköld & Hou 1991; Hou & Bergström 1995; Ramsköld & Chen 1998; Zhao Yuan-long *et al.* 1999b; Steiner *et al.* 2012; Ma *et al.* 2012a; Smith, M.R. & Ortega-Hernández 2014; Smith, M.R. & Caron 2015.

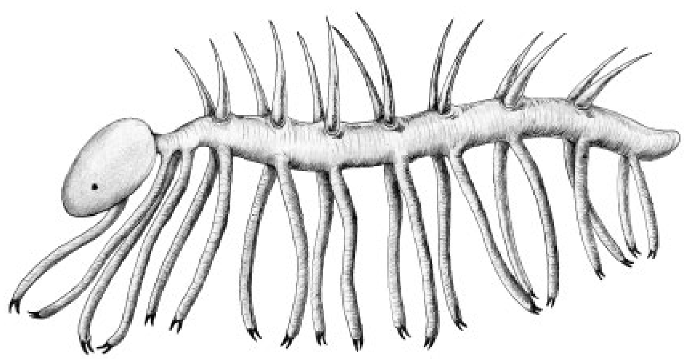


Figure 18.10 Reconstruction of ***Hallucigenia fortis*** (modified from Hou *et al.* 2004a).

Figure 18.11 ***Hallucigenia fortis***. **(a)** RCCBYU 10248, ×8.7; Mafang, Haikou, Kunming. **(b)** RCCBYU 10246a, ×8.2; Mafang, Haikou, Kunming. **(c)** RCCBYU 10246b, ×9.7; Mafang, Haikou, Kunming.

(a)

(b)

(c)

Genus *Luolishania* Hou & Chen, 1989

Luolishania longicruris Hou & Chen, 1989

This is one of the most anatomically complex Cambrian lobopodians, known from at least 60 individuals. As with other Chengjiang lobopodians, the fossils of *Luolishania longicruris* are preserved in fine-grained mudstone and are strongly flattened, with some structures retaining a low three-dimensional relief. Specimens compressed dorsoventrally and laterally reveal quite different features, so when interpreting morphology it is essential to take into consideration the original orientation and taphonomic effects.

Complete specimens are from 8 mm to 1.5 cm long. The head is round and elongated in dorsoventral aspect, but ellipsoidal in lateral profile, separated from the trunk by a constriction. It is covered by a thin head shield and possesses a pair of antenniform outgrowths in front of a pair of eyes. The eyes are situated dorsolaterally on the head and are suggested to consist of two to three visual units within each eye (Ma *et al.* 2012a). The trunk is relatively long and slender, up to 1 mm in width, and tapers posteriorly to a short, bluntly rounded projection behind the last pair of legs. The trunk surface carries fine annulations and setae, except at the areas where the legs and sclerites are attached. Fifteen sets of sclerites are arranged along the body, each set composed of three individual spines arranged transversely (one dorsal and two lateral). One of these sets is on the head, just behind the eyes, with a relatively large basal area and short spine; the others sets are above each pair of legs, with relatively short, thorn-shaped spines, except the third to fifth sets which are notably longer. Between each set of trunk sclerites, there are three barb-shaped projections similarly arranged in the middle of each trunk segment. Fourteen to sixteen pairs of legs are situated ventrolaterally beneath the trunk, each possessing setae and four distal claws. The first five pairs of legs are long, slender, covered by dense setae, and with straight, needle-shaped claws; the other, more posterior legs are much shorter, thicker, less spiny, and with strong, hook-like claws. Thus the differentiated sclerites, legs, claws, and leg interspaces of *L. longicruris* define morphologically distinct regions of the body (tagmata): a distinct head and a trunk divided into two sections (Ma *et al.* 2009). The mouth is terminal, leading to a straight and simple gut that extends through the entire length of the body.

L. longicruris was originally described from a single dorsoventrally compressed specimen (Hou & Chen 1989b). Subsequently over 50 additional specimens have been recovered, which allowed a revised comparison with other lobopodians (Ma *et al.* 2009). Consequently *Miraluolishania haikouensis* Liu & Shu *in* Liu *et al.*, 2004 is considered to be a junior synonym of *L. longicruris*, which is the only known species of the genus. *Luolishania* has been placed in the lobopodian Family Luolishaniidae, which also includes Collins' monster from the Burgess Shale of Canada, *Acinocricus* from the Emu Bay Shale, Australia, and *Collinsium* from the Xiaoshiba biota, China (Ma *et al.* 2009, 2014c; Yang Jie *et al.* 2015). Luolishaniidae has been suggested to share close affinities with the lobopodians *Hallucigenia*, *Onychodictyon*, and *Cardiodictyon*, also found in the Chengjiang biota.

The distinct morphological differences in the anterior and posterior legs of *L. longicruris* indicate a functional difference. Evidence from the gut also indicates that this animal was clearly not a mud eater, but fed on rich organic matter. Some specimens of *L. longicruris* have been found with fossil sponges, indicating a possible ecological association. Based on all available evidence, *L. longicruris* is suggested to have led a filter-feeding lifestyle: the stout posterior legs, with strong hook-shaped claws, help to anchor the posterior part of the body firmly to a suitable medium (e.g., a sponge) thus enabling the anterior body with its elongated spiny legs to move around freely in the search for food (possibly organic particles in the water).

This species is known from several localities of the Chengjiang biota in Yunnan Province.

Key references

Hou & Chen 1989b; Liu Jian-ni *et al.* 2004; Ma *et al.* 2009, 2012a.

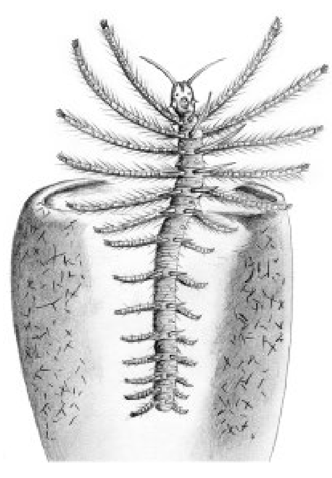
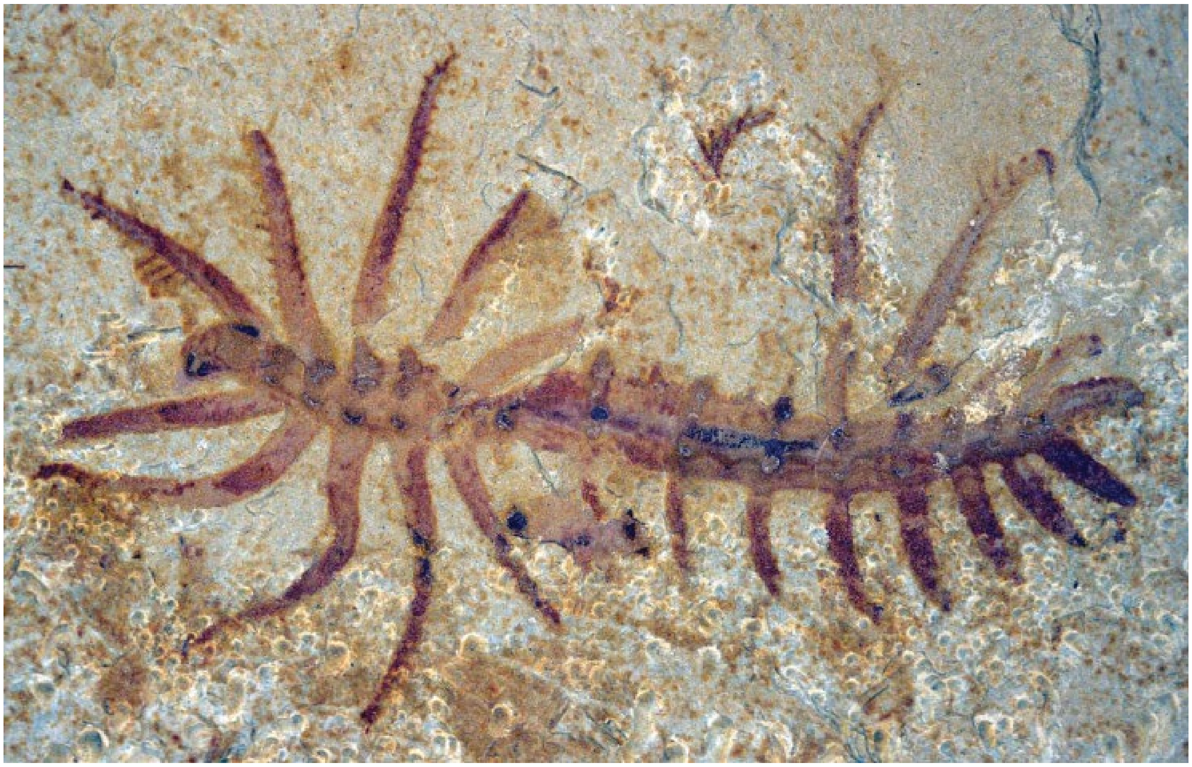
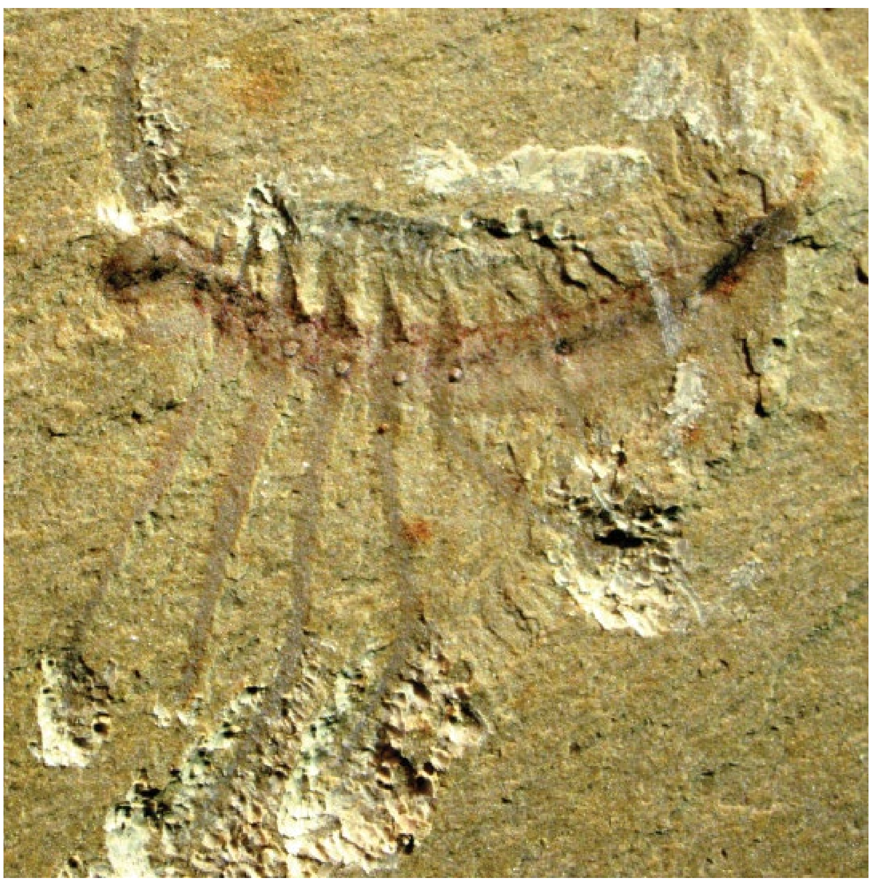


Figure 18.12 Reconstruction of ***Luolishania longicruris*** (after Ma *et al.* 2009) and associated sponge.



(a)



(b)

Figure 18.13 ***Luolishania longicruris***. **(a)** RCCBYU 10242, ×10.4; Mafang, Haikou, Kunming. **(b)** YKLP 11272a, ×12.4; Mafang, Haikou, Kunming.

Genus *Antennacanthopodia* Ou & Shu *in* Ou *et al.*, 2011

Antennacanthopodia gracilis Ou & Shu *in* Ou *et al.*, 2011

Antennacanthopodia gracilis is an extremely rare Cambrian lobopodian species, with only two specimens found so far. Both specimens are known from part and counterpart and are preserved in dorsoventral aspect. In contrast against the yellow mudstone matrix, the soft tissues are preserved in purplish black and the hard parts are in reddish brown.

The holotype is 1.4 cm long. The body tapers slightly toward both ends and consists of a differentiated head and an elongated trunk. The head appears round in shape with an unsclerotized frontal projection. It bears two pairs of slender, gently curved, and anterolaterally pointed antenniform outgrowths, which are interpreted as the frontal and second antennae (Ou *et al.* 2011). A pair of black, subrounded spots symmetrically situated on the bases of the frontal antennae are suggested to be a pair of putative lateral eyes. The trunk is devoid of obvious annuli and sclerites, but its surface bears transverse rows of tiny spines. Nine pairs of stout walking legs splay ventrolaterally on both sides of the trunk. Thorn-like, sharply pointed spines are arranged in at least seven annuli on the surface of each walking leg. No claws are observed, but a sclerotized, disk-shaped structure at the distal end of each leg is interpreted as a leg pad (Ou *et al.* 2011). The straight, longitudinal, purplish-black broad band running through the body is interpreted as the alimentary canal. Some sediment infill is found at the posterior part of the pharynx and in the entire esophagus. The trunk extends beyond the last pair of walking legs. A pair of soft cirriform structures attached to the posterior end of the body are suggested to be posterior appendicules (Ou *et al.* 2011).

A. gracilis is the only known species of *Antennacanthopodia*. This genus shares some similarities with another Chengjiang lobopodian, *Luolishania*, both of which have a well-defined head with antenniform outgrowths and paired lateral eyes. However, in comparison to all other Cambrian lobopodians, *A. gracilis* shows most similarities to the living Onychophora, including the position, shape, and proportion of its tapered frontal antennae, its putative eyes, and stout walking legs with leg pads (Ou *et al.* 2011). These close affinities are also supported by the latest phylogenetic analyses, in which *A. gracilis* is often resolved as the sister taxa to the living Onychophora (Ma *et al.* 2014c; Smith, M.R. & Ortega-Hernández 2014), and sometimes falls within the same clade as *Luolishania*.

The stout legs with leg pads exclude the possibility that they were used as an attachment disk or a holdfast. Instead, they appear functionally comparable to the onychophoran spiny walking pads, which are used to walk over smooth substrates (Ou *et al.* 2011). The sediment infill in the alimentary canal indicates that the animal might be an omnivore, feeding on the surface of the sea floor.

This species is only known from the Chengjiang biota in Yunnan Province.

Key references

Ou *et al.* 2011; Ma *et al.* 2014c; Smith, M.R. & Ortega-Hernández 2014.

Figure 18.14 ***Antennacanthopodia gracilis*****.** **(a)** ELEL EJ081876a, ×11.0; Erjie section, Kunyang, Yunnan. **(b)** ELEL EJ081876b, ×15.3; Erjie section, Kunyang.

(a) (b)

19 Anomalocaridids

Anomalocaridids are one of the most celebrated clades of invertebrate fossils. The first material described was *Anomalocaris* from the middle Cambrian Burgess Shale (Whittington & Briggs 1985) and nearly all representatives are recorded from Cambrian rocks, including five species from the Chengjiang biota. Elsewhere, other anomalocaridids comprise the genera *Caryosyntrips*, *Hurdia*, and *Peytoia* from the Cambrian of North America (e.g., Daley *et al.* 2013), *Tamisiocaris* from the early Cambrian of Greenland (Vinther *et al.* 2014), the very large *Aegirocassis* from the Ordovician of Morocco (Van Roy & Briggs 2011; Van Roy *et al.* 2015), and the anomalocaridid-like survivor *Schinderhannes* from the Devonian of Germany (Kühl *et al.* 2009).

Anomalocaridid morphology involves giant size in many species: they are the largest known Cambrian animals, with some attaining a body length of a meter or more. Consequently their ecology and their position in the trophic structure of communities have attracted much debate and popular attention. Morphological features characteristic of the group include large frontal head appendages, a ventral mouth encircled by overlapping plates, stalked compound eyes, a trunk with pairs of lateral lobes, and, posteriorly, a segmented tail, which in some species bears a pair of long delicate trailers (cerci). Both neural anatomy and sophisticated digestive anatomy are preserved in some anomalocaridids (Cong *et al.* 2014; Vannier *et al.* 2014). Most anomalocaridids are considered to be nektobenthic predators and scavengers, swimming and using their sophisticated visual system (Paterson *et al.* 2011) and frontal appendages to grasp food and transfer it to the mouth (Chen Jun-yuan *et al.* 2007b). *Anomalocaris* may have used suction for food ingestion (Daley & Bergström 2012). In contrast, the morphology of *Tamisiocaris* indicates that some anomalocaridids were actively swimming suspension feeders, using a sweep-net method to capture food (Vinther *et al.* 2014), while the Ordovician witnessed the evolution of giant filter-feeding anomalocaridids (Van Roy *et al.* 2015).

The phylogenetic position of anomalocaridids within the Arthropoda is controversial (Daley *et al.* 2013; Haug *et al.* 2012b; Legg *et al.* 2013; Edgecombe & Legg 2013; Vinther *et al.* 2014), with the most recent analysis placing them within the stem of the Euarthropoda (Van Roy *et al.* 2015). The origin of arthropodization, a key innovation in arthropod evolution, is seen in *Anomalocaris* and relatives (Legg *et al.* 2012). Anomalocaridids have been shown to bear separate ventral and dorsal flaps on each trunk segment, interpreted as homologous with the biramous nature of the trunk limbs of other arthropods (Van Roy *et al.* 2015). As a particularly distinctive group of arthropods, anomalocaridids are treated here in a separate chapter.

Genus *Anomalocaris* Hou, Bergström & Ahlberg, 1995

Anomalocaris saron Hou, Bergström & Ahlberg, 1995

The remains of more than 100 individuals are known, but (almost) complete specimens of *Anomalocaris saron* are very rare. Typical finds are of fragmented specimens and isolated elements, especially remains of the frontal appendages, which in some individuals are estimated to be at least 20 cm long.

A pair of frontal appendages, a pair of large, stalked, presumed compound eyes attached dorsolaterally, and ventral mouthparts are prominent features of the head. The ventrally situated oral cone consists of a circlet of overlapping plates of various sizes surrounding the mouth. Each frontal appendage consists of many short podomeres, most of which have a prominent inner pair of spines each of which is multispinose. The relatively weakly cuticularized slender body has 11 imbricated pairs of elongate lateral lobes (so-called swimming flaps), behind which there is a tail fan composed of overlapping paired blades trailing a pair of long, slender cerci.

The Cambrian Fossils of Chengjiang, China: The Flowering of Early Animal Life, Second Edition. Hou Xian-guang, David J. Siveter, Derek J. Siveter, Richard J. Aldridge, Cong Pei-yun, Sarah E. Gabbott, Ma Xiao-ya, Mark A. Purnell, Mark Williams.

Lanceolate scale-like structures were originally described as occurring on the dorsal surface of the body and delicate dorsal filaments have been interpreted as gills by some authors.

In many phylogenetic analyses *Anomalocaris* is placed as a close relative of *Amplectobelua* (Legg *et al*. 2013; Vinther *et al*. 2014).

Mouthpart and other morphological differences between anomalocaridid species suggest various feeding strategies, with *Anomalocaris* possibly using suction to draw food into the mouth and ingesting it either whole or cut up (Daley & Bergström 2012; Daley *et al*. 2013). Complex paired digestive glands are present in *Anomalocaris* (Vannier *et al.* 2014).

A. saron is unknown outside the Chengjiang biota, but *Anomalocaris* has also been reported from slightly younger strata in two areas in Yunnan Province (Zhang Xing-liang *et al*. 2001; Wang Yuan-yuan *et al*. 2013). *Anomalocaris canadaspis*, the type species, occurs in the middle Cambrian Burgess Shale of British Columbia.

Key references

Chen Jun-yuan *et al*. 1994; Hou *et al*. 1995, 1999, 2004a; Chen Jun-yuan & Zhou 1997; Chen Jun-yuan 2004; Daley *et al*. 2013; Legg *et al*. 2013.

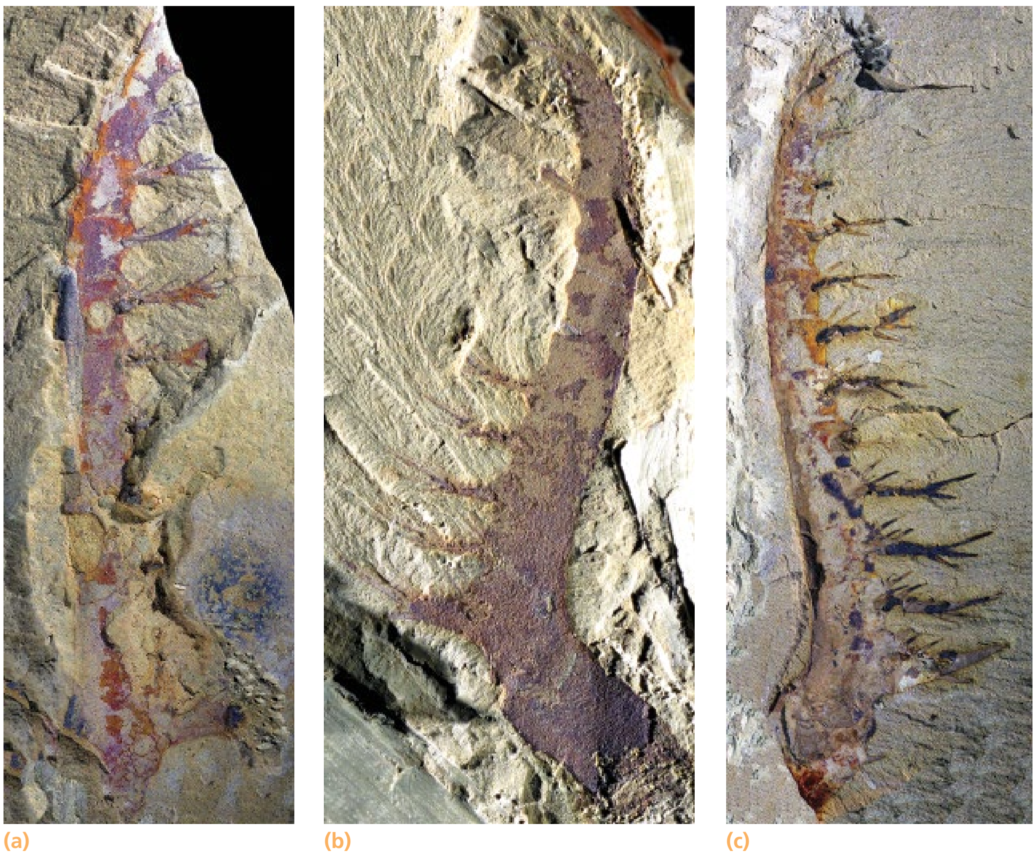


Figure 19.1 ***Anomalocaris saron***. (a) YKLP 13884, ×4.2; Ercaicun, Haikou, Kunming. (b) YKLP 13885, ×4.6; Mafang, Haikou, Kunming. (c) YKLP 13886a, ×3.2; Ercaicun, Haikou, Kunming.

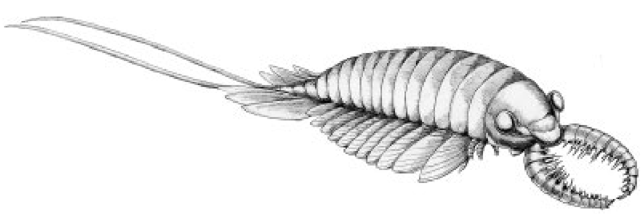


Figure 19.2 Reconstruction of ***Anomalocaris saron*** (based on material of Chen *et al*. 1994 and Hou *et al*. 1995; after Hou *et al.* 2004a).

Genus *Amplectobelua* Hou, Bergström & Ahlberg, 1995

Amplectobelua symbrachiata Hou, Bergström & Ahlberg, 1995

Amplectobelua symbrachiata is normally found as fragmented material and isolated elements, mostly frontal (grasping) appendages. Over 200 individuals are represented, but include only four or five relatively complete specimens.

Some isolated frontal appendages are about 15 cm long, and the overall length of the species is estimated to be up to 1 m, excluding the long pair of terminal furcae. The species supposedly resembles *Anomalocaris* in the number and venation of the lateral flaps in its body, and in its tail fan morphology and long furcae (Chen Jun-yuan *et al.* 1994). It purportedly differs in the smaller size and details of its anterior appendages, in having a wider body trunk with larger flaps, and having more anteriorly positioned eyes. A complicated mouth area is reported to consist of a circle of plates set symmetrically with large, elaborate teeth. The podomeres of the frontal appendage bear pairs of simple spines, with two spines on the distal podomere and an exceptionally long spine near the proximal end of the appendage.

Phylogenetic analysis resolves *Amplectobelua* species as near relatives of *Anomalocaris (*Legg *et al*. 2013; Van Roy *et al*. 2015).

With their large frontal appendages and circle of plates forming an oral cone, most anomalocaridids have conventionally been considered to be apex predators in the Cambrian seas (Chen Jun-yuan *et al*. 2007b). The robust, spiny, frontal appendage of *A. symbrachiata* probably had a grasping function (Haug *et al*. 2012b) and the species was probably a predator-cum-scavenger although endorsement of this interpretation awaits detailed study of its mouthparts.

Amplectobelua is one of several anomalocaridid genera recognized from the Chengjiang biota. *A. symbrachiata* is recorded only from Yunnan Province. A congeneric species, *Amplectobelua stephanensis*, is known from the middle Cambrian Burgess Shale of British Columbia (Daley & Budd 2010).

Key references

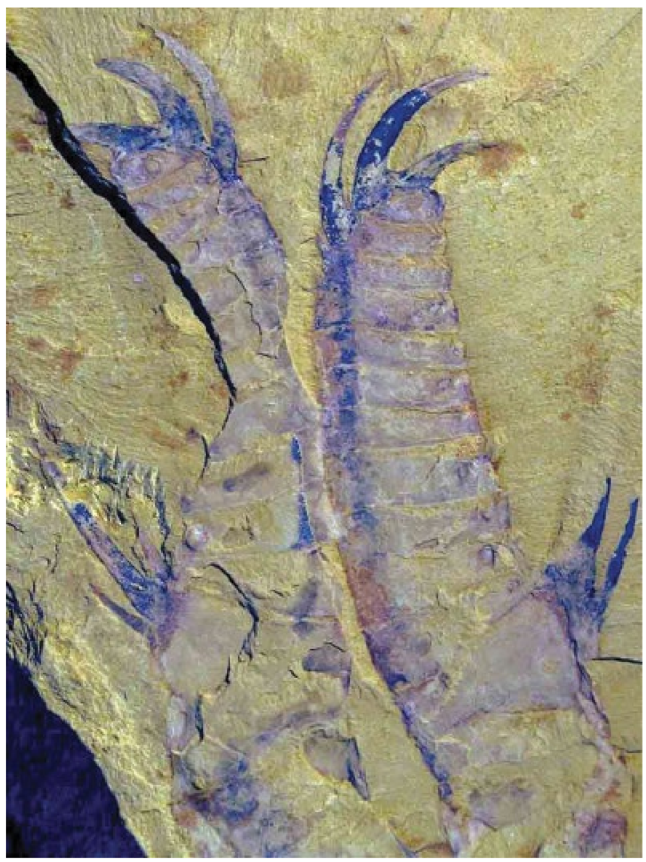
Chen Jun-yuan *et al*. 1994, 1996; Hou *et al*. 1995, 1999, 2004a; Chen Jun-yuan & Zhou 1997; Chen Jun-yuan 2004; Daley & Budd 2010; Daley & Bergström 2012; Haug *et al.* 2012b; Daley *et al*. 2013; Legg *et al*. 2013.

Figure 19.3 ***Amplectobelua symbrachiata.*** **(a)** YKLP 13887, ×0.9; Ercaicun, Haikou, Kunming. **(b)** YKLP 13888, ×2.1; Mafang, Haikou, Kunming. **(c)** NIGPAS 115346, ×3.7; Mafang, Haikou, Kunming. **(d)** YKLP 13889, ×2.5; Mafang, Haikou, Kunming.

(a)

(b)

(c)



(d)

Genus *Lyrarapax* Cong, Ma, Hou, Edgecombe & Strausfeld, 2014

Lyrarapax unguispinus Cong, Ma, Hou, Edgecombe & Strausfeld, 2014

This small anomalocaridid species is known from three largely complete specimens. Its preservation is exceptional even for Chengjiang biota fossils. In addition to features that are relatively common in Chengjiang arthropods, such as a digestive tract, it also preserves details of muscle blocks and the brain.

The body is up to 8 cm in length. The head bears a dorsal carapace, large, stalked, and club-shaped compound eyes of similar morphology to those in *Anomalocaris canadensis*, and has a large, ventrally opening mouth cone. The only appendages in the head or trunk are the pair of frontal appendages, which are short, arthropodized, and bear ventral spines on each podomere. The neck is distinct, consisting of four segments, behind which a paddle-shaped body flap of the first trunk segment is succeeded by a series of 10 additional segments each with successively narrowing body flaps. Bands of setal blades occur dorsally. The last segment provides a tail fan, which consists of three pairs of blades.

Many of the anatomical features of *Lyrarapax unguispinus* are diagnostic of anomalocaridids. Based on shared derived characters of especially the pincer-like frontal appendages, *L. unguispinus* shows closest affinity with *Amplectobelua* (Van Roy *et al.* 2015), which also occurs in the Chengjiang biota. Details of the preserved eyes, the dorsal, segmented brain, and associated neural features chart the segmental arrangement of the anomalocaridid head and its appendages. The brain organization and neural origin of the paired pre-ocular frontal appendages in anomalocaridids matches that in Onychophora and allows elucidation of the transformation of these appendages and allied nerves in more derived arthropods.

L. unguispinus may have obtained its food in a similar way to many other anomalocaridid species, using its spinose frontal appendages to scavange and to grasp prey.

Lyrarapax is known only from its type species. *L. unguispinus* is so far recorded from two localities, both in the Haikou district of Yunnan Province.

Key references

Cong *et al.* 2014; Van Roy *et al.* 2015.

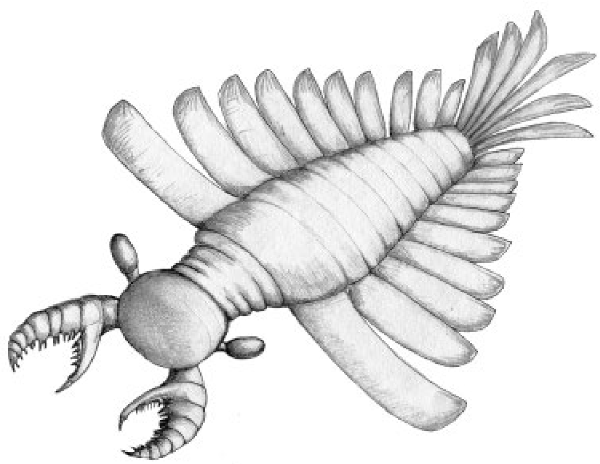
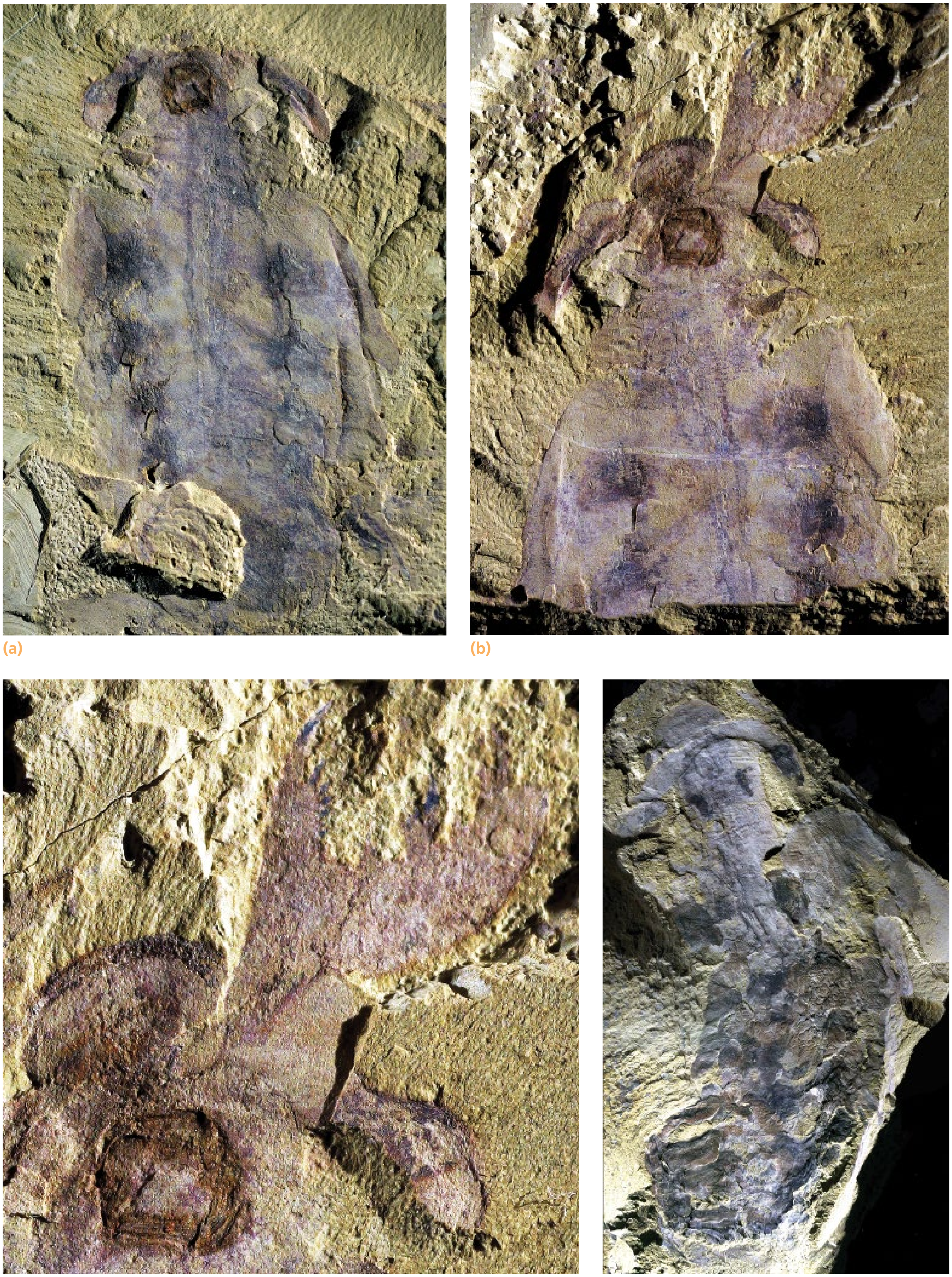


Figure 19.4 Reconstruction of ***Lyrarapax unguispinus***.

Figure 19.5 ***Lyrarapax unguispinus***. **(a)** YKLP 13304b, ×3.0; Ercaicun, Haikou, Kunming. **(b)**, **(c)** YKLP 13304a, ×3.8, ×9.6; Ercaicun, Haikou, Kunming. **(d)** YKLP 13306a, ×1.3; Ercaicun, Haikou, Kunming.



(a) (b) (c) (d)

Genus *Cucumericrus* Hou, Bergström & Ahlberg, 1995

Cucumericrus decoratus Hou, Bergström & Ahlberg, 1995

This species is known from only a few specimens. Typically only a single branch of the trunk appendage and associated fragments of cuticle are preserved. The overall length of the animal is unknown.

The single branch of the trunk appendage was originally described as having three parts (Hou *et al.* 1995): a basal region (protopod), from which stems an elongate gradually tapered ramus (ramipod), and a laterally extensive laminar structure (striated appendage flap). The basal part of the appendage has a series of small, medially facing endites on the inner margin. The trunk appendage has been reinterpreted as possibly a limb of euarthropod type, consisting of basipod, endopod, and exopod (Haug *et al.* 2012b). In the original description the type specimen of *C. decoratus* was depicted to have several fragmentary patches of cuticle surfaced with what was interpreted as scales.

Since its original description the scant material *of Cucumericrus decoratus* has been considered to be of an anomalocaridid (Hou *et al.* 1995, 1999, 2004a, 2006b; Chen Jun-yuan & Zhou 1997). That view is supported by a recent morphological and phylogenetic analysis (Van Roy *et al.* 2015), which also affirmed anomalocaridids as basal stem euarthropods and homologized the ventral limb and associated scaly dorsal cuticle (presumed flaps with setal blades) of *Cucumericrus* with the euarthropod biramous limb.

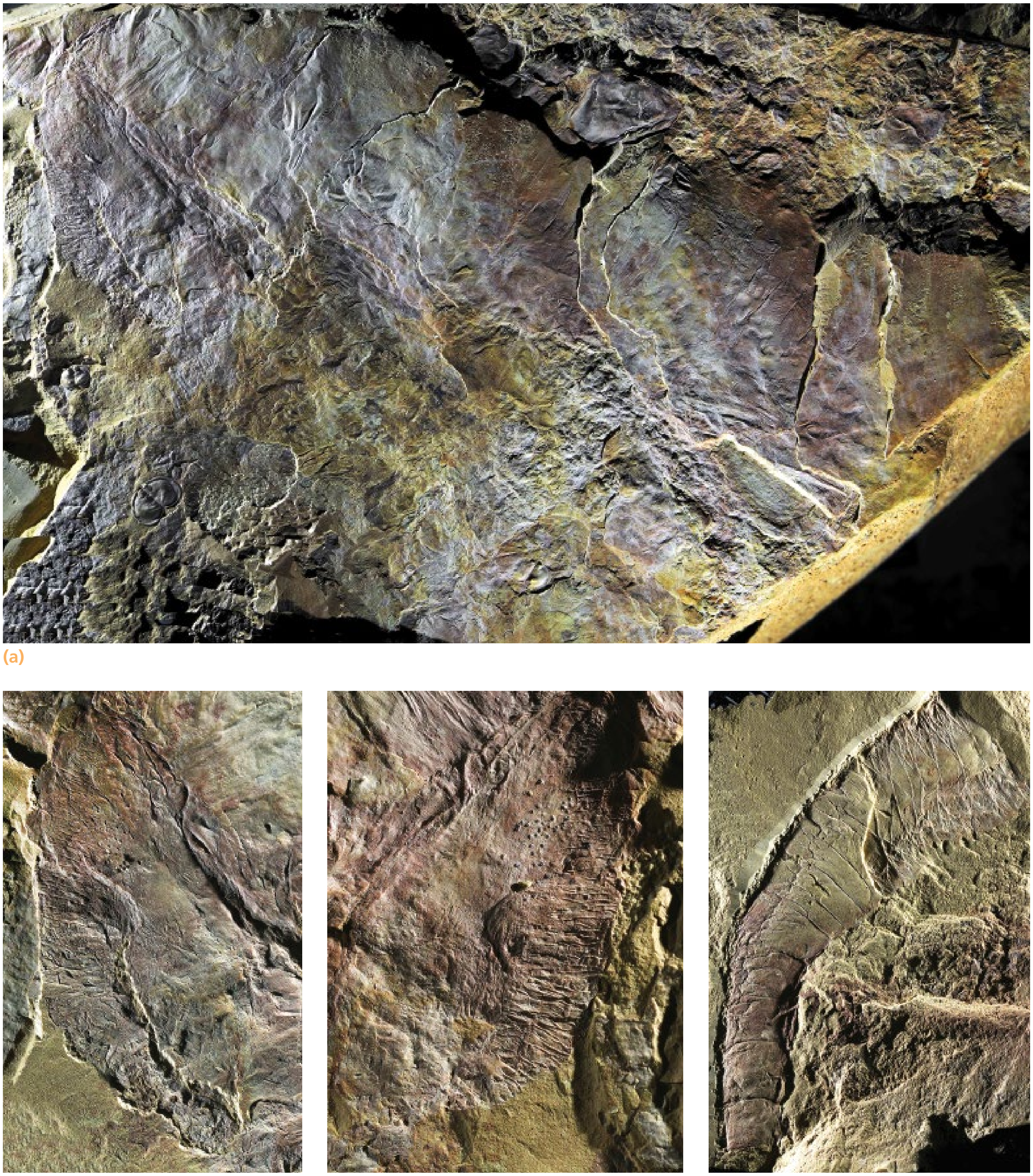
The interpretation of its paleoecology is problematical because of the limited amount of morphological detail known about the species. Most anomalocaridids are active predators.

C. decoratus is the only known species of its genus and is not recorded outside the Chengjiang biota.

Key references

Hou *et al.* 1995, 1999, 2004a; Chen Jun-yuan & Zhou 1997; Van Roy *et al.* 2015.

Figure 19.6 ***Cucumericrus decoratus***. **(a)** A series of appendage flaps, patches of dorsal scales, and (at upper, left-side edge) an appendage (see Hou *et al.* 1995, figure16.B). NIGPAS 115352a, ×1.5; Maotianshan, Chengjiang. **(b)** The appendage. NIGPAS 115352a, ×2.7; Maotianshan, Chengjiang. **(c)** The counterpart of the appendage. NIGPAS 115352b, ×2.7; Maotianshan, Chengjiang. **(d)** NIGPAS 115351, ×1.3; Maotianshan, Chengjiang.



(a) (b) (c) (d)

20 Euarthropoda

Euarthropods are by far the most species-rich and ecologically diverse living animals, and include such familiar groups as beetles, spiders, and crabs. They are characterized by their segmented body, chitinous cuticle forming an external skeleton that is sometimes biomineralized, jointed limbs, well-developed sensory systems, and a life cycle involving molting. The adjoining plates of cuticle (sclerites) that form the exoskeleton consist of dorsal (tergite) and ventral (sternite) parts. Some euarthropods (e.g., myriapods: millipedes and centipedes) have limbs with a single (uniramous) branch, whilst others have biramous limbs with inner (endopod) and outer (exopod) branches. The latter include the trilobites, numerous pancrustaceans such as shrimps, barnacles, and crabs, and some chelicerates (xiphosurans). The Chelicerata embraces xiphosurids (horseshoe crabs), eurypterids (sea scorpions), and arachnids (spiders and scorpions).

The extant euarthropod fauna comprises the pancrustaceans, chelicerates, and myriapods. Pancrustaceans include the hexapods (insects), though these are not represented in the Chengjiang biota. Trilobites (Cambrian-Permian), ostracods, and other pancrustacean groups in which the cuticle is mineralized with calcium carbonate comprise most of the fossil record of arthropods. Molecular and morphological evidence yields many models of arthropod phylogeny (e.g., Regier *et al.* 2010; Legg *et al.* 2013; Edgecombe & Legg 2014), but all scientists agree that arthropods are monophyletic.

Euarthropods form the major numerical component of the Chengjiang biota and they are also the most species-rich group. They comprise some five anomalocaridid species and some lobopodian taxa – basal stem euarthropod clades (see Chapters 18 and 19) – and about 80 other recorded species. Our arrangement of these in general follows the phylogenetic scheme of Legg *et al.* (2013), which includes an anatomically disparate group of animals that are considered as stem euarthropods, more derived than the anomalocaridids, but not having acquired the full suite of crown euarthropod characteristics. Within the stem of Euarthropoda are several bivalved arthropods (e.g., *Isoxys, Jugatacaris*), the Fuxianhuida (*Fuxianhuia, Chengjiangocaris*), antennate megacheirans (e.g., *Fortiforceps, Jianfengia*), and Megacheira (e.g., *Alalcomenaeus*). Though relationships within and between these different groupings often remain uncertain, some of these stem euarthropods are important for determining the early evolution of, for example, euarthropod cardiovascular and neural anatomy, now documented in detail from *Fuxianhuia* (Ma *et al.* 2012b, 2014b) and *Alalcomenaeus* (Tanaka *et al.* 2013).

The artiopodans constitute nearly one-quarter of the species diversity of the Chengjiang euarthropod fauna, and are represented by at least 18 species; this group includes the familiar trilobites and trilobitomorphs. The latter animals are characterized by their subelliptical head shields and trunks composed of multiple tergites, the trunk often ending in a long terminal tail-spine. Trilobites went on to be one of the most successful euarthropod groups, appearing in the fossil record some 521 million years ago and surviving in the Paleozoic oceans for some 270 million years. Chengjiang artiopodans include taxa, in addition to the trilobites, with long stratigraphic records, such as the Aglaspidida.

Much less well represented amongst Chengjiang euarthropods are stem mandibulate animals (Mandibulata = Myriapoda + Pancrustacea). In this category are the tiny bradoriids *Kunmingella* and *Kunyangella*. Nevertheless, analysis of the brain and cardiovascular system of *Fuxianhuia* shows similarities to crown-group euarthropods, particularly Mandibulata (Ma *et al.* 2012b, 2014b), suggesting a more crown-ward position of *F. protensa* than is depicted in Legg *et al.* (2013), or that the central nervous system and cardiovascular structures of mandibulate euarthropods retained many ancestral characteristics. Similarly, the neural anatomy of *Alalcomenaeus* shows important correspondences with those of crown group chelicerates like the horseshoe crab. Accordingly, *Alalcomenaeus* was placed within the total group Chelicerata by Tanaka *et al.* (2013), and thus within the euarthropod crown. These latter examples serve to illustrate how our understanding of the details of euarthropod phylogeny remains in flux.

The Cambrian Fossils of Chengjiang, China: The Flowering of Early Animal Life, Second Edition. Hou Xian-guang, David J. Siveter, Derek J. Siveter, Richard J. Aldridge, Cong Pei-yun, Sarah E. Gabbott, Ma Xiao-ya, Mark A. Purnell, Mark Williams.

Genus *Isoxys* Walcott, 1890

Isoxys paradoxus Hou, 1987

Isoxys paradoxus is relatively rare and, unlike its Chengjiang associates *Isoxys auritus* and *Isoxys curvirostratus*, is known only from carapaces.

The thin, elongate, bivalved carapace has a straight spine at both the anterodorsal and posterodorsal corners. The posterior spine is longer than the bivalved part of the carapace. Including both spines, carapace length can exceed 10 cm. *I. paradoxus* can easily be distinguished from *I. auritus* by the unequal and total length of its spines. The carapace of *Isoxys curvirostratus* is distinguished from other species of the genus by having a curved anterior spine (Vannier & Chen 2000).

The biogeographical distribution and paleoecology of *Isoxys* are discussed under *I. auritus*. *I. paradoxus* is unknown outside of the Chengjiang biota.

Key references

Hou 1987c; Hou *et al*. 1999, 2004a.

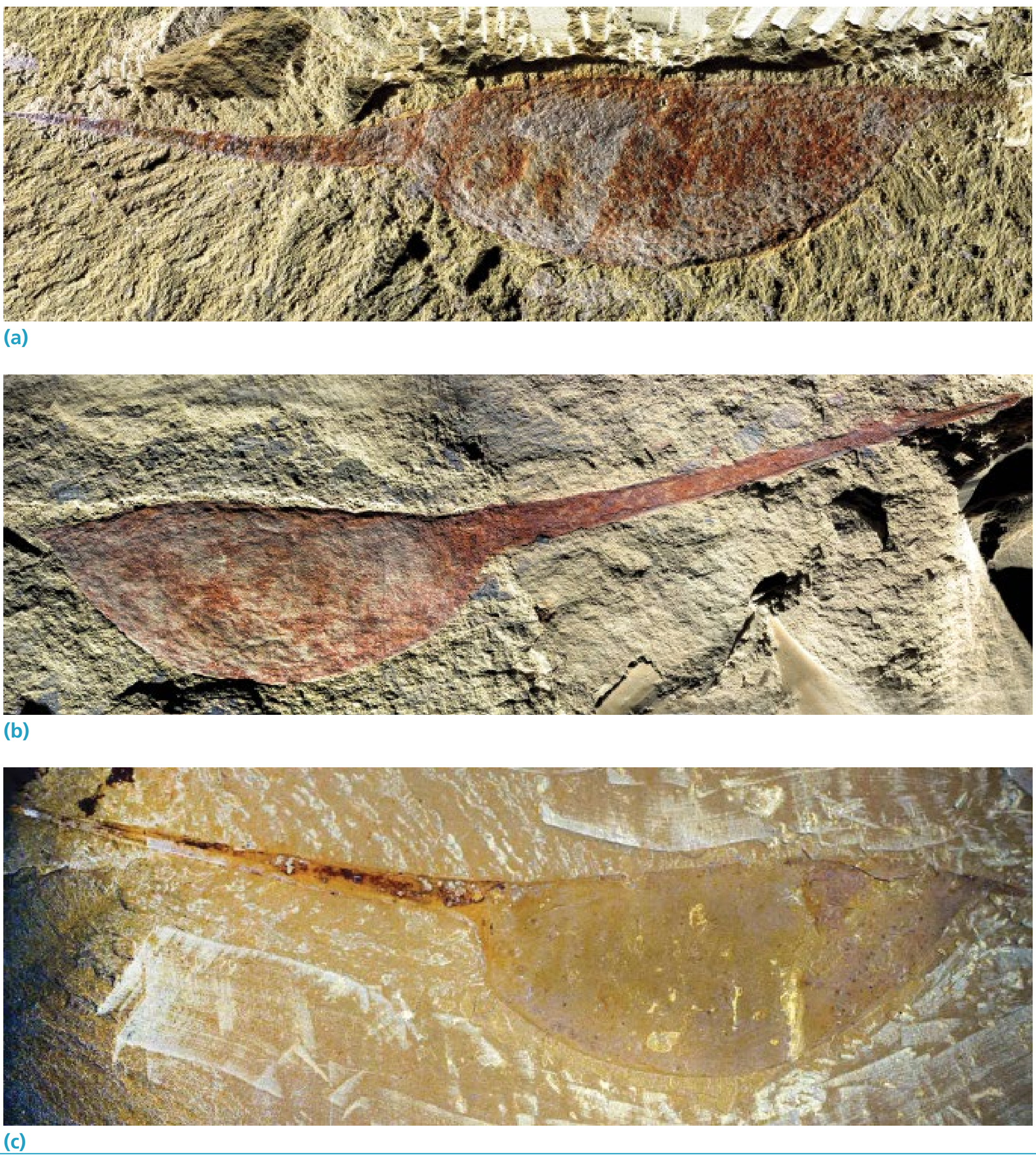


Figure 20.1 ***Isoxys paradoxus***. **(a)** YKLP 13906, ×1.9; Mafang, Haikou, Kunming. **(b)** YKLP 13907, ×1.5; Mafang, Haikou, Kunming. **(c)** RCCBYU 10263, ×2.8; Xiaolantian, Chengjiang.

Isoxys auritus (Jiang, 1982)

Isoxys auritus is one of three *Isoxys* species known from the Chengjiang biota, the others being *I. curvirostratus* and *I. paradoxus*. *I. auritus* is very common, and several specimens preserve soft parts (Fu *et al.* 2014b). Its thin, elongate, and bivalved carapace can be more than 4 cm long and is extended into spines of subequal length at the anterodorsal and posterodorsal corners. An ornament of fine reticulation occurs on the carapace.

Exceptionally preserved material from the Chengjiang (Fu *et al.* 2011, 2014b), Burgess Shale (García-Bellido *et al.* 2009b), Sirius Passet (Stein *et al.* 2010), and Emu Bay Shale (García-Bellido *et al.* 2009a) Lagerstätten shows a long segmented body for *Isoxys*, with a pair of forwardly projecting stalked eyes. The frontal appendages are known in five species, including in *I. auritus*, in which they are elongate, slim, and antenniform, and appear to insert into the post-ocular (second, deutocerebral) segment of the head (Fu *et al.* 2014b); these appendages and the eyes protrude beyond the anterior edge of the carapace. Behind the frontal appendages of *I. auritus* there are up to 11 biramous appendages with endopods that are composed of up to six (possibly seven) podomeres, and with paddle-shaped exopods that bear long setae on their posterior margin (Fu *et al.* 2014b).

Fu *et al.* (2014b) described the ontogeny of *I. auritus*, recognizing juveniles with large antennae and eyes, only seven pairs of post-antennular appendages, and a carapace that lacked reticulate ornament. They also suggested that sexual dimorphism in the adult was manifested in differences in carapace micro-ornament.

The morphology of the first appendage differs between *Isoxys* species suggesting that in some taxa it had a raptorial function, whilst in others (including *I. auritus*) it had a sensory function. This has led some authors to question whether the species assigned to *Isoxys* represent a single genus (Fu *et al.* 2014b), though a detailed cladistic analysis (Legg & Vannier 2013) suggested a monophyletic taxon. The uniformity of the biramous appendages indicates that *Isoxys* is not very derived, and the most recent analyses of its morphology place it at the base of the Arthropoda (Legg & Vannier 2013; Legg *et al.* 2013).

The well-developed respiratory structures of certain *Isoxys* suggest an active swimming mode of life (Fu *et al.* 2011). Some *Isoxys* preserve a series of bulbous glands in the mid-gut that may have served for food storage, and this may signal a carnivorous or scavenging mode of feeding (Legg & Vannier 2013).

Isoxys is a component of the earliest arthropod faunas worldwide, species being recorded from early Cambrian strata in Spain, Siberia, South Australia, and Southwest China and also from the early and middle Cambrian of Laurentian North America (Williams *et al.* 1996; Vannier & Chen 2000; Stein *et al.* 2010). Paleogeographically, *Isoxys* seems to be restricted to tropical and subtropical regions. *I. auritus* is known only from the Chengjiang biota.

Key references

Jiang 1982; Shu *et al.* 1995b; Hou *et al.* 1999, 2004a; Fu *et al.* 2014b.

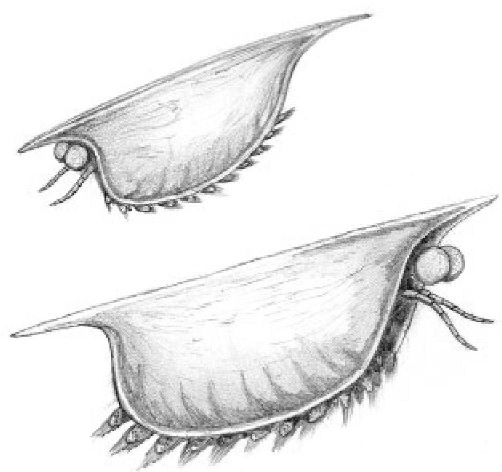


Figure 20.2 Reconstruction of ***Isoxys auritus*** (based on data of Vannier & Chen 2000 and Hou *et al.* 2004a).

Figure 20.3 ***Isoxys auritus***. **(a)** YKLP 13902, ×5.8; Mafang, Haikou, Kunming. **(b)** YKLP 13903, ×2.7; Maotianshan, Chengjiang. **(c)** YKLP 13905, ×2.4; Huangjiazhuang, Chengjiang.

(a)

(b)

(c)

Genus *Pectocaris* Hou, 1999

Pectocaris spatiosa Hou, 1999

Pectocaris spatiosa, a relatively rare taxon, is one of two species of this genus from the Chengjiang biota, the other being *P. eurypetala* (Hou & Sun 1988). *Jugatacaris agilis* Fu & Zhang, 2011, may be the same species as *P. spatiosa*.

The elongate carapace tapers gently anteriorly. The posterior end and part of the dorsal margin of the largest carapace are not preserved, but its total dimensions are estimated to be a little over 9 cm long and 5 cm high. It is therefore one of the largest bivalved arthropods of the Chengjiang biota.

At the front of the animal is a pair of compound eyes that extend beyond the anterior edge of the carapace, together with the remains of the proximal parts of annulate antennae and possibly part of the gut. The carapace encloses what are interpreted to be least 50 segments, some of which have associated biramous appendages, but the details of these limbs are difficult to discern. Each endopod seems to be long and narrow, and consists of many podomeres. Several delicate setae of the exopods are also preserved. The four posterior-most segments covered by the carapace are longer than the others and appear to lack appendages. Protruding posteriorly behind the carapace is part of the trunk comprising many short segments and a long telson ending in a pair of blade-like rami.

Pectocaris has been considered as a possible branchiopod crustacean based on its supposed possession of a uniramous first and second antennae, biramous appendages with a blade-like exopod, its many and short head and thoracic segments, and its possession of abdominal segments without limbs (Hou 1999; Hou *et al*. 2004b). Others have questioned the interpretation of the appendages (Budd 2002). Phylogenetic analysis (Legg *et al*. 2012) places *Pectocaris* as a stem euarthropod close to *Jugatacaris* (see summary in Giribet & Edgecombe 2013), resemblances between these two taxa being a polypodous multi-segmeted trunk, a large number of podomeres on the appendages, and paddle-like furcal rami.

Its thin carapace, prominent eyes, slender endopods, and broad telson flukes suggest that *Pectocaris* may have been a nektonic swimmer (Hou *et al*. 2004b). The species is known only from the Chengjiang biota of Chengjiang County.

Key references

Hou & Sun 1988; Hou 1999; Hou *et al*. 1999, 2004a, 2004b.

Figure 20.4 ***Pectocaris spatiosa.*** **(a)** RCCBYU 10178, ×3.4; Mafang, Haikou, Kunming. **(b)** YKLP 13908, ×2.5; Mafang, Haikou, Kunming. **(c)** YKLP 13909b, ×4.0; Xiaolantian, Chengjiang.

(a)

(b)

(c)

Genus *Shankouia* Chen, Wang, Maas & Waloszek *in* Chen, 2004

Shankouia zhenghei Chen, Wang, Maas & Waloszek *in* Chen, 2004

This species is known from several tens of specimens. They range up to about 8 cm long and probably represent different growth stages. Complete and fragmentary individuals are represented, most in the form of part and counterpart. Appendages and other soft parts are preserved in a few specimens.

The body is elongate and has at least 41 segments. The head consists of two segments. The more anterior segment has a small tergite and bears two, laterally inserted stalked eyes. The second segment bears an expansive, shield-like tergite that covers the first six trunk tergites (body segments 3–8). Ventrally, the second segment bears the first pair of appendages, slender forward-projecting antennae. Just behind the antennal insertions there is a mouth and ventral plate, the hypostome. Except for the first six tergites each trunk tergite is convex medially and has lateral extensions, giving a trilobed appearance to the dorsal exoskeleton. Each post-oral segment bears a pair of appendages. The appendage consists of a long, gently tapering, multipodomere inner branch and a shorter, flap-like, subovoid exopod with fine marginal spines. The trunk ends in a conical portion bearing a pair of large triangular lateral flaps and two smaller flaps terminally.

This species name was apparently made available by Chen *et al*. in Chen Jun-yuan (2004), which has priority over the same name published by Chen *et al*. in Waloszek *et al*. (2005). The taxa *Liangwangshania biloba* Chen, 2005 and *S. zhenghei* appear to represent a single species. *Shankouia* is also morphologically similar to the Chengjiang genera *Fuxianhuia* and *Chengjiangocaris*. They lack, and also have, several characteristic features of euarthropods (Waloszek *et al*. 2005; Edgecombe & Legg 2013), and phylogenetic analysis resolves these Fuxianhuiida as stem euarthropods (Legg *et al*. 2012, 2013; Edgecombe & Legg 2014).

S. zhenghei possibly used the pediform inner branches of its limbs to walk and the flap-like outer branches to glide slowly at the sea bottom (Waloszek *et al*. 2005). The exopods probably also had a respiratory function. The form of the posterior cone and associated flaps suggests it could have functioned for steering and as a stabilizer (Chen Jun-yuan *et al*. 2007b). The lack of functionally differentiated appendages indicates that *S. zhenghei* used its appendages almost exclusively for locomotion and not to transport or manipulate food. It was perhaps an unspecialized omnivore.

Only one species of *Shankouia* is known. *S. zhenghei* occurs at Anning and Haikou in Yunnan Province.

Key references

Chen Jun-yuan 2004; Waloszek *et al*. 2005.

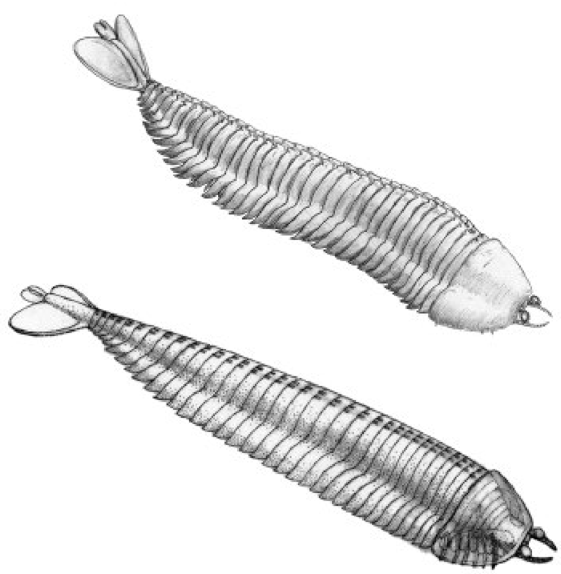
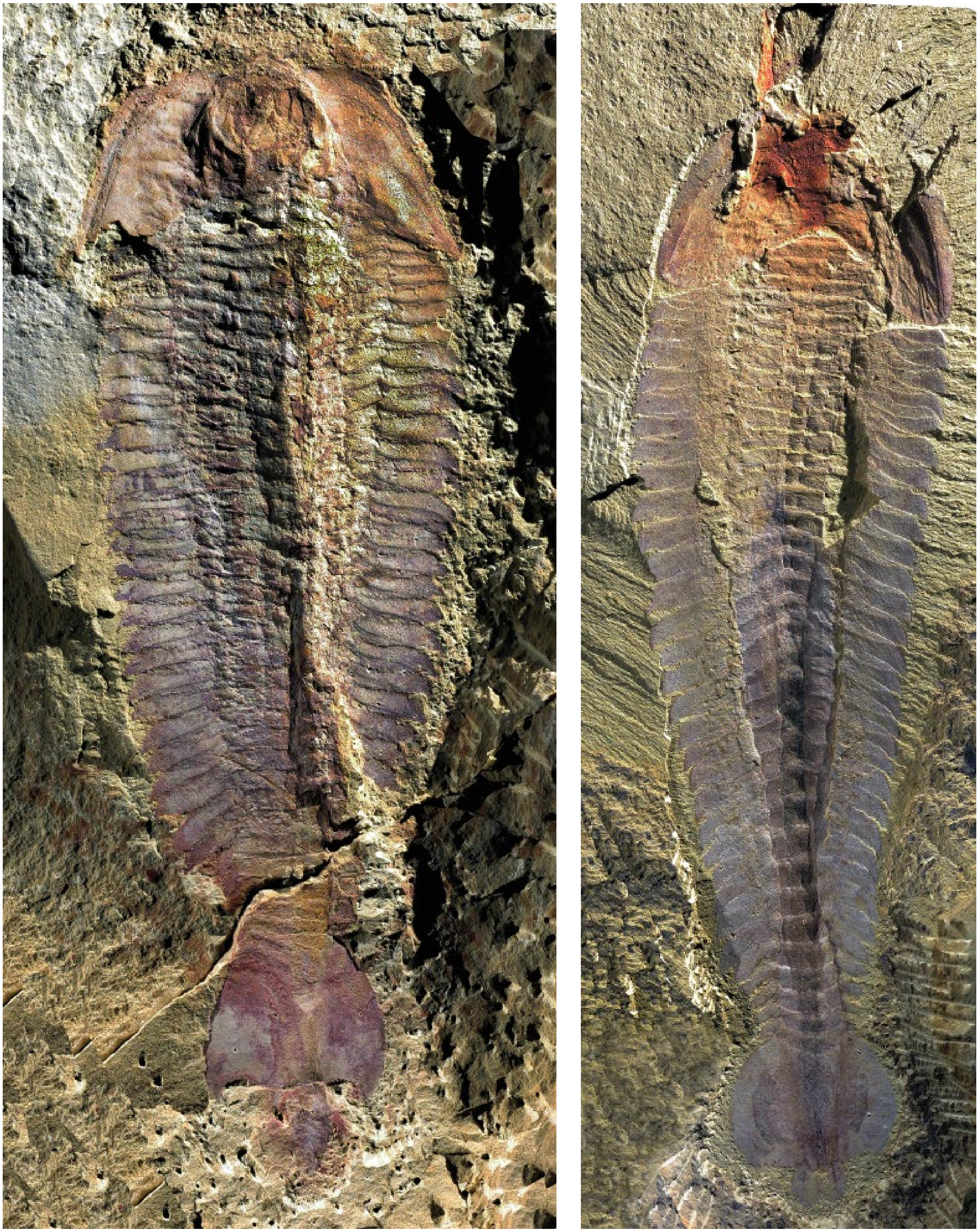


Figure 20.5 Reconstruction of ***Shankouia zhenghei*** (modified from Waloszek *et al*. 2005).

Figure 20.6 ***Shankouia zhenghei***. **(a)** YKLP 10421, ×3.0; Xiaolantian, Chengjiang. **(b)** YKLP 13910, ×3.3; Ercaicun, Haikou, Kunming.



(a) **(b)**

Genus *Chengjiangocaris* Hou & Bergström, 1991

Chengjiangocaris longiformis Hou & Bergström, 1991

Chengjiangocaris longiformis is known from several specimens, which preserve details of the dorsal exoskeleton and soft parts.

C. longiformis does not exceed 10 cm in length. The anterior region is covered by a short carapace, beyond which project a pair of stalked eyes that, by comparison with the slightly younger *Chengjiangocaris kunmingensis* from Yunnan Province, likely originate from an anterior sclerite (Yang Jie *et al*. 2013). Behind these, and also projecting beyond the anterior end of the carapace, there is a pair of uniramous antennae whose podomeres narrow toward the distal end. In *C. kunmingensis,* the frontal pair of antennae are followed posteriorly by a pair of enlarged, backward-directed uniramous appendages: these have not yet been identified in *C. longiformis*. The thorax of *C. longiformis* comprises five short tergites. Behind the thorax, the trunk has another 17 tergites (abdomen) plus a triangular-shaped terminal element. The trunk lacks obvious differentiation into a broad middle part and a slender posterior part. The endopods in the trunk are simple, each consisting of about 20 uniform podomeres and a small conical end-piece. The exopod is a simple rounded flap, lacking setae or bristles. The appendages are much more closely spaced than the trunk tergites (Hou & Bergström 1997), resulting in a segmental mismatch, though the exact pattern of the mismatch in *C. longiformis* is not known.

Based on the morphology of the carapace, thorax, and appendages Hou and Bergström (1997) suggested an affinity with *Fuxianhuia*. This relationship has been sustained by recent morphological (Yang Jie *et al*. 2013) and phylogenetic analysis (Legg *et al*. 2013), which united *Chengjiangocaris* and *Fuxianhuia* in the fuxianhuiids, demonstrated close similarities in their head appendages – particularly their possession of a specialized post-antennal appendage – and resolved their phylogenetic position as stem euarthropods (see also Waloszek *et al*. 2005). The positions of the antennae and specialized post-antennal appendages in *Chengjiangocaris* are likely segmentally homologous to the deutocerebral and tritocerebral appendages of crown-group euarthropods (Yang Jie *et al*. 2013). The Chengjiang taxon *Cambrofengia yunnanensis* Hou *et al*., 1999 may be based on detached appendages of *C. longiformis*.

The habitat and benthic mode of life of *C. longiformis* may have been similar to that of the related *Fuxianhuia,* which has been interpreted as a highly mobile forager.

C. longiformis is the only representative of its genus in the Chengjiang biota. *C. kunmingensis*, the only other known congeneric species, occurs in the Xiaoshiba Lagerstätte of Yunnan Province (Yang Jie *et al*. 2013).

Key references

Hou & Bergström 1991, 1997; Hou *et al*. 1999, 2004a; Waloszek *et al*. 2005; Legg *et al*. 2013; Yang Jie *et al*. 2013.

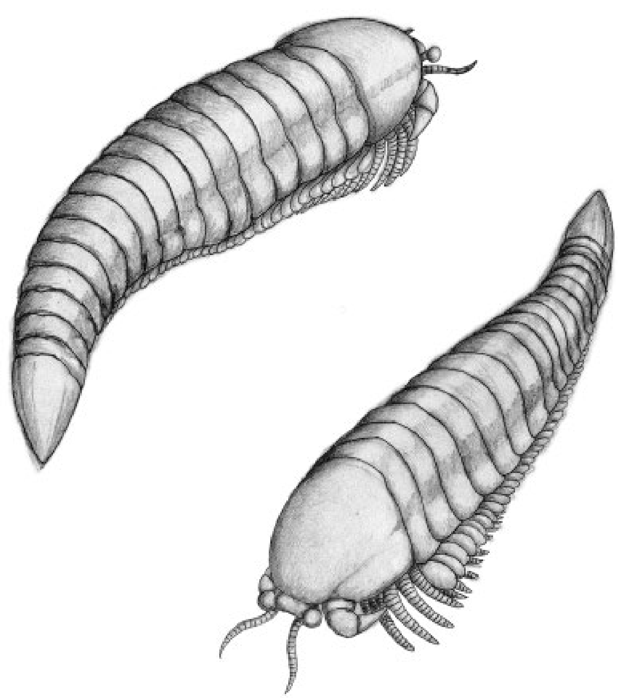


Figure 20.7 Reconstruction of ***Chengjiangocaris longiformis*** (modified from Hou *et al.* 2004a).

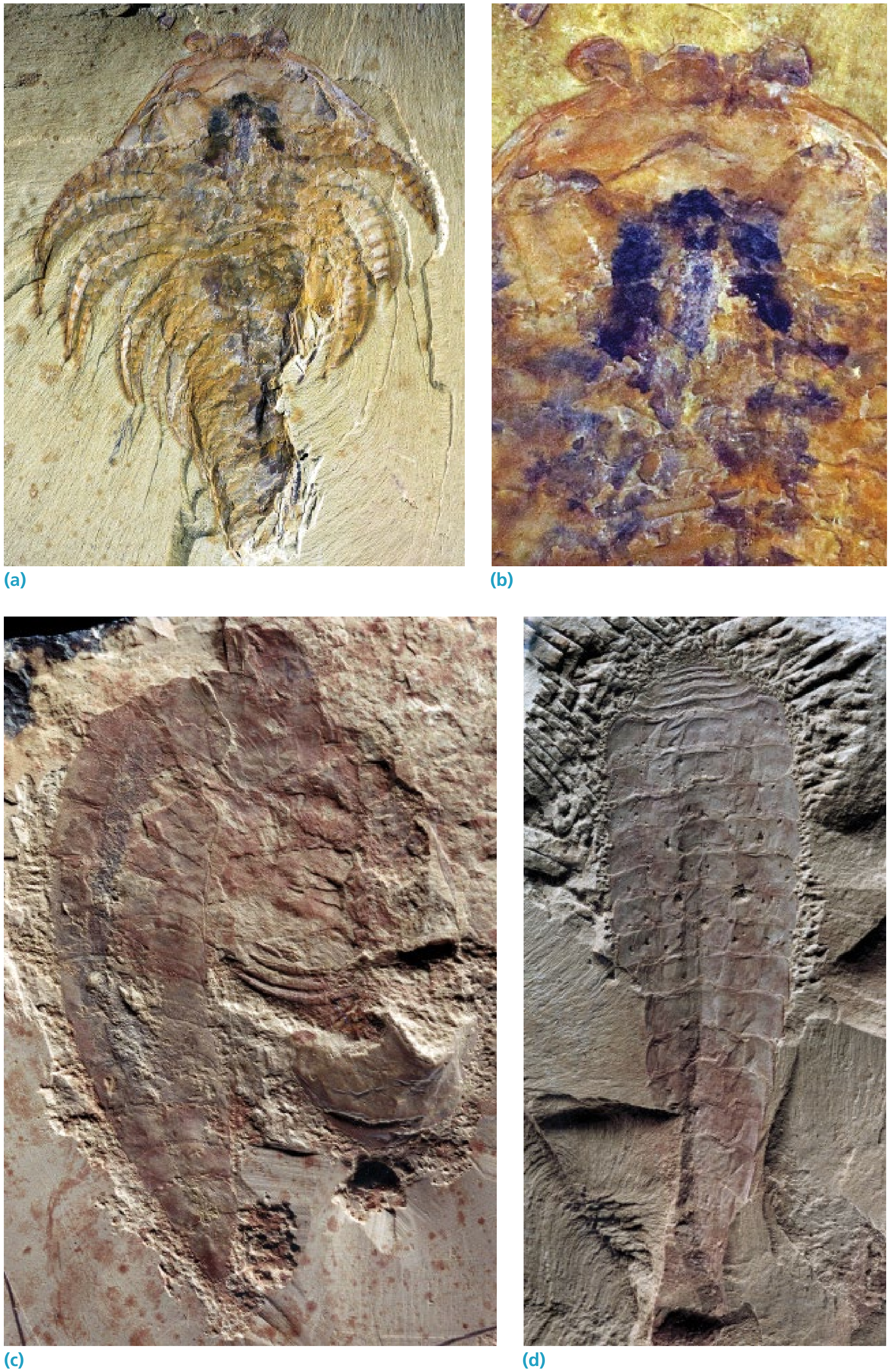


Figure 20.8 ***Chengjiangocaris longiformis***. **(a), (b)** NIGPAS 10256, ×2.0, ×4.6; Xiaolantian, Chengjiang. **(c)** NIGPAS 115359, ×2.1; Xiaolantian, Chengjiang. **(d)** NIGPAS 110837, ×1.5; Maotianshan, Chengjiang.

Genus *Fuxianhuia* Hou, 1987

Fuxianhuia protensa Hou, 1987

Fuxianhuia protensa is known from hundreds of well-preserved specimens, the largest being about 11 cm long. Specimens are typically preserved dorsoventrally flattened.

The short semicircular head shield, which is suggested to be composed of two hemi-shields, covers the anterior-most four segments of the body. The anterior-most segment bears a pair of stalked lateral eyes projecting anterior to the head shield, with optic nerves that extend backward to connect with the first segment of the brain (the protocerebrum). The second segment bears a pair of uniramous post-ocular antennae, which also clearly connect via nerve tracts to the brain (Ma *et al*. 2012b). The first post-antennal segment shows paired curved articulated appendages flanking the mouth, corresponding to a third pair of nerve tracts from the brain. In the closely related, slightly younger species *Fuxianhuia xiaoshibaensis*, also from Yunnan Province, these uniramous limbs comprise three podomeres (Yang Jie *et al*. 2013). The presence of three successive pairs of nerve roots leading to the optic lobes, paired uniramous antennae, and paired post-antennal appendages, demonstrates that the brain of *F. protensa* comprised three parts: protocerebrum, deutocerebrum, and tritocerebrum. *F. protensa* possessed a simple tube gut extending from the mouth to the last segment of the abdomen.

The thorax of *F. protensa* comprises up to about 17 segments, with the first two to three smaller segments covered by the head shield. The thoracic segments bear broad paratergal folds. An abruptly narrowed abdomen consists of 13 to 14 segments with a terminal spine flanked by a pair of shorter lateral spines. The biramous appendages of the thorax have an endopod of at least 15 podomeres and a flap-like exopod with smooth margins. Although some 16 to 18 thoracic tergites carry appendages, there appear to be as many as 35 to 45 pairs of appendages in total, with two to four pairs of appendages for each tergite of the thorax (Hou & Bergström 1997; compare Chen Jun-yuan *et al*. 1995b).

F. protensa preserves evidence for a complex cardiovascular system with segmentally arranged lateral extensions in the trunk originating from a midline structure, which is interpreted as the heart (Ma *et al*. 2014b). Paired frontal arteries extend forward beneath the head shield and provide an elaborate system of tributaries that extend to the brain, eyes, and antennae.

Hou and Bergström (1997) assigned *Fuxianhuia* to a new family and a new superclass, Proschizoramia, which they characterized as a group at an early stage in the evolution of arthropods with biramous limbs. *Fuxianhuia* has been regarded as a basal euarthropod (Chen Jun-yuan *et al*. 1995b; Edgecombe & Ramsköld 1999a) and a possible early chelicerate (Wills 1996). Another analysis resolved this genus as an upper stem euarthropod close to the Chengjiang genus *Pectocaris* (Budd 2002). Recent morphological (Yang Jie *et al*. 2013) and phylogenetic analyses (Legg *et al*. 2013) have united *Chengjiangocaris* and *Fuxianhuia* in the fuxianhuiids and have demonstrated close similarities in their head appendages – particularly their possession of a specialized post-antennal appendage – and recognized their position as upper stem euarthropods (Edgecombe & Legg 2014; see also Waloszek *et al*. 2005). The brain and cardiovascular system of *F. protensa* show similarities to crown-group euarthropods, particularly Mandibulata (Ma *et al*. 2012b, 2014b), suggesting a more crown-ward position of *F. protensa* or indicating that the central nervous system and cardiovascular structures of mandibulates retained many ancestral characteristics.

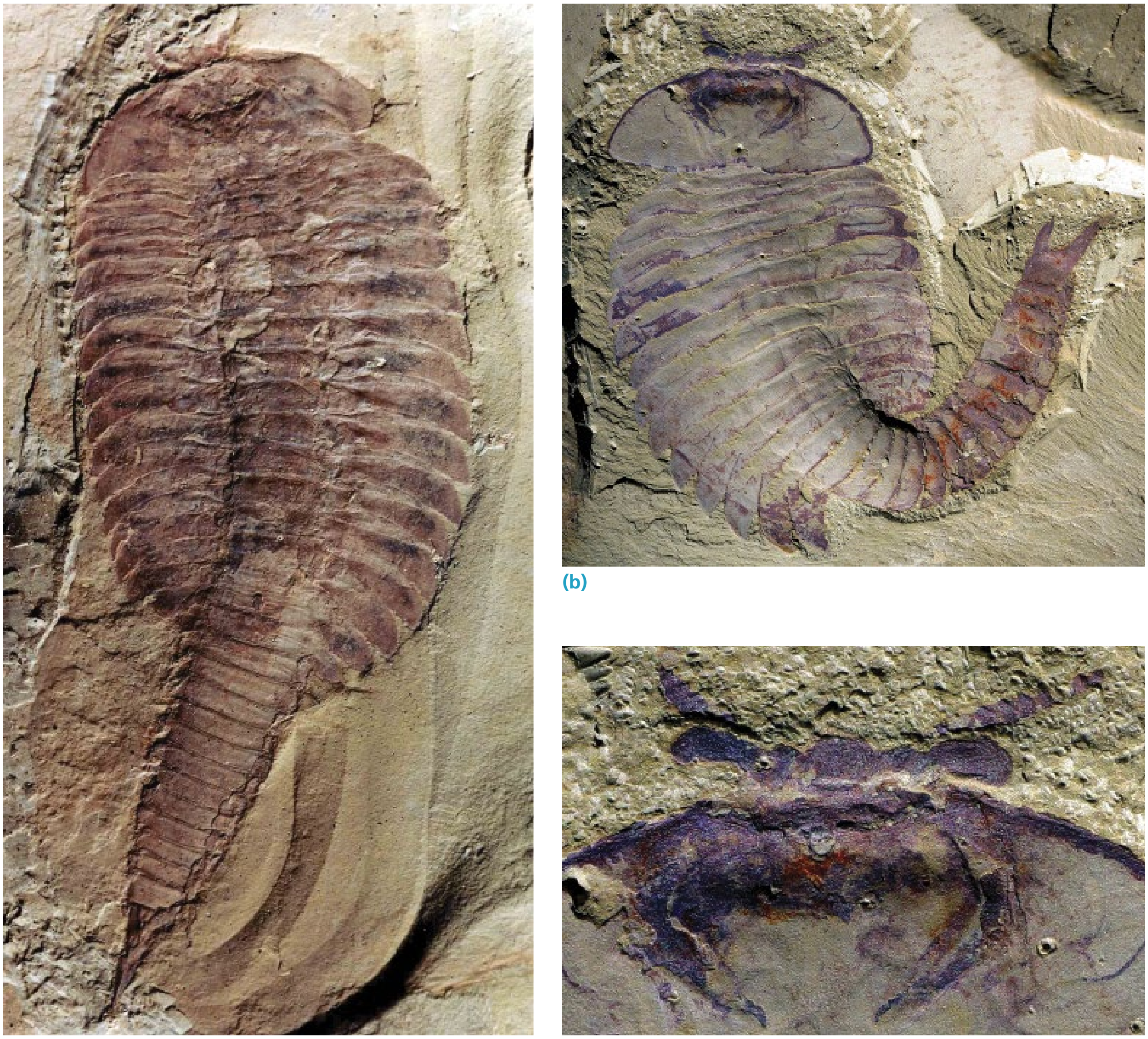
F. protensa clearly had excellent vision, with its eyes situated on stalks that were able to rotate (Ma *et al*. 2012b). The species may have been a highly mobile forager, employing visual and olfactory perception, a view supported by the rich system of arteries associated with its brain, which suggests a demand for oxygen required by networks integrating information from well-developed visual and antennal sensory systems (Ma *et al*. 2014b). The articulation and morphology of the specialized second appendage pair suggest that *Fuxianhuia* may have used a type of sweep feeding (Yang Jie *et al*. 2013).

F. protensa is unknown outside the Chengjiang biota.

Key references

Hou 1987b; Chen Jun-yuan *et al*. 1995b; Wills 1996; Chen Jun-yuan & Zhou 1997; Hou & Bergström 1997; Bergström & Hou 1998; Hou *et al*. 1999, 2004a; Budd 2002, 2008b; Waloszek *et al*. 2005; Ma *et al*. 2012b, 2014b.

Figure 20.9 ***Fuxianhuia protensa***. **(a)** NIGPAS 110826, ×1.4; Maotianshan, Chengjiang. **(b), (c)** YKLP 11321, ×2.3, ×6.2; Ercaicun, Haikou, Kunming.



(a) (b) (c)

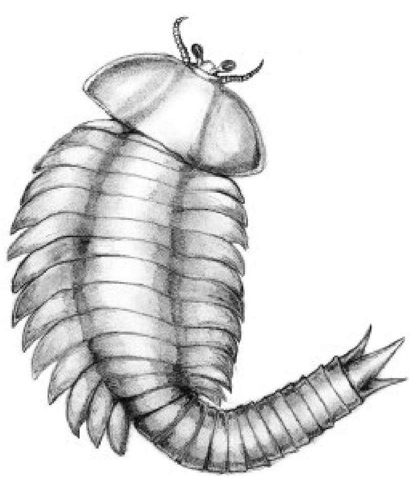


Figure 20.10 Reconstruction of ***Fuxianhuia protensa*** (modified from Hou *et al*. 2004a).

Genus *Pseudoiulia* Hou & Bergström, 1998

Pseudoiulia cambriensis Hou & Bergström, 1998

Only two specimens of *Pseudoiulia cambriensis* are known. Both are laterally compressed and incomplete. The head is unknown.

The type specimen, which is about 3.7 cm long and 5 mm high, shows an elongate trunk with 31 homonymous segments, plus what appears to be the terminal element, which may be incomplete. The body seems to have been strongly vaulted in cross-section. The appendages are poorly preserved suggesting that they were weakly sclerotized. Setiferous fragments and elongate flaps bearing marginal setae represent parts of the exopods; the endopods are not known.

Based on its elongate body, *P. cambriensis* has been compared with myriapods, but the absence of the head means that there are no preserved mandibles, tentorium, or Tömösváry organs that could qualify such an affinity (Edgecombe 2004). Despite the absence of its head, the trunk of *Pseudoiulia* shows striking similarities with the arthropods *Kootenichela* Legg, 2013 and *Worthenella* Walcott, 1911 from the middle Cambrian of British Columbia, Canada. These three taxa are united by possessing an elongate trunk each with 25 or more segments, and have appendages with subtriangular exopod flaps fringed with fine setae (Legg 2013). *Kootenichela* has large pedunculate eyes, a possible antenna-like appendage, and large raptorial appendages. Phylogenetic analysis resolves *Kootenichela* and *Worthenella* as sister taxa within a paraphyletic Megacheira clade (Legg 2013), or as antennate megacheirans (Legg *et al*. 2013). In both analyses *Kootenichela* and *Worthenella* are upper stem euarthropods, an assignment that might also be applicable to *Pseudoiulia*.

Although there is insufficient evidence to deduce the mode of life of *P. cambriensis,* the presence of well-developed mid-gut glands in the possibly related *Kootenichela* may, by inference, indicate a scavenging or predatory mode of life for *Pseudoiulia* (see Legg 2013).

P. cambriensis is known only from the Chengjiang biota.

Key references

Hou & Bergström 1998; Hou *et al*. 1999, 2004a.

Figure 20.11 ***Pseudoiulia cambriensis***. **(a)** RCCBYU 10270, ×4.0; Mafang, Haikou, Kunming. **(b)** YKLP 13912, ×3.3; Mafang, Haikou, Kunming.

(a) (b)

Genus *Fortiforceps* Hou & Bergström, 1997

Fortiforceps foliosa Hou & Bergström, 1997

This species is known from some 20 specimens, some excellently preserved. Appendages and other soft-parts are normally present.

Opinions vary regarding the exact nature of several morphological features of this species. The body is long and slender, reaching a length of about 4 cm excluding appendages. Large stalked eyes and a pair of forwardly projecting great appendages emerge from under the front edge of the short head shield. Possible antennae, with a club-like termination, have been recorded from some specimens. The great appendage consists of a two-part proximal peduncle connected by an elbow joint to a distal claw comprising four podomeres each with a long spine on the inner side. At least three additional pairs of biramous appendages occur on the head. The trunk has about 20 segmental tergites each with a pair of biramous appendages consisting of a long, multi-podomere inner branch and a flap-like outer branch fringed with fine small setae. Posteriorly there is a broad, fan-like telson edged with fine bristles and consisting of a median region flanked by a pair of longer lateral blades.

As a short great appendage arthropod (megacheiran) *Fortiforceps* is allied to genera such as the Chengjiang *Jianfengia*, *Tanglangia*, and *Leanchoilia.* The monotypic genera *Fortiforceps, Jianfengia*, and *Tanglangia* are each based on sparse material and it has been suggested that at least *Fortiforceps* and *Jianfengia* might represent a single species (Haug *et al.* 2012a). Megacheirans are generally considered to be either stem euarthropods (e.g., Legg *et al.* 2012, 2013; Edgecombe & Legg 2014) or as part of the chelicerate group in the broad sense (e.g., Chen Jun-yuan *et al.* 2004; Cotton & Braddy 2003; Dunlop 2006; Haug *et al.* 2012a, 2012b; Liu Yu *et al.* 2014). The neural pattern of the head preserved in a specimen of the megacheiran *Alalcomenaeus* from Chengjiang indicates homology between the great appendage and the chelicera and corresponds most closely to the nervous system of Chelicerata of all extent arthropods (Tanaka *et al.* 2013).

This species was probably carnivorous. The morphology of its great appendage has been compared to the great appendage of later developmental stages of the Burgess Shale megacheiran *Yohoia tenui,* which possibly captured prey like the living spearer-type mantis shrimp, using the elbow-joint of the great appendage in a jack-knifing mechanism (Haug *et al.* 2012b). Some specimens show a simple intestine present from the middle part of the head to the end of the trunk. The paddle-like outer branch of the trunk limbs suggests that it was likely to be a swimmer.

Fortiforceps is known only from its type species and is unknown outside the Chengjiang biota.

Key references

Hou & Bergström 1997; Hou *et al.* 1999, 2004a; Chen Jun-yuan 2004; Chen Jun-yuan *et al.* 2004; Dunlop 2006; Haug *et al.* 2012b.

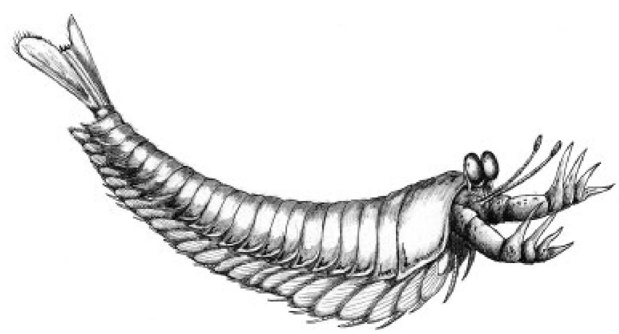
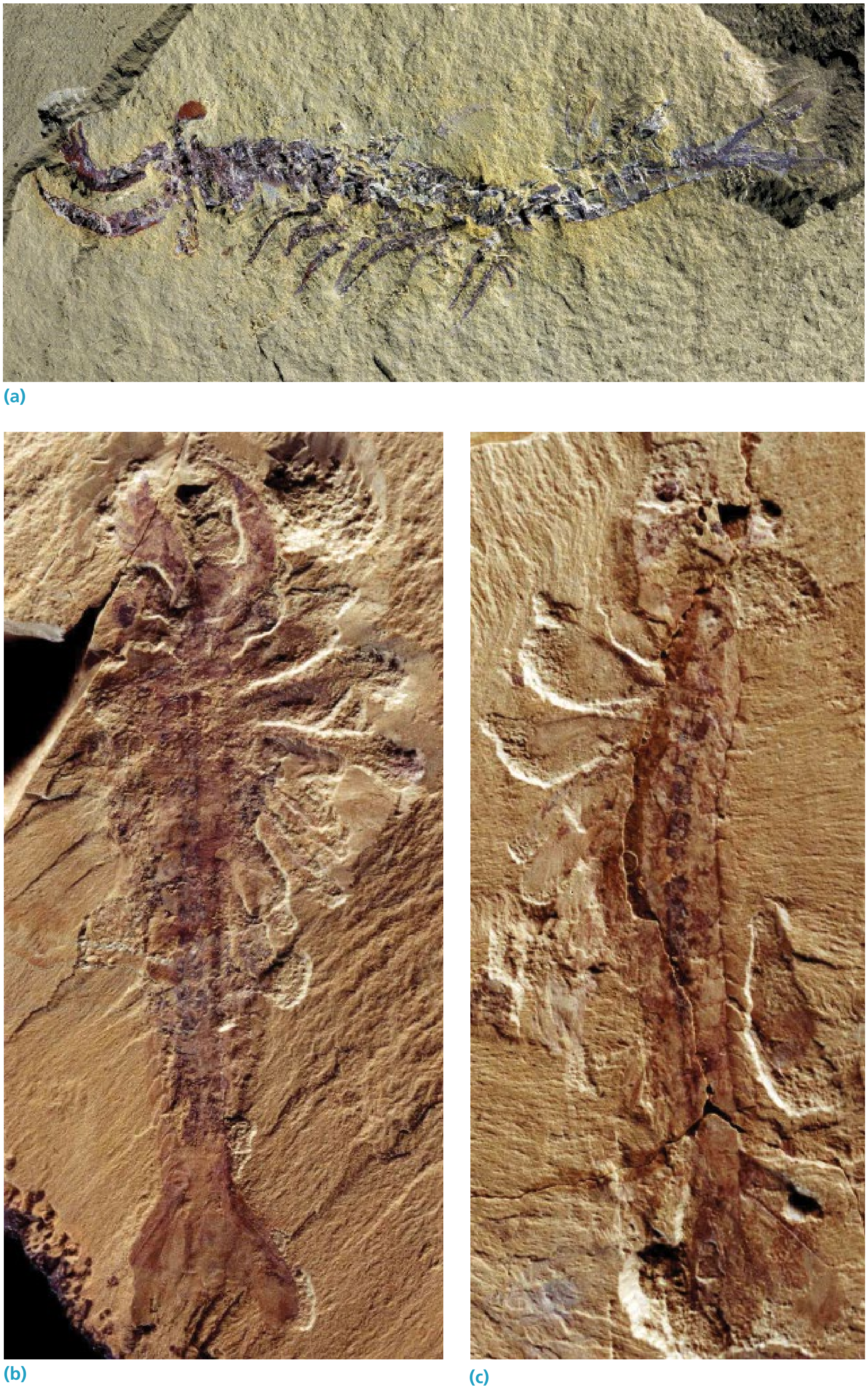


Figure 20.12 Reconstruction of ***Fortiforceps foliosa*** (modified from Hou & Bergström 1997).

Figure 20.13 ***Fortiforceps foliosa*. (a)** YKLP 11351a, ×3.7; Ercaicun, Haikou, Kunming. **(b)** NIGPAS 115373, ×3.3; Maotianshan, Chengjiang. **(c)** NIGPAS 115372, ×3.3; Maotianshan, Chengjiang.



(a)
(b)
(c)

Genus *Occacaris* Hou, 1999

Occacaris oviformis Hou, 1999

This species is known only from a single, laterally compressed, incomplete specimen. Much of the head region and soft anatomy is missing, but remains of the carapace, parts of the appendages, and posterior parts of the body are preserved.

The specimen is small, measuring some 1.5 cm long including the limbs projecting from the carapace. The carapace is bivalved, smooth, about 8 mm long and 6 mm high and subovoid in lateral aspect. The valves cover the head and anterior parts of the body and appear to be thin and unmineralized. A pair of stalked eyes jut forward outside the carapace. Projecting from behind the carapace are the remains of possibly three trunk tergites and a telson. The exact number and detailed nature of the appendages is debatable. The best-preserved appendage is presumed to be a great appendage, consisting of a proximal bipartite peduncle articulated by a weak elbow joint to a claw comprising four or five spine-bearing elements (Haug *et al.* 2012b). Other authors have interpreted this appendage as a displaced inner limb branch (see Haug *et al.* 2012b). The original description of *Occacaris oviformis* recognized a pair of multi-annulate antennae in front of the great appendages (an interpretation questioned by later authors), and the scant remains of multi-segmented limbs presumably representing the inner branch of biramous head and trunk appendages. Posteroventrally, the remnants of three setiferous flaps were considered to be parts of the exopods of appendages.

Based primarily on features of the head, *Occacaris* and the closely related *Fortiforceps* were resolved as stem euarthropods (Budd 2002). That placement for megacheirans is supported in a comprehensive phylogenetic analysis of arthropods (Legg *et al.* 2012, 2013; Edgecombe & Legg 2014). Alternatively, based on morphological considerations, in particular the evolution of the form of the great appendage, others claim a chelicerate affinity for these and other short great appendage arthropods (e.g., Chen Junyuan *et al.* 2004; Cotton & Braddy 2003; Dunlop 2006; Haug *et al.* 2012b). The latter view has been endorsed by preserved neuroanatomical evidence in material from the Chengjiang Lagerstätte (Tanaka *et al.* 2013).

Occacaris was perhaps an active predator. It may have used its spinose great appendage in a jack-knife fashion to capture small animals (Haug *et al.* 2012b). As knowledge of most of its appendages is scant, its mode of locomotion is uncertain.

The only known specimen is from Maotianshan, near Chengjiang town.

Key references

Hou 1999; Hou *et al.* 1999, 2004a; Haug *et al.* 2012b.

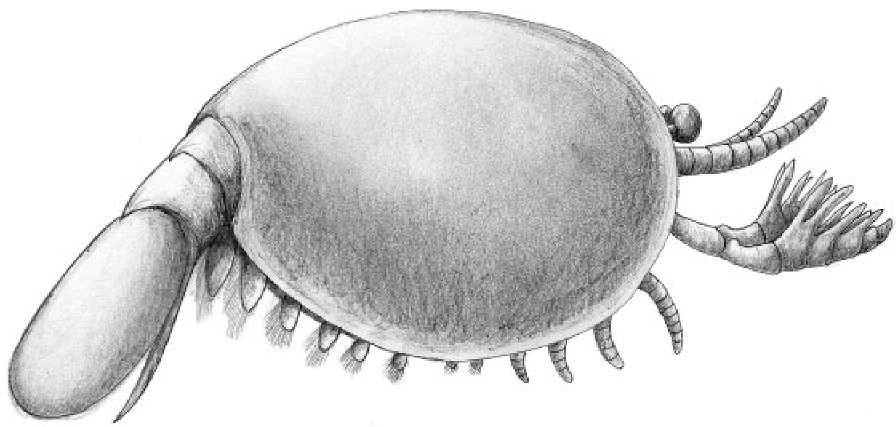
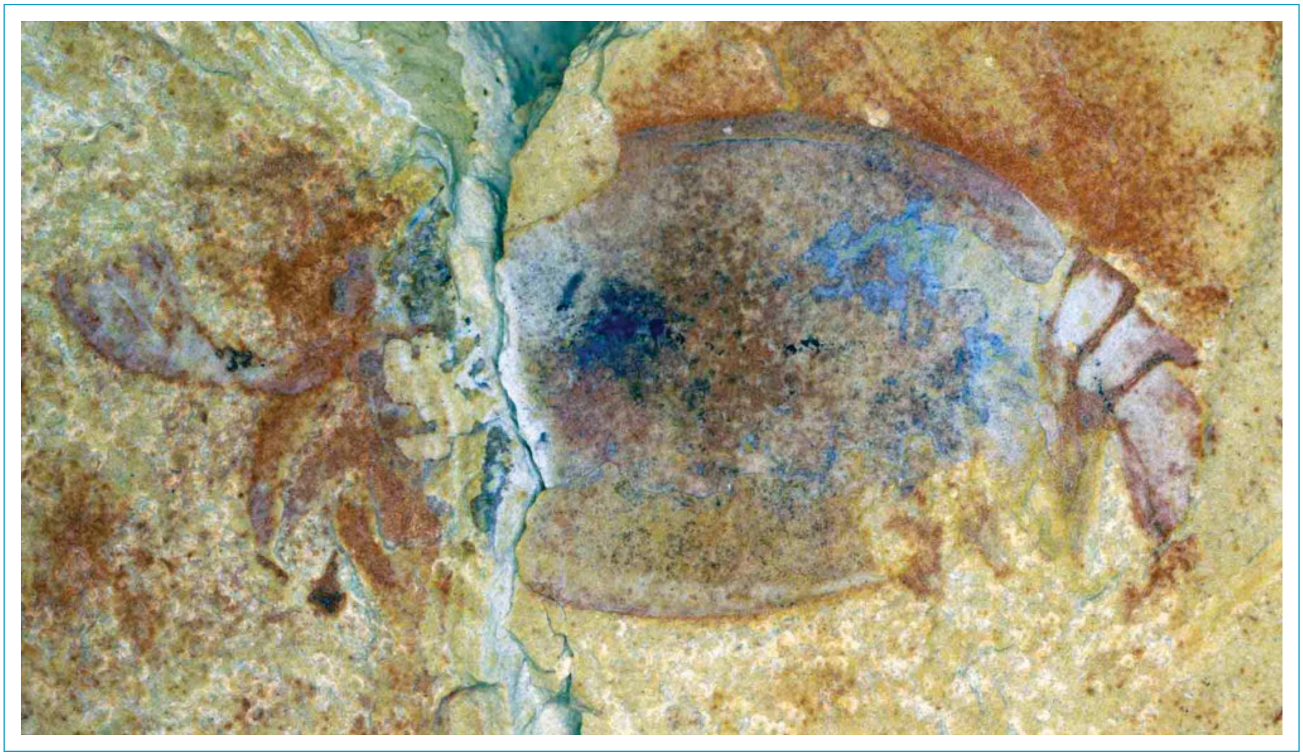


Figure 20.14 Reconstruction of ***Occacaris oviformis*** (general aspect based on Bergström & Hou 2005; great appendage morphology also after Haug *et al.* 2012b).

Figure 20.15 ***Occacaris oviformis***, NIGPAS 115408, ×13.0; Maotianshan, Chengjiang.



Genus *Forfexicaris* Hou, 1999

Forfexicaris valida Hou, 1999

Forfexicaris valida is very rare, known with certainty from only two specimens. They are laterally flattened, with one specimen having appendage remnants in front of the thin, concentrically wrinkled valves.

In lateral aspect the valves have a subcircular outline and a straight dorsal margin with gently rounded angles anteriorly and posteriorly. The carapace of the type specimen is about 1.5 cm long; the second specimen is 1.2 cm long. A pair of supposed eyes project from the anterior margin of the carapace. Reconstruction of the type specimen records a well-developed short great appendage consisting of at least four elements, some with elongate spines (Hou 1999; Vannier *et al*. 2006). Fragmentary remains of a few paddle-shaped structures preserved in front of the valves, each bearing a marginal row of delicate setae, are presumed to be parts of exopods of biramous appendages. The corresponding endopods are unknown, as is the morphology of the hind part of the body.

F. valida was established as the only member of the Family Forfexicarididae. Although poorly known, the species can be tentatively placed among other Chengjiang forms with a short great appendage (megacheirans), such as *Fortiforceps foliosa* and *Occacaris oviformis*. Indeed, Hou (1999) compared *F. valida* to *Occacaris oviformis*, and the question of whether these two forms might in fact be one species has been mooted (Haug *et al*. 2012b). Some authors regard megacheirans as stem euarthropods (e.g., Legg *et al*. 2012, 2013). Alternative, morphological-based analyses assign megacheirans to the Chelicerata, in a scenario in which the great appendage is considered to be the precursor of chelicerae (e.g., Chen Jun-yuan *et al*. 2004; Cotton & Braddy 2003; Dunlop 2006; Haug *et al*. 2012b).

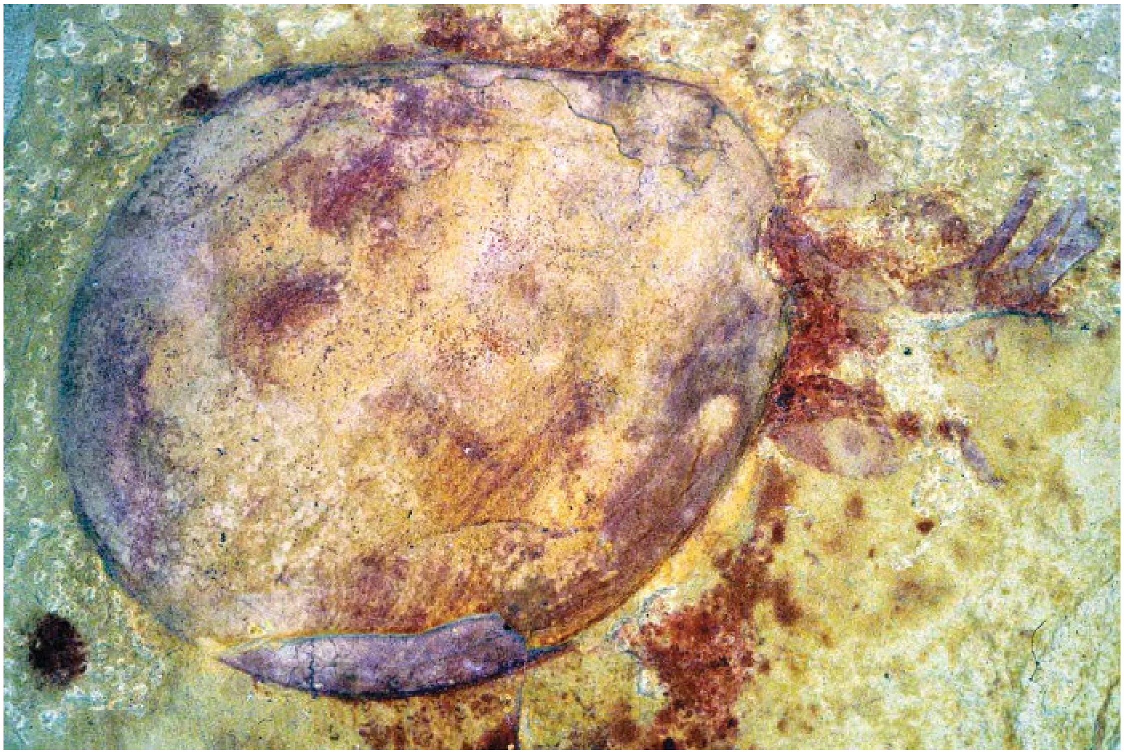
With the limited available material, little can be inferred concerning locomotion and other aspects of the mode of life of *F. valida*. Most likely the great appendage functioned as a raptorial limb, to obtain prey and other items of food.

The species is known only from the Chengjiang area.

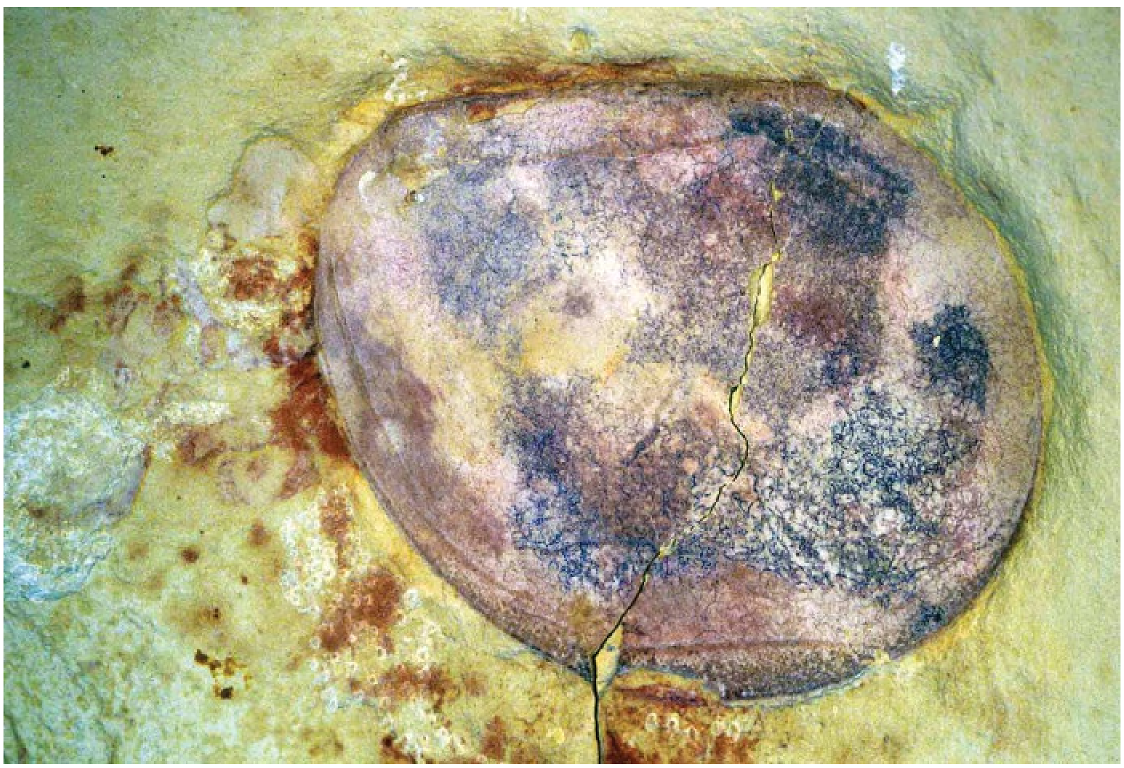
Key references

Hou 1999; Hou *et al*. 1999, 2004a.

Figure 20.16 ***Forfexicaris valida***. **(a)** NIGPAS 115409a, ×13.6; Xiaolantian, Chengjiang. **(b)** NIGPAS 115409b, ×13.6; Xiaolantian, Chengjiang.



(a)



(b)

Genus *Jianfengia* Hou, 1987

Jianfengia multisegmentalis Hou, 1987

Jianfengia multisegmentalis is known from several tens of specimens, which range up to 2 cm long. They are preserved compressed in both lateral and dorsoventral aspect and show details of the soft-parts.

J. multisegmentalis has a short head, a trunk with about 22 segmental tergites, and a telson (Hou 1987a; Dunlop 2006). A few wrinkles may indicate the presence of at least three segments in the head. The head shield bends down anteriorly, is transversely vaulted, and extends into a short, probably ventrolaterally directed pleural fold. The trunk tergites are of simple shape and transversely rounded. The telson seems to be a narrow, more or less parallel-sided rod-like structure with a pointed end. The great appendage and a pair of probable stalked eyes project beyond the anterior part of the head. The great appendage consists of a proximal bipartite peduncle articulated via an elbow-type joint with a distal claw consisting of four spinose podomeres (Haug *et al*. 2012b). The head and the trunk contain a total of 25 other pairs of (biramous) appendages. The long, slender endopods consist of many podomeres with a spine-like tip. Each exopod appears to be an elongate flap that carries long setae on the outer edge. The alimentary canal is often preserved as a darker tract in the trunk region and as an oval area in the head.

J. multisegmentalis is morphologically similar in many respects to the Chengjiang taxa *Fortiforceps foliosa* and *Tanglangia longicaudata* and it has been suggested that they may be growth stages of a single species (Haug *et al*. 2012a). It was also noted that the great appendage of *J. multisegmentalis* bears close resemblance to the early developmental stages of the great appendage in *Yohoia tenuis* from the Burgess Shale. In some analyses these and other so-called short great appendage arthropods resolve as closely related stem euarthropods (Budd 2002; Legg *et al*. 2012, 2013). An opposing view, supported by fossil neurological evidence (Tanaka *et al*. 2013), places them as part of the evolution of chelicerates, in which the great appendage evolved into the chelicera of king crabs, scorpians, and their relatives (e.g., Chen Jun-yuan *et al*. 2004; Dunlop 2006; Haug *et al*. 2012b).

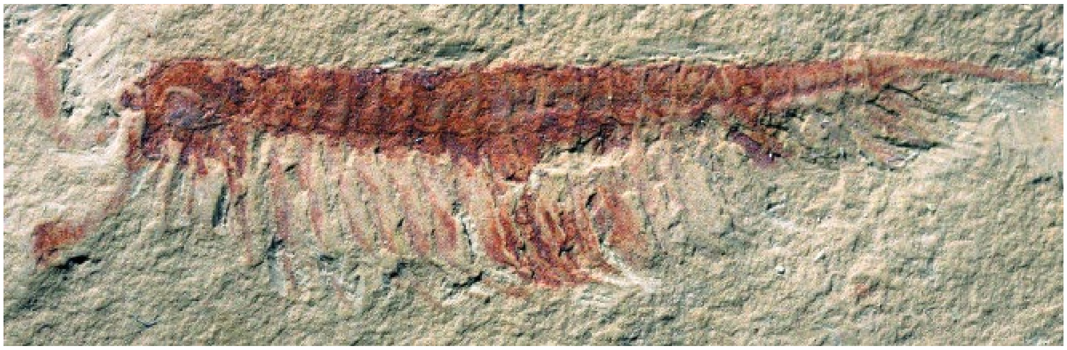
J. multisegmentalis may have had a lifestyle like that of the living predatory mantis shrimp (Chen Jun-yuan *et al*. 2004, 2007b; Haug *et al*. 2012b). They have similar tail fins and the pronounced elbow joint in the great appendage in both species facilitates a jack-knife mechanism for use in hunting at or near the sea bottom. The prominent eyes in *J. multisegmentalis* could have been effective in detecting prey. Its long, slender trunk endopods may have been used for walking. The exopods may have been used in swimming.

J. multisegmentalis is known only from the Chengjiang Lagerstätte.

Key references

Hou 1987a; Chen Jun-yuan & Zhou 1997; Hou *et al*. 1999, 2004a; Chen Jun-yuan 2004; Chen Jun-yuan *et al*. 2004; Dunlop 2006; Haug *et al*. 2012b.

Figure 20.17 ***Jianfengia multisegmentalis*****.** **(a)** NIGPAS 10012, ×6.6; Maotianshan, Chengjiang. **(b)** YKLP 13914, ×7.5; Maotianshan, Chengjiang. **(c)** YKLP 13915, ×9.8; Mafang, Haikou, Chengjiang. **(d)** YKLP 13916, *circa* ×7.9; Mafang, Haikou, Chengjiang.



(a)

(b)

(c)

(d)

Genus *Tanglangia* Luo & Hu *in* Luo, Hu, Chen, Zhang & Tao, 1999

Tanglangia longicaudata Luo & Hu *in* Luo, Hu, Chen, Zhang & Tao, 1999

This species has been described on the basis of a few specimens, most of which are well preserved. Exoskeletons range up to 4 cm in length.

The narrow, elongate body comprises a head shield, trunk, and a telson (Luo & Hu *in* Luo *et al*. 1999; Xu Guang-hui 2004). The head has a subelliptical outline and bears a frontal pair of great appendages, behind which there are possibly three pairs of biramous appendages. The great appendage seemingly consists of a proximal peduncle articulated in elbow-joint fashion with a distal claw comprising four podomeres each bearing a spine. A pair of stalked eyes project in front of the head shield. The trunk is divided into about 13 segmental tergites and bears pairs of biramous appendages details of which are obscure. The simple, narrow, telson is almost as long as the entire trunk region.

In overall morphology *Tanglangia longicaudata* resembles the Chengjiang species *Jianfengia multisegmentalis* and *Fortiforceps foliosa*. It differs from both species especially by having many fewer trunk segments and a relatively much longer telson. Nevertheless, it has been questioned whether two or even all three of these taxa represent nothing more than growth stages of the same species (Haug *et al*. 2012b).

Most analyses determine such short great appendage arthropods as either stem euarthropods (Legg *et al*. 2012, 2013) or as derivatives of the stem lineage of chelicerates in the strict sense (Chen Jun-yuan *et al*. 2004; Cotton & Braddy 2003; Maas *et al*. 2004; Dunlop 2006; Haug *et al*. 2012b; Tanaka *et al*. 2013).

The ecology of *T. longicaudata* is poorly understood. It was presumably carnivorous, perhaps a sea bottom dweller, using its great appendage to hunt for food with a jack-knife mechanism as envisaged for Cambrian mantis shrimp-like predators (Chen Jun-yuan *et al*. 2004, 2007b; Haug *et al*. 2012b).

The species is known from localities in the Haikou and Chengjiang areas of Yunnan Provence. A slightly younger species of *Tanglangia* occurs in the Emu Bay Shale, indicating biogeographic connections between early Cambrian biotas of Australia and South China (Paterson *et al*. 2015a).

Key references

Luo & Hu *in* Luo *et al*. 1999; Hou *et al*. 2004a; Chen Jun-yuan *et al*. 2004; Xu Guang-hui 2004; Haug *et al*. 2012b.

Figure 20.18 ***Tanglangia longicaudata***. **(a)** YKLP 13917, ×6.1; Ercaicun, Haikou, Kunming. **(b)** YKLP 13918, ×5.4; Ercaicun, Haikou, Kunming. **(c)** RCCBYU 10268, ×4.6; Ma'anshan, Chengjiang.

(a)

(b)

(c)

Genus *Parapeytoia* Hou, Bergström & Ahlberg, 1995

Parapeytoia yunnanensis Hou, Bergström & Ahlberg, 1995

Parapeytoia yunnanensis is a rare species, known only from a few almost complete articulated specimens and about 10 isolated frontal and trunk appendages.

The species has a pair of great appendages on the head and has been interpreted as having two or three other pairs of (biramous) appendages on the head and possibly 13 segments, with legs, in the trunk (Haug *et al.* 2012b). The great appendage consists of a proximal part of two elements and a distal claw of four parts each bearing a long, finger-like spine on the inner side of the appendage. The mouth area is ring-like, consisting of radially arranged structures. The trunk limbs are large and have a basal part in the form of a huge flat plate with tiny and larger spines along the inner edge, from which extends a leg-like branch composed of at least eight podomeres (Hou *et al.* 1995; Chen Jun-yuan *et al.* 2007b). Seemingly continuous with the basipod there is a laterally extensive flap. According to one interpretation, the dorsal side of *P. yunnanensis* has transverse sets of lanceolate scales.

This species was originally described as an anomalocaridid, and no primary taxonomic analysis has been undertaken of this species since it was erected. However, *P. yunnanensis* is now generally placed as a short great appendage arthropod. This species and other megacheirans with a clearly developed elbow joint in the great appendage, such as the Chengjiang *Occacaris* and *Fortiforceps* and *Yohoia* from the Burgess Shale, are chelicerates according to several morphological-based analyses (Chen Jun-yuan *et al.* 2004; Dunlop 2006; Haug *et al.* 2012b) supported by fossil neurological evidence (Tanaka *et al.* 2013). Other, phylogenetic studies resolve megacheirans as stem euarthropods (Legg *et al.* 2012, 2013).

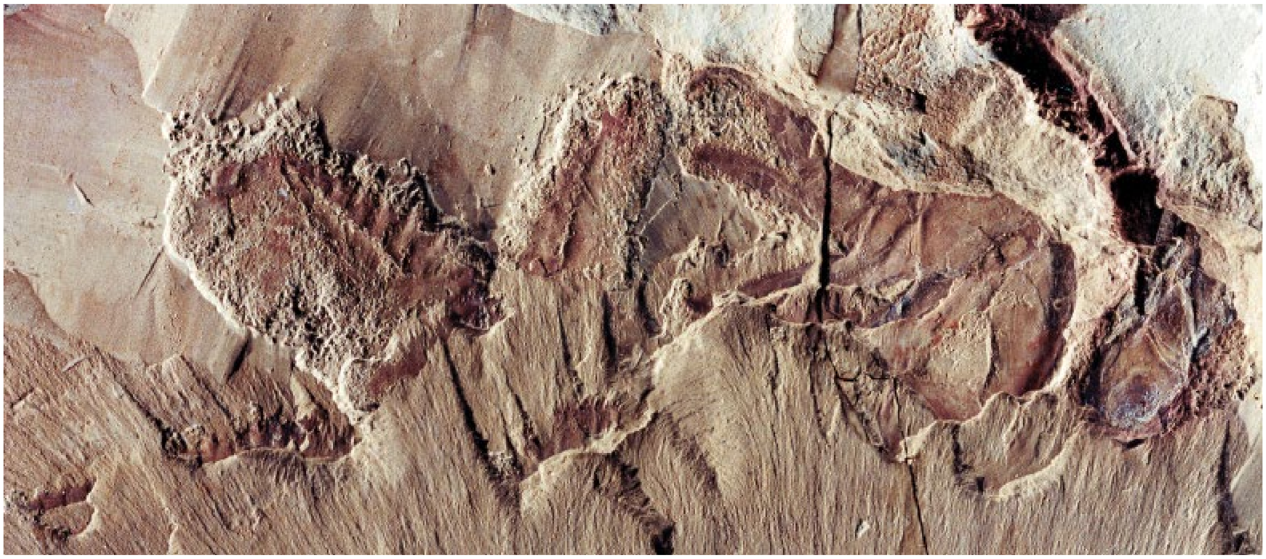
P. yunnanensis probably had a mobile scavanging and predatorial lifestyle, at or near the sea bottom (Chen Jun-yuan *et al.* 2007b; Haug *et al.* 2012b), perhaps like that of the present-day mantis shrimp. The spinose great appendages could have been used to capture live animals and other items of food.

P. yunnanensis is known only from the Chengjiang fauna.

Key references

Hou *et al.* 1995, 1999, 2004a; Chen Jun-yuan 2004; Haug *et al.* 2012b.

Figure 20.19 ***Parapeytoia yunnanensis***. **(a)** Ventral view, part. NIGPAS 115334b, ×1.7; Maotianshan, Chengjiang. **(b)** Ventral view, counterpart, showing grasping appendages, mouth, sternites and other pairs of appendages. NIGPAS 115334a, ×1.8; Maotianshan, Chengjiang.


(a)


(b)

Genus *Haikoucaris* Chen, Waloszek & Maas, 2004

Haikoucaris ercaiensis Chen, Waloszek & Maas, 2004

Haikoucaris ercaiensis was originally described from just three specimens, including one almost 4 cm long with well-preserved soft parts. There is now a total of about 20 specimens known, all of which are relatively complete.

Behind the semicircular head shield there is a trunk region of 13 tergites and a short spatula-like telson with a pointed tip. The tergites have short, fairly rounded, lateral margins. The anterior-most head segment bears a pair of great appendages. Each consists of a bipartite peduncle proximally and, distally, a claw of three elements each elongated into a spine. There are three more pairs of appendages in the head, but their details are obscure; most probably they are morphologically similar to the trunk appendages. Unstalked, anterolaterally directed eyes occur at the front of the head. All of the trunk segments have a pair of biramous appendages. Each appendage comprises a rigid basipod, a leaf-shaped setiferous exopod, and an endopod most likely of seven podomeres.

Phylogenetic analysis places *H. ercaiensis* close to many other short great appendage stem euarthropod genera known from the Chengjiang biota, such as *Alalcomenaeus*, *Leanchoilia*, and *Parapeytoia*, and also *Yohoia* from the Cambrian Burgess Shale (Legg *et al.* 2012, 2013). Features such as body shape, number of trunk segments, and especially the detailed morphology of the great appendage differentiate these and allied genera. An alternative scenario of affinity emphasizes the purported similarity (homology) between the (short) great appendages and the chelicerae of king crabs, pycnogonids, and relatives (Chen Jun-yuan *et al.* 2004; Cotton & Braddy 2003; Dunlop 2006; Haug *et al.* 2012b). Compared to the chelicerate chelicera, *H. ercaiensis* seemingly has just one less element in the claw of its great appendage. Evidence from neuroanatomy preserved in Chengjiang fossils has given support for a chelicerate affinity for short great appendage arthropods (Tanaka *et al.* 2013).

It seems likely that the great appendages were used as raptorial appendages to obtain prey, probably at or near the sea bottom. The slender body and large exopods suggest a swimming mode of locomotion. The morphological variation amongst the short great appendage arthropods suggests that each may have been adapted for a specific hunting strategy and/or a particular prey (Chen Jun-yuan *et al.* 2004, 2007b; Haug *et al.* 2012b).

As indicated by the generic name, *H. ercaiensis* is known from localities in the Haikou area of the Chengjiang Lagerstätte.

Key references

Chen Jun-yuan *et al.* 2004; Chen Jun-yuan 2004; Haug *et al.* 2012b.

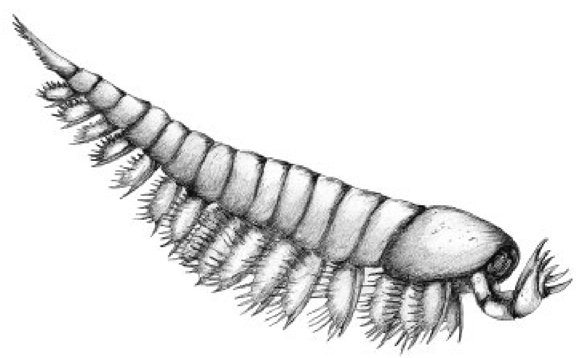
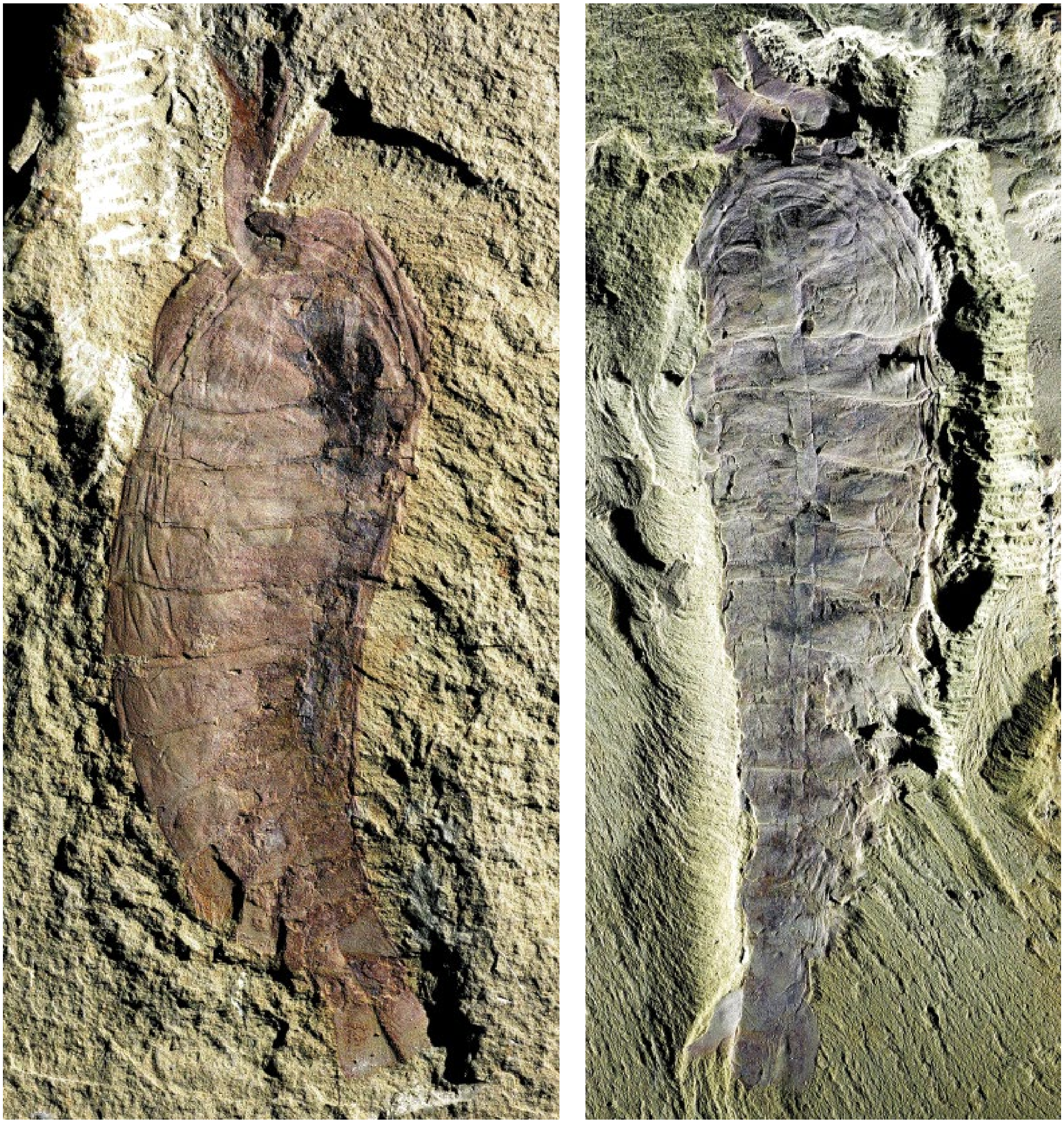


Figure 20.20 Reconstruction of ***Haikoucaris ercaiensis*** (modified from Chen Jun-yuan *et al.* 2004).

Figure 20.21 ***Haikoucaris ercaiensis*.** **(a)** YKLP 13920, ×4.0; Mafang, Haikou, Kunming. **(b)** YKLP 13921a, ×3.2; Mafang, Haikou, Kunming.



(a) (b)

Genus *Alalcomenaeus* Simonetta, 1970

Alalcomenaeus sp. of Tanaka, Hou, Ma, Edgecombe & Strausfeld, 2013

Alalcomenaeus sp. was originally described from three incomplete specimens, one of which is notable for preserving the neural structures of the head and trunk (Tanaka *et al*. 2013).

Alalcomenaeus sp. has a head shield with nearly straight anterior and posterior margins and with an overall trapezoidal shape, narrowing anteriorly. Paired eyes, each about 0.75 mm wide, are preserved each side of the midline, protruding just beyond the anterior margin of the shield. Each eye contains some 160 to 250 lenses. Each eye pair is clearly connected to the anterior (protocerebral) part of the head via a single optic nerve (Tanaka *et al*. 2013). *Alalcomenaeus* sp. has four pairs of head appendages. The frontal, uniramous great appendage, which is probably inserted into the second (deutocerebral) segment of the head (Tanaka *et al*. 2013), projects well beyond the anterior margin of the head shield; it was probably flagellate in the manner of the Burgess Shale *Alalcomenaeus cambricus* Simonetta, 1970. It is followed by three biramous appendages; by analogy to the appendages of *A. cambricus* these likely comprise an inner, segmented endopod and an outer flap-like exopod fringed by spines (Briggs & Collins 1999). Beyond the head shield there are 11 trunk segments, each with a pair of biramous appendages, which by analogy to *A. cambricus* were probably similar to those of the head. The appendages of trunk segments 9 to 11 become successively shorter toward the posterior end of the animal. Body segment 11 terminates in a broad, ovoid, paddle-shaped telson.

The head shield with its straight anterior margin and the ovoid paddle-shaped telson serve to distinguish *Alalcomenaeus* sp. from the closely related *Leanchoilia* Walcott, 1912, whilst the Australian (Emu Bay Shale) *Oestokerkus* Edgecombe *et al*., 2011 is differentiated by its forked telson. Phylogenetic analysis placed *Alalcomenaeus* within the Megacheira great appendage arthropods (Legg *et al*. 2013), and as such, *Alalcomenaeus* would be considered an upper stem euarthropod. However, the neural anatomy of *Alalcomenaeus* sp. shows important correspondences with those of crown group chelicerates like the horseshoe crab *Limulus*, especially the connection of the eye-pairs to the protocerebrum via a single optic nerve, and in the possession of fused cerebral and trunk ganglia. *Alalcomenaeus* was placed within the total group Chelicerata (Tanaka *et al*. 2013), and thus within the euarthropod crown.

Alalcomenaeus has been interpreted both as a benthic scavenger and as an active predator on soft-bodied organisms at or near the surface of the seabed. Its multi-annulated and flagellate great appendage would likely have been sensory, whilst its more substantive biramous head and trunk appendages could have been used for capturing and tearing at prey (Briggs & Collins 1999).

Many more specimens of *Alalcomenaeus* sp. remain to be described from the Chengjiang biota. *Alalcomenaeus* is also common in the Burgess Shale (Briggs & Collins 1999).

Key references

Walcott 1912; Simonetta 1970; Briggs & Collins 1999; Edgecombe *et al*. 2011a; Tanaka *et al*. 2013; Legg *et al*. 2013.

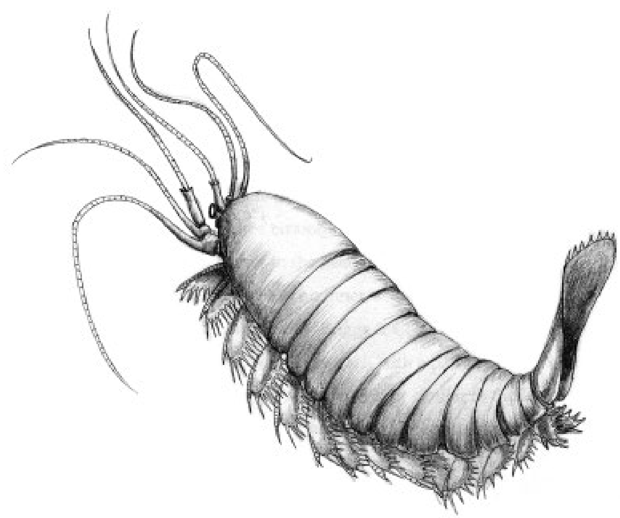


Figure 20.22 Reconstruction of ***Alalcomenaeus*** sp. (based on new specimens from Chengjiang, and ***Alalcomenaeus cambricus*** in Briggs & Collins 1999).

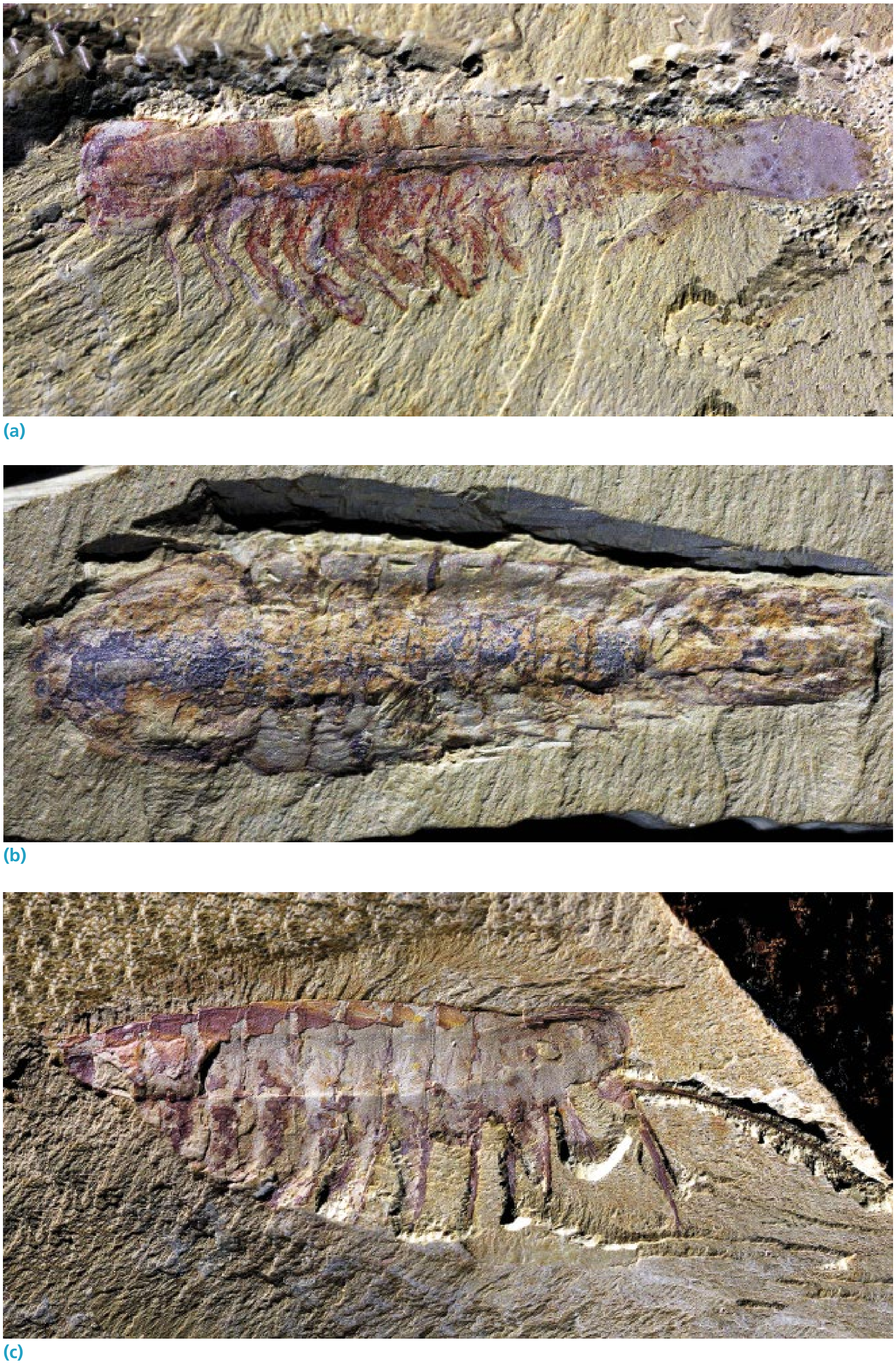


Figure 20.23 ***Alalcomenaeus*** sp. **(a)** YKLP 11076, ×6.9; Ercaicun, Haikou, Kunming. **(b)** YKLP 11075, ×5.9; Mafang, Haikou, Kunming. **(c)** YKLP 11077b, ×3.7; Ercaicun, Haikou, Kunming.

Genus *Leanchoilia* Walcott, 1912

Leanchoilia illecebrosa (Hou, 1987)

Leanchoilia illecebrosa is one of the most common arthropods of the Chengjiang biota. It is known from hundreds of specimens, including juveniles, from several localities. Many specimens show beautifully preserved appendages and other soft parts, in lateral and dorsal aspect, including fine details of the eyes and the gut.

The body is typically about 2–5 cm long. The head has three pairs of biramous appendages behind a frontal great appendage composed of a two-segmented proximal peduncle and four distal podomeres, three of which each bears a long flagellum (Hou & Bergström 1997; Liu Yu *et al*. 2007). Two stalked ventral eyes and two pairs of ventral median eyes have been reported (Schoenemann & Clarkson 2012). The head shield is succeeded by a trunk containing 11 tergites, each with a pair of biramous appendages consisting of slender endopods and two-part, flap-like exopods edged with a splay of long spines. Marginal spines also fringe the flat, elongate, dagger-like telson.

The phylogenetic position of the short great appendage arthropods (megacheirans), such as *Leanchoilia*, is contentious. Some authors have resolved them as stem euarthropods (e.g., Legg *et al*. 2012, 2013; Edgecombe & Legg 2014). Others have claimed an affiliation with the chelicerates *sensu lato* based on the idea that the frontal appendage is a morphological forerunner of a chelifore or chelicera (e.g., Chen Jun-yuan *et al*. 2004; Cotton & Braddy 2003; Haug *et al*. 2012a, 2012b; Liu Yu *et al*. 2014). Exceptionally preserved evidence of the nervous system in Chengjiang material of the closely related genus *Alalcomenaeus* indicates a deutocerebral innervation for the great appendage, thus corroborating its homology with chelicera and supporting an assignment to the chelicerate total group (Tanaka *et al.* 2013).

L. illecebrosa is generally regarded as a probable predator, using the short great appendage as a raptorial limb (e.g., Haug *et al*. 2012a, 2012b). Niche differentiation during the ontogeny of the species was also possibly developed (Liu Yu *et al.* 2014). The well-developed exopod limb branches suggest that it was an efficient swimmer. The downward-oriented stalked eyes, covered by the head shield, have been suggested to indicate a benthic mode of life. The supposed presence of a mud-filled gut in certain specimens has been used to speculate an entirely different interpretation of how *L. illecebrosa* obtained its food, by deposit feeding activities (Bergström 2001; Liu Yu *et al*. 2007), but such occurrences probably reflect the permineralization of (sediment-free) mid-gut glands subsequently replaced by clay minerals (Butterfield 2002).

L. illecebrosa is known only from the Chengjiang biota. The Chengjiang species *Leanchoilia asiatica*, *Dianchia mirabilis*, *Yohoia sinensis*, and *Zhongxinia speciosa* are very likely synonyms of *L. illecebrosa*. Other leanchoiliid species occur in the Cambrian of Canada (e.g., Haug *et al*. 2012a) and Australia (Edgecombe *et al*. 2012).

Key references

Hou 1987a; Hou & Bergström 1997; Hou *et al.* 1999, 2004a; Chen Jun-yuan 2004; Liu Yu *et al.* 2007, 2014; Haug *et al.* 2012a.

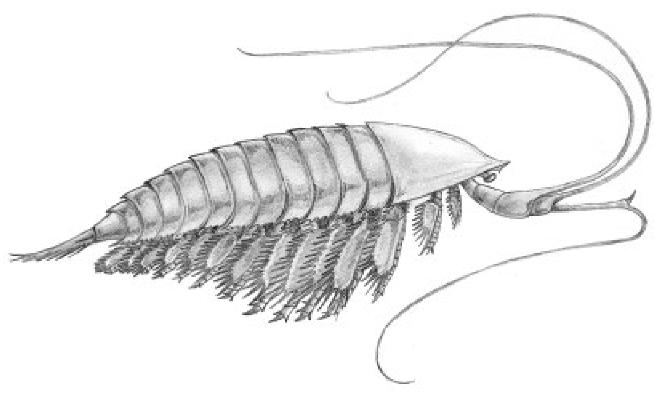


Figure 20.24 Reconstruction of ***Leanchoilia illecebrosa*** (modified from Liu Yu *et al*. 2007).

Figure 20.25 ***Leanchoilia illecebrosa*.** **(a)** NIGPAS 115367, ×4.3; Jianbaobaoshan, near Dapotou, Chengjiang. **(b)** YKLP 13923, ×3.1; Mafang, Haikou, Kunming. **(c)** YKLP 13925, ×5.1; Mafang, Haikou, Kunming.


(a)


(b)


(c)

Genus *Retifacies* Hou, Chen & Lu, 1989

Retifacies abnormalis Hou, Chen & Lu, 1989

This large arthropod is found as more or less complete exoskeletons and as isolated head shields and tail shields. Specimens number several tens of individuals, some of which have appendages and traces of the gut preserved. Inclusive of the antennae and the posterior tail the largest individuals are estimated to be over 55 cm long (Hou & Bergström 1997).

The dorsal surface of the entire exoskeleton has an irregular polygonal mesh-like ornament not seen in any other Chengjiang arthropod. Behind the short, wide somewhat featureless head shield there are 10 overlapping thoracic tergites, each pointed distally. The exoskeleton has a weakly convex, narrow axial region, a large, wide pygidium with a tiny pair of marginal spines, and a long, segmented spine-like tail. Ventrally, near the prominent hypostome, small club-shaped putative eyes are set on simple stalks, projecting beyond which are a pair of long, setiferous, finely segmented antennae. Behind the antennae there are supposedly 18 pairs of biramous appendages (Hou & Bergström 1997), 3 in the head, 10 in the thorax, and 5 in the pygidium. All of the biramous appendages are morphologically similar to each other, differing only in size and spacing. The inner branch of each appendage consists of stout podomeres, each with a multispinose inner edge. The exopod consists of a crescent-shaped proximal flap fringed by a splay of about 20 long, imbricated lamellar setae that are edged with tiny bristles distally.

Initial views on the affinity of *Retifacies abnormalis* drew comparison with helmetiids and naraoiids (Delle Cave & Simonetta 1991; Hou & Bergström 1997). A later assessment of Cambrian arachnomorphs concluded that a naraoiid-*Retifacies* grouping was paraphyletic (Edgecombe & Ramsköld 1999b) and placed *Retifacies* close to the Burgess Shale genera *Sidneyia* and *Emeraldella*. A comprehensive phylogenetic analysis of fossil arthropods (Legg *et al*. 2013; see also Paterson *et al*. 2012) determined that the retifaciids, including the Chengjiang genera *Squamacula* and *Pygmaclypeatus*, were basal stem chelicerates. *Retifacies longispinus* Luo & Hu *in* Luo *et al*., 1997 is a probable junior synonym of *R. abnormalis*.

This large, subovoid-shaped, relatively flat species was possibly nektobenthic. The robust endopod could have functioned for walking and the fan-like outer branch may have partly been used for swimming. The traditional idea that the filamentous exopods of such lamellipedians (Hou & Bergström 1997) were also used as gills has been questioned (Suzuki *et al*. 2008). The serrated inner edge of each endopod could have functioned in predation and scavenging. That sediment infills part of the gut in one specimen may hint at other feeding strategies (Hou & Bergström 1997).

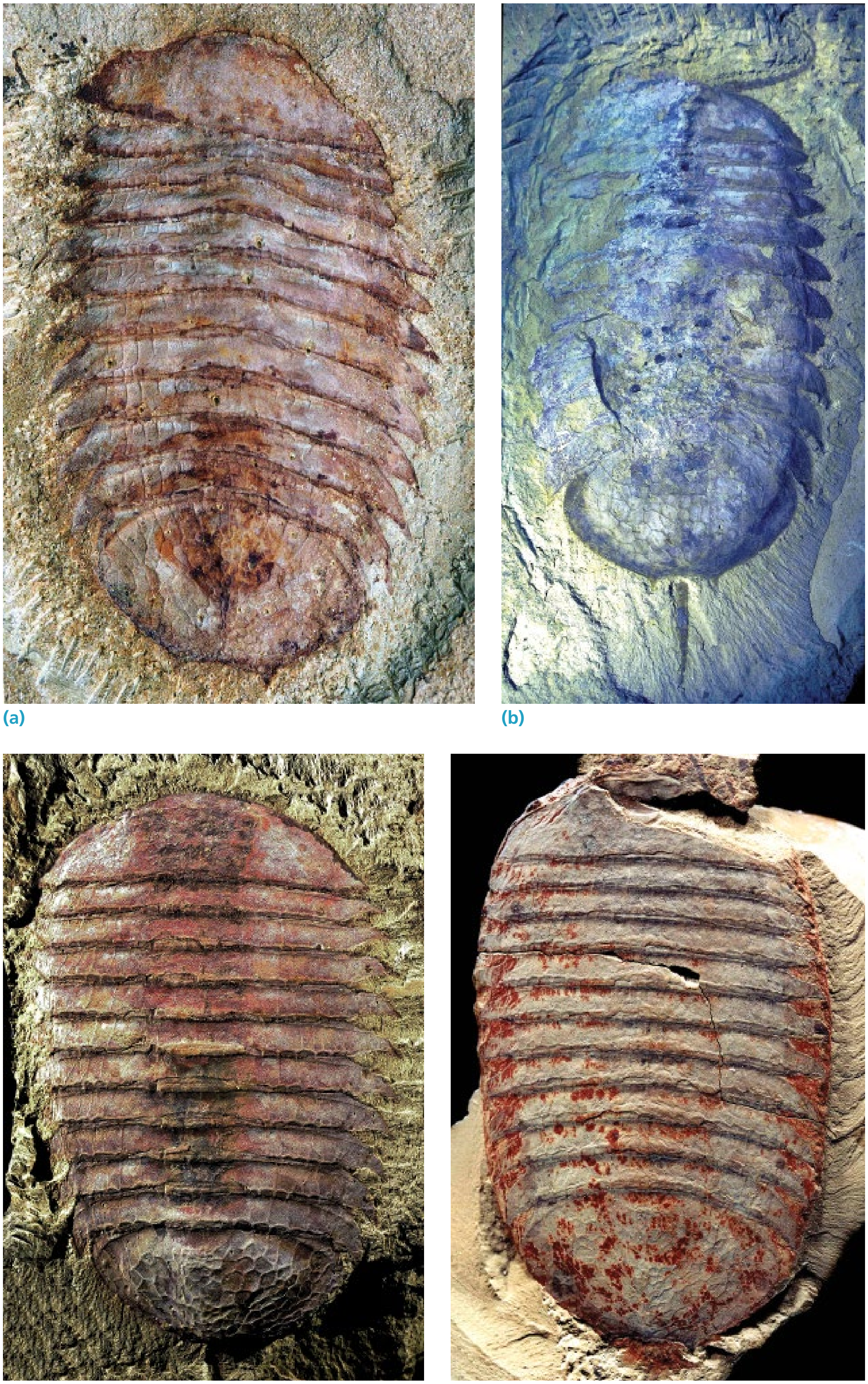
Retifacies is known from only the type species, which is not recorded outside the Chengjiang biota.

Key references

Hou *et al*. 1989, 1999, 2004a; Chen Jun-yuan *et al*. 1996; Hou & Bergström 1997; Chen Jun-yuan & Zhou 1997; Edgecombe & Ramsköld 1999b; Chen Jun-yuan 2004; Legg *et al*. 2013.

Figure 20.26 Reconstruction of ***Retifacies abnormalis*** (modified from Hou & Bergström 1997).

Figure 20.27 ***Retifacies abnormalis*. (a)** YKLP 13926, ×1.7; Ercaicun, Haikou, Kunming. **(b)** YKLP 13927, ×1.1; Ercaicun, Haikou, Kunming. **(c)** RCCBYU 10285, ×1.9; Mafang, Haikou, Kunming. **(d)** NIGPAS 115390, ×1.4; Maotianshan, Chengjiang.



(a) (b) (c) (d)

Genus *Pygmaclypeatus* Zhang, Han & Shu, 2000

Pygmaclypeatus daziensis Zhang, Han & Shu, 2000

This species is quite rare. It was erected on the basis of two dorsoventrally flattened, mostly complete specimens with limited remains of soft parts. A total of some 10 specimens are now known.

The surface of the exoskeleton appears to be smooth. Its width is greater than its length, with maximum width occurring across the wide, short head shield. There is no evidence of eyes. Below the head shield there is a hypostome joined to the inner edge of a probable rostral plate. A narrow doublure extends all around the exoskeleton. There are six, overlapping thoracic tergites. The exoskeleton has a poorly defined axial region and axial furrows are hardly discernible. A large, slightly vaulted tail shield has three weakly defined segmental boundaries in the axial region. Some specimens have the gut preserved in the form of a mud-filled axial structure. Possible traces of gut caeca are also evident. Other remains of soft parts include the antenna, round eyes that project just in front of the head shield, and attachment structures or arthrodial membranes of the limbs.

Pygmaclypeatus shows similarity in overall shape to the Chengjiang retifaciid *Squamacula* Hou & Bergström, 1997 (Zhang Xing-liang *et al*. 2004). Phylogenetic analysis supports a close affinity between *Pygmaclypeatus* and stem chelicerates of the Retifaciida such as *Retifacies* Hou *et al*., 1989 (Paterson *et al*. 2012; Legg *et al*. 2013).

The overall shape and dorsoventrally low elevation of its exoskeleton suggest that *P. daziensis* would be suited to a benthic mode of life. The species is known only from the Haikou region, Kunming.

Key references

Zhang Xing-liang *et al*. 2000; Paterson *et al*. 2012; Legg *et al*. 2013.

Figure 20.28 ***Pygmaclypeatus daziensis***. **(a)** YKLP 13928, ×5.9; Ercaicun, Haikou, Kunming. **(b)** YKLP 13929, ×3.4; Ercaicun, Haikou, Kunming. **(c)** YKLP 13930, ×5.0; Ercaicun, Haikou, Kunming.

(a) (b) (c)

Genus *Squamacula* Hou & Bergström, 1997

Squamacula clypeata Hou & Bergström, 1997

This species of relatively small arthropod was originally recorded on the basis of only two specimens, but at least six subsequently discovered specimens now enable a fuller assessment of its morphology (Zhang Xing-liang *et al.* 2004). In addition to the somewhat featureless dorsal exoskeleton, appendages and parts of the gut are also preserved.

The exoskeleton is weakly vaulted overall. It ranges up to 2.2 cm in length and its width is slightly less. The head shield is wide and short, the thorax comprises 10 overlapping tergites each of which is pointed distally and covers a somite, and the pygidium is tiny and subovoid in dorsal aspect. There is no discrete axial region to the exoskeleton and there is no evidence of eyes. The head shield has an enormous doublure, which has been interpreted by some authors to function in helping the animal to move through sediment. A pair of multi-segmented, uniramous appendages occur on the head, and each thoracic somite carries a pair of biramous limbs on a spinose limb base. The distal-most of seven podomeres comprising the endopod bears distal spines. Setae border the flap-like exopods. Tail shield appendages are also preserved, and are shaped like the thoracic appendages. The gut is observed as a sediment-filled axial tract, and there are also laterally adjacent traces of midgut glands.

Based on morphological similarities with its Chengjiang associate *Retifacies abnormalis*, *S. clypeata* was erected as a putative retifaciid (Hou & Bergström 1997). Recent analysis (Legg *et al.* 2013) confirms that assignment and resolves the Retifaciida as basal within the stem chelicerates. Its nearest relative is the only other known *Squamacula* species, *S. buckorum* from the Early Cambrian Emu Bay Shale Lagerstätte of Australia (Paterson *et al.* 2012).

S. clypeata has a dorsoventrally flat morphology, and possibly hunted and scavenged near the sea bed (Zhang Xing-liang *et al.* 2004). Its spinose endopods could be used for walking and comminuting food, and its filamentous exopods would appear to function for swimming and possibly respiration.

S. clypeata is known only from Yunnan Province, at localities near Haikou and at Maotianshan.

Key references

Hou & Bergström 1997; Hou *et al.* 1999, 2004a; Zhang Xing-liang *et al.* 2004; Paterson *et al.* 2012; Legg *et al.* 2013.

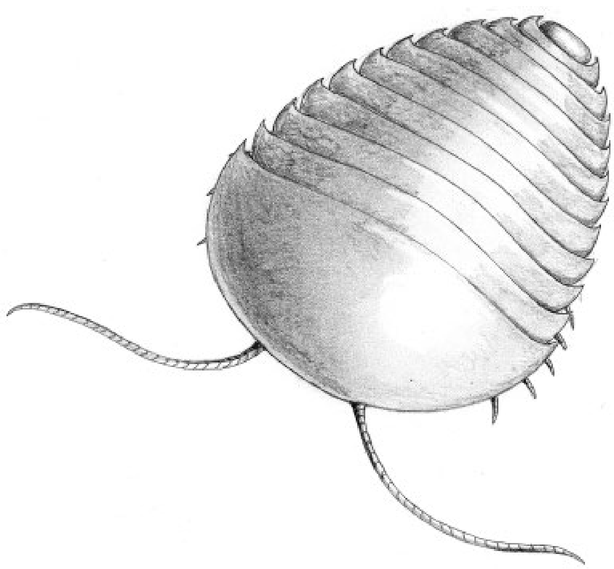
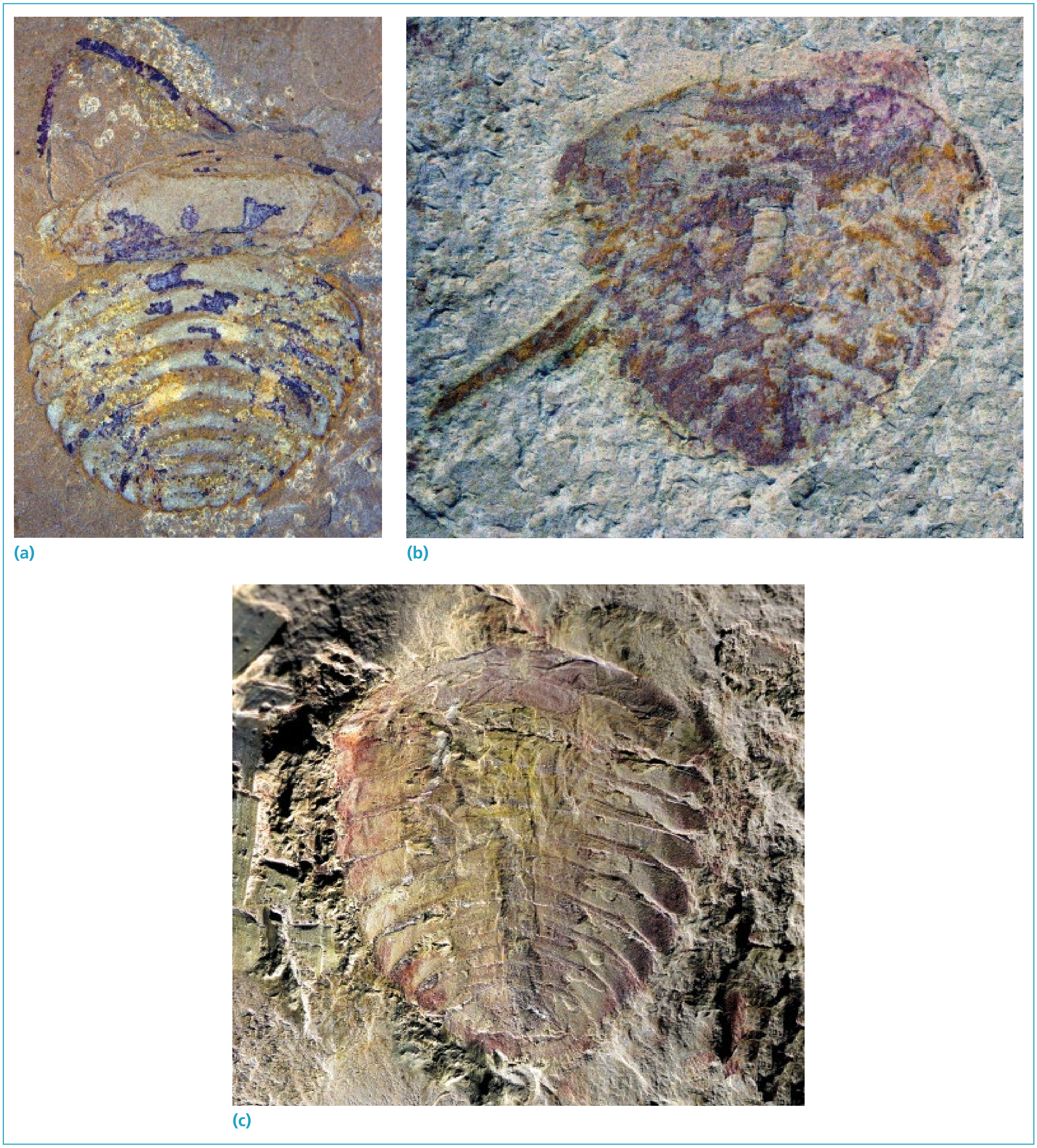


Figure 20.29 Reconstruction of ***Squamacula clypeata*** (modified from Hou *et al.* 2004a).

Figure 20.30 ***Squamacula clypeata*. (a)** NIGPAS 115393, ×6.5; Maotianshan, Chengjiang. **(b)** NIGPAS 11549, ×9.4; Xiaolantian, Chengjiang. **(c)** RCCBYU 10286, ×4.3; Xiaolantian, Chengjiang.



(a) (b) (c)

Genus *Urokodia* Hou, Chen & Lu, 1989

Urokodia aequalis Hou, Chen & Lu, 1989

Urokodia aequalis is known from about 20 specimens, some of which are well preserved. The exoskeleton is up to 4 cm long.

The elongate exoskeleton consists of head and tail shields with a long trunk of about 14 essentially similar tergites. The head shield bears a pair of anterior spines and three pairs of lateral spines, all of which project forward. The trunk tergites extend into short spines. The tail shield is approximately equal in size to the head shield. Based on one complete specimen and several isolated tergites the tail shield was originally considered to be morphologically similar to the head shield both in the number and form of the (posteriorly directed) spines. A subsequently found, complete *Urokodia* specimen from Anning, Yunnan Province (Zhang Xing-liang *et al*. 2002), was assigned to *U. aequalis*. However, it differs in having two large paired spines and many small spines on the tail, and therefore it is not certain that it represents the same species as *U. aequalis*. The only known soft part of *Urokodia* is a possible stout antenna.

The affinity of *Urokodia* is problematical because knowledge of its ventral appendages and other soft parts is lacking. It shows general similarity with the Burgess Shale *Mollisonia* Walcott, 1912. That comparison is supported by phylogenetic analysis that resolves both genera as closely allied trilobitomorphs, a clade of stem chelicerates (Legg *et al*. 2013).

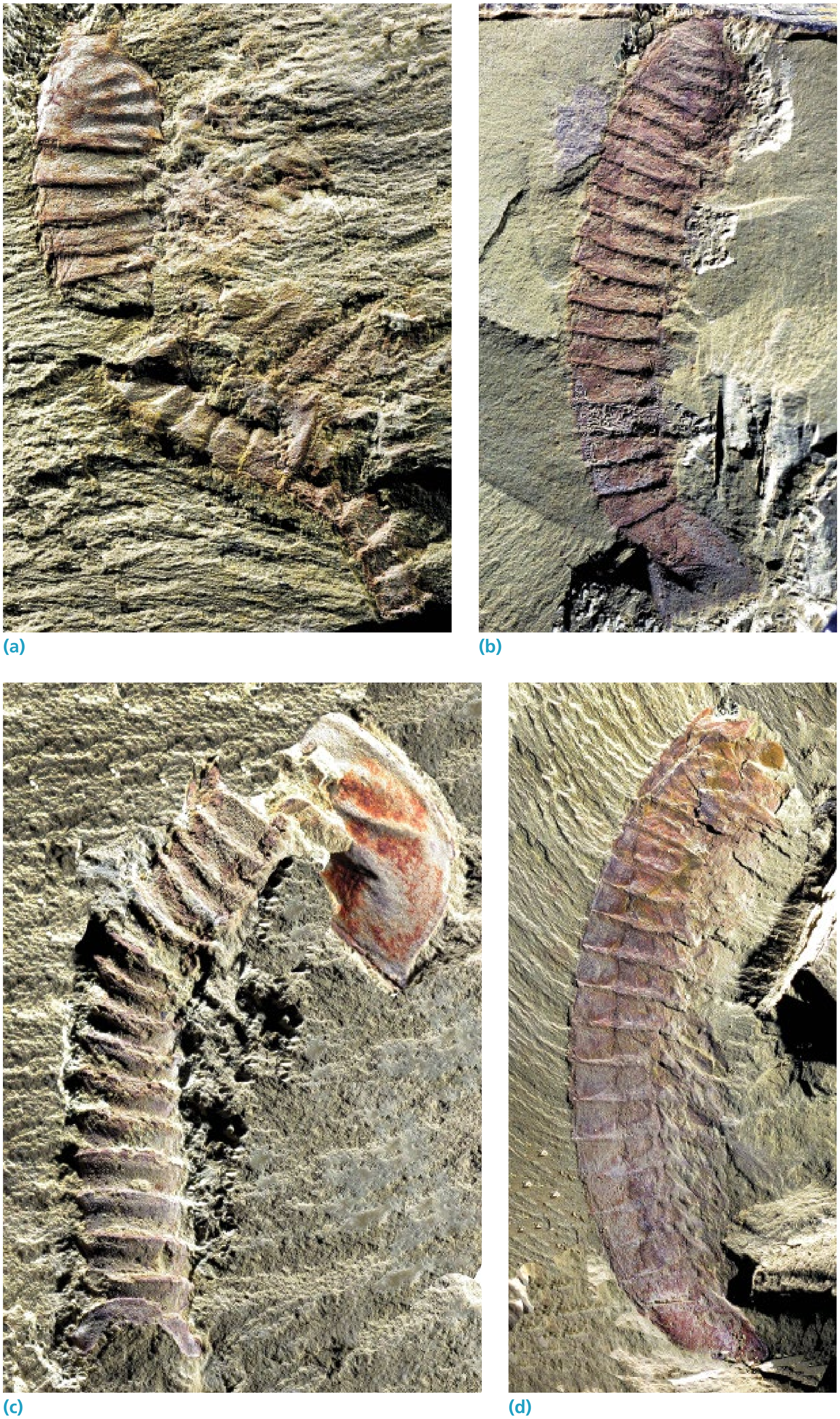
The overall form of its exoskeleton indicates that *U. aequalis* probably lived on the sea floor. Since its appendages are unknown, so too is its mode of feeding.

The species is only known from the Chengjiang biota and occurs in the Chengjiang and possibly Haikou areas.

Key references

Hou *et al*. 1989, 1999, 2004a; Chen Jun-yuan *et al*. 1996; 1999, Zhang Xing-liang *et al*. 2002.

Figure 20.31 ***Urokodia aequalis***. **(a)** YKLP 13931, ×3.6; Mafang, Haikou, Kunming. **(b)** YKLP 13933, ×2.6; Ercaicun, Haikou, Kunming. **(c)** YKLP 13932, ×5.1; Ercaicun, Haikou, Kunming. **(d)** YKLP 13934, ×4.1; Ercaicun, Haikou, Kunming.


(a) (b) (c) (d)

Genus *Sinoburius* Hou, Ramsköld & Bergström, 1991

Sinoburius lunaris Hou, Ramsköld & Bergström, 1991

Sinoburius lunaris is the only known species of this genus, and specimens are rare. The exoskeleton lacked mineralization. Its overall morphology, with a head shield, thorax, and tail shield, and with clear axial and pleural regions, is reminiscent of trilobites.

Adults are small, the largest being about 1.2 cm long. *S. lunaris* has a broad, overall crescent-shaped head shield that is extended posteriorly into genal spines that flank the trunk. It possesses a pair of large, stalked, oval-shaped compound eyes, which are accommodated in exoskeleton bulges mediolaterally on the head shield. Opinions differ about the possible presence of a fissure extending (as in *Xandarella*) from each eye to the lateral margin of the head shield in *S. lunaris* (Chen Jun-yuan *et al.* 1996; Hou & Bergström 1997; Edgecombe & Ramsköld 1999b). Behind putative antennae there are at least four pairs of long, laterally directed biramous appendages in the head.

The trunk comprises seven tergites, and posteriorly there is a single well-defined tail shield bearing two lateral spines on each side of its margin, and terminated by a long axial spine. A single pair of biramous appendages is associated with each thoracic tergite (Hou & Bergström 1997), whilst the tail shield may cover as many as 10 segments, the first six bearing biramous appendages.

Several authors have considered *Sinoburius* to be closely related to the Chengjiang trilobitomorph xandarellids *Xandarella* and *Cindarella* (Hou & Bergström 1997; Ramsköld *et al.* 1997; Edgecombe & Ramsköld 1999b; Paterson *et al.* 2010, 2012; Legg *et al.* 2013), though this opinion is not held by Stein *et al.* (2013), who, amongst other factors, considered the possession of a head shield extended into genal spines to be an important difference. In contrast to *Xandarella* and *Cindarella,* in *Sinoburius* there is only one pair of appendages in each trunk tergite.

Sinoburius has been interpreted as a benthic deposit feeder (Hou & Bergström 1997). By analogy to *Cindarella* (see Zhao Fang-chen *et al.* 2013), the advanced visual system of *Sinoburius* also suggests an animal able to find food either by scavenging or predation in low light conditions.

Known occurrences of *S. lunaris* are restricted to the Chengjiang biota.

Key references

Hou *et al.* 1991, 1999, 2004a; Chen Jun-yuan *et al.* 1996; Chen Jun-yuan & Zhou 1997; Ramsköld *et al.* 1997; Hou & Bergström 1997; Edgecombe & Ramsköld 1999b.

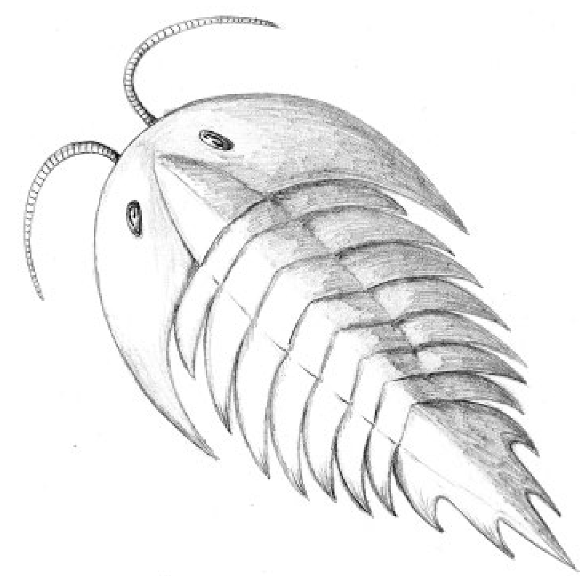
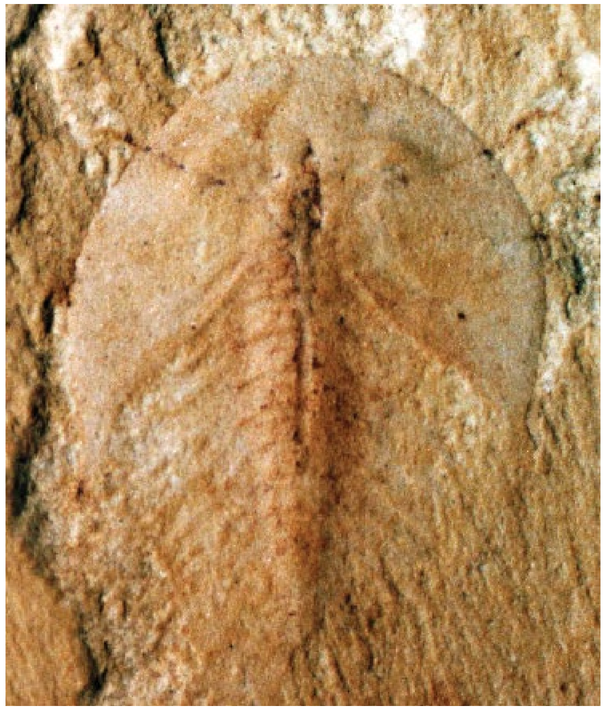


Figure 20.32 Reconstruction of ***Sinoburius lunaris*** (modified from Hou *et al.* 2004a).

Figure 20.33 ***Sinoburius lunaris***. **(a)** NIGPAS 115287, ×9.7; Maotianshan, Chengjiang. **(b)** NIGPAS 115288, ×15.4; Maotianshan, Chengjiang.

(a)



(b)

Genus *Acanthomeridion* Hou, Chen & Lu, 1989

Acanthomeridion serratum Hou, Chen & Lu, 1989

This is a rare species, originally described from eight specimens, all of which are dorsoventrally flattened.

Acanthomeridion serratum is up to 3.5 cm long and almost parallel-sided. Its head shield has a rounded anterior margin. The trunk has 11 smooth, well-defined tergites that extend laterally to form posteriorly directed spines that are especially long in the posterior tergites. The posterior-most tergite has a marked medial furrow housing a long, narrow spine. The appendages and soft parts of the animal are unknown.

Because of the lack of information on its appendages, the affinity of this species is not clear, though at least one phylogenetic analysis has suggested a relationship with the petalopleurans and xandarellids (Legg *et al.* 2013). A Family and Order was established on the basis of the monotypic *Acanthomeridion* (Hou & Bergström 1997).

The shape of its body indicates that *A. serratum* probably lived on the sea floor. The lack of knowledge of its appendages makes it difficult to interpret its mode of feeding.

Acanthomeridion is unknown outside the Chengjiang biota.

Key references

Hou *et al.* 1989, 1999, 2004a; Hou & Bergström 1997; Legg *et al.* 2013.

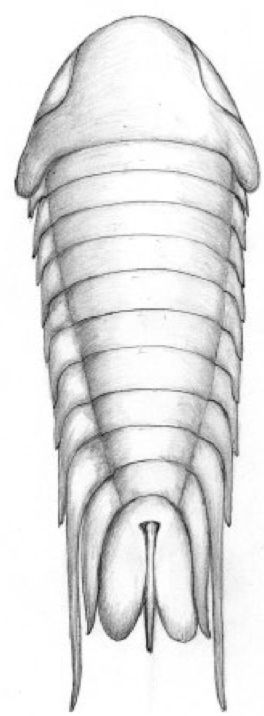


Figure 20.34 Reconstruction of ***Acanthomeridion serratum*** (based on Hou & Bergström 1997).

Figure 20.35 ***Acanthomeridion serratum***. **(a)** RCCBYU 10290, ×3.5; Maotianshan, Chengjiang. **(b)** YKLP 11118, ×4.1; Mafang, Haikou, Kunming.

(a) (b)

Genus *Cindarella* Chen, Ramsköld, Edgecombe & Zhou *in* Chen *et al*. 1996

Cindarella eucalla Chen, Ramsköld, Edgecombe & Zhou *in* Chen *et al*. 1996

Fossils of *Cindarella eucalla* are commonly preserved dorsoventrally flattened. The exoskeleton lacks mineralization and is up to 13 cm long excluding appendages. The Chengjiang species *Almenia spinosa* Hou & Bergström, 1997 may be the same species as *C. eucalla* (Edgecombe & Ramsköld 1999b).

As in the closely related Chengjiang genus *Xandarella* Hou *et al*., 1991, *C. eucalla* has a large semi-elliptical head shield. In *Cindarella* this head shield belongs to only the first five (antennal plus four post-antennal) segments, and its posterior part is extended as a carapace-like fold to cover an additional six anterior trunk segments (Ramsköld *et al*. 1997). The head displays a pair of long antennae that protrude beyond the anterior of the head shield. Large, stalked ventral eyes originate near the front of the lateral and anterior margins of the hypostome and also extend latero-anteriorly beyond the front of the head shield: each compound eye consists of over 2000 lenses (Zhao Fang-chen *et al*. 2013).

The trunk has 21 to 23 tergites; a median ridge extends into the terminal spine on the posterior three trunk tergites. The gut can be traced from near the hypostome to close to the posterior margin of the terminal tergite.

C. eucalla shows a decoupling of tergites and segments in the trunk (Ramsköld *et al*. 1997). The anterior six trunk tergites correspond to single segments and, like the four post-antennal head segments, each bears a pair of biramous appendages. Posterior of trunk tergite 6, each tergite covers more than one appendage pair, with a lack of correspondence between tergite boundaries and segment boundaries. The number of appendages per tergite increases progressively posteriorly.

Cindarella and *Xandarella* formed the basis of the Xandarellida (Chen Jun-yuan *et al*. 1996; Hou & Bergström 1997; Ramsköld *et al*. 1997), a group of trilobitimorphs (Legg *et al*. 2013). The two genera resolve as sister taxa in phylogenetic analyses (Paterson *et al*. 2010; Stein *et al*. 2013; Legg *et al*. 2013). *Cindarella* differs from *Xandarella* in the number of its head segments and in having eyes that extend laterally from under the margin of the head shield.

The advanced visual system of *C. eucalla* (Zhao Fang-chen *et al*. 2013) indicates an animal able to find food either by scavenging or predation in low light conditions. With its refined vision, *C. eucalla* would also have been able to avoid predators.

C. eucalla is known only from the Chengjiang biota.

Key references

Chen Jun-yuan *et al*. 1996; Chen Jun-yuan & Zhou 1997; Ramsköld *et al*. 1997; Edgecombe & Ramsköld 1999b; Hou *et al*. 2004a; Zhao Fang-chen *et al*. 2013.

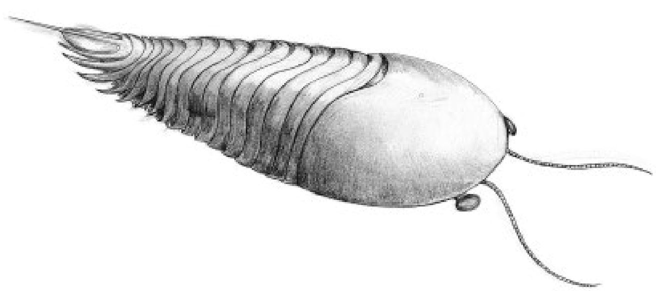
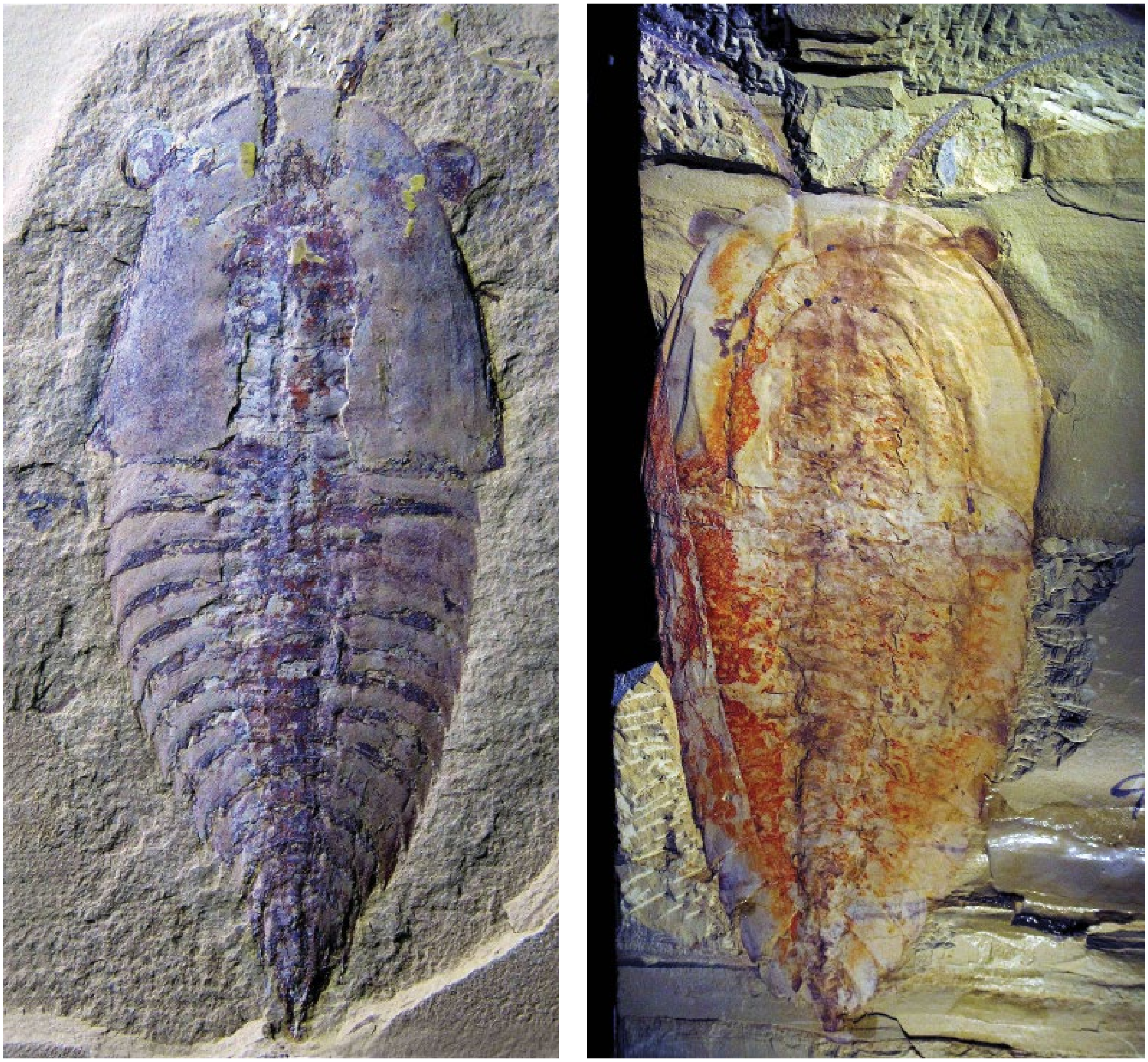


Figure 20.36 Reconstruction of ***Cindarella eucalla*** (modified from Hou *et al*. 2004a).

Figure 20.37 ***Cindarella eucalla***. **(a)** YKLP 13935, ×2.6; Jianshan, Haikou, Kunming. **(b)** RCCBYU 10288, ×1.1; Mafang, Haikou, Kunming.



(a) **(b)**

Genus *Xandarella* Hou, Ramsköld & Bergström, 1991

Xandarella spectaculum Hou, Ramsköld & Bergström, 1991

The exoskeleton of *Xandarella spectaculum* was unmineralized and is typically preserved dorsoventrally flattened. Complete specimens are greater than 5 cm long.

X. spectaculum possesses a large semi-elliptical head shield that is extended posteriorly to overlap the anterior part of the trunk, where there is a small axial tergite. The head has six pairs of biramous appendages behind the long multi-annulate antennae that protrude beyond the anterior end of the head shield. Paired compound eyes are stalked, based ventrally, and are considered morphologically similar to the eyes of *Cindarella* and *Sinoburius* (Edgecombe & Ramsköld 1999b). The eyes are configured to see through a round, raised exoskeleton bulge in the dorsal part of the exoskeleton. A fissure extends from each eye to the lateral margin of the head shield; this feature is reminiscent of the dorsal facial suture in trilobites.

Behind the small axial tergite are a further 11 tergites, the trunk being terminated by an axial spine arising from the terminal tergite. As with *Cindarella*, the anterior trunk tergites, including the small axial tergite, are associated with a single biramous appendage pair, but posterior from trunk tergite 7 there is a decoupling of this pattern, with tergite 8 covering two pairs of appendages, tergite 9 covering four pairs of appendages, and tergite 10 covering five appendages; possibly as many as 12 pairs of appendages are covered by the terminal tergite (Hou & Bergström 1997). The biramous appendages consist of an endopod with many podomeres, some bearing small spines. Lamellar setae are attached to the distal podomeres of the exopods.

It was considered that the four posterior-most tergites of *X. spectaculum* define a tail shield (Hou & Bergström 1997), an interpretation adopted by Paterson *et al.* (2010) in their phylogenetic analysis of artiopodan arthropods. Some phylogenetic analyses resolve xandarellids (*Xandarella* and *Cindarella* Chen *et al.* 1996) and *Sinoburius* Hou *et al.*, 1991 – three Chengjiang genera – as closely related taxa (Hou & Bergström 1997; Ramsköld *et al.* 1997; Edgecombe & Ramsköld 1999b; Paterson *et al.* 2010; Legg *et al.* 2013), though this is not universally accepted (see Stein *et al.* 2013). Xandarellids resolve within the Trilobitomorpha *sensu stricto* in the analysis of Legg *et al.* (2013).

X. *spectaculum* has been interpreted as a deposit-feeding animal (Hou & Bergström 1997). By analogy to *Cindarella* (see Zhao Fang-chen *et al.* 2013), the advanced visual system of *X. spectaculum* suggests an animal able to find food either by scavenging or predation in low light conditions.

X. spectaculum is known only from lower Cambrian strata of Yunnan Province.

Key references

Hou *et al.* 1991, 1999, 2004a; Chen Jun-yuan & Zhou 1997; Hou & Bergström 1997; Ramsköld *et al.* 1997; Bergström & Hou 1998; Edgecombe & Ramsköld 1999b.

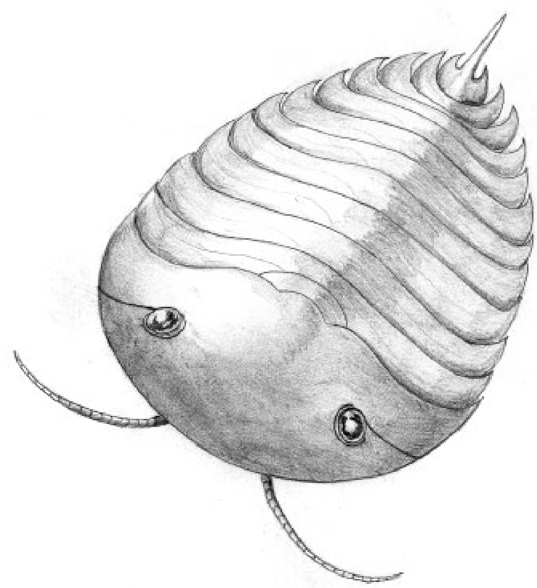


Figure 20.38 Reconstruction of ***Xanderella spectaculum*** (modified from Hou *et al.* 2004a).

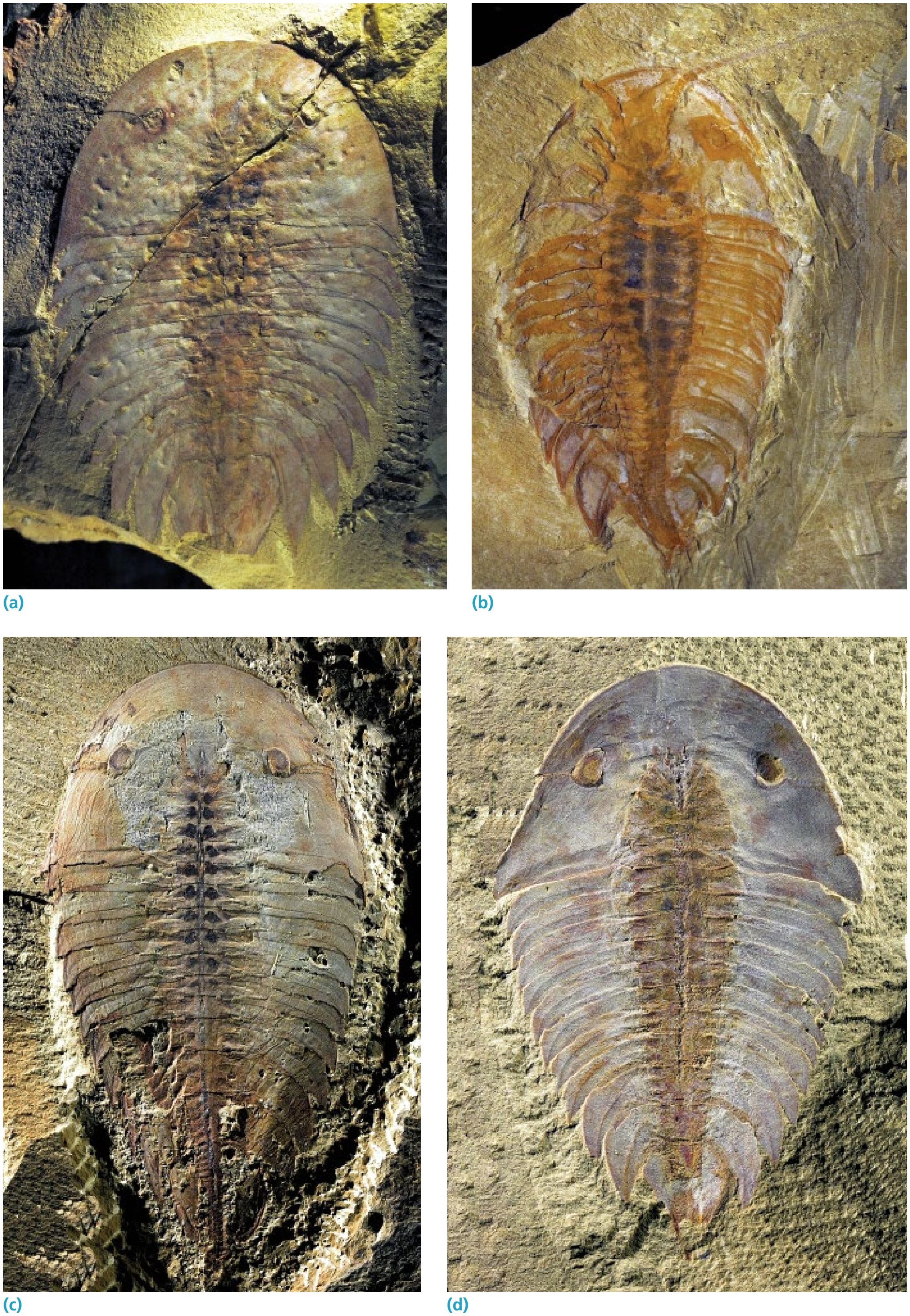


Figure 20.39 ***Xanderella spectaculum***. **(a)** YKLP 13936, *circa* ×2.1; Mafang, Haikou, Kunming. **(b)** YKLP 13937, ×1.7; Xiaolantian, Chengjiang. **(c)** YKLP 13938, ×2.2; Mafang, Haikou, Kunming. **(d)** YKLP 13939, ×3.0; Ercaicun, Haikou, Kunming.

Genus *Skioldia* Hou & Bergström, 1997

Skioldia aldna Hou & Bergström, 1997

Skioldia aldna is a rare species known from just a few specimens, the largest of which are over 10 cm long. The exoskeleton appears to be weakly mineralized at best.

The dorsal exoskeleton is fused into a single, broadly suboval-shaped shield much of which is bordered by tiny spines. It is mostly featureless apart from a weakly defined axis and furrows that demarcate some 13 segments that meet edge-to-edge and are lost at the margin. The middle (thoracic) part of the exoskeleton has about nine segments, whose boundaries are longer than those on the putative head and tail regions. A pair of eyes occurs close to the anterior margin, adjacent to a well-developed axial sclerite (rostral plate) behind which there is a putative hypostome. The multisegmented antenna curves back under the exoskeleton. It is succeeded by paired biramous appendages under each segment, as seen impressed on the dorsal surface of the exoskeleton. Long lamellar setae are discernible on the presumed exopods, but further details of appendage morphology are not yet documented.

This species of Trilobitomorpha *sensu stricto* has closest affinity with a group of Cambrian genera (the clade Conciliterga) that includes *Saperion*, *Kuamaia*, and *Haifengella* from Chengjiang, *Helmetia* and *Tegopelte* from British Columbia, and *Australimicola* from Australia (Hou & Bergström 1997; Edgecombe & Ramsköld 1999b; Paterson *et al*. 2013; Legg *et al*. 2013; Zhao Fang-chen *et al*. 2014b). The boundaries of the anterior trunk tergites are reflexed anteriorly in these genera. Elements of the dorsal exoskeleton of *Skioldia* appear to be more fused together than in *Kuamaia*, but less merged than in *Saperion*. The exoskeleton of *Skioldia* and *Kuamaia* differ in shape, and the marginal spines in *Skioldia* are much smaller and the tergites are more indistinct.

S. aldna is dorsoventrally flat, and may have been nektobenthic, with a mode of life much the same as species of *Saperion* and *Kuamaia*.

Skioldia is known only from one species and the Chengjiang biota.

Key references

Hou & Bergström 1997; Edgecombe & Ramsköld 1999b; Hou *et al*. 1999, 2004a; Legg *et al*. 2013.

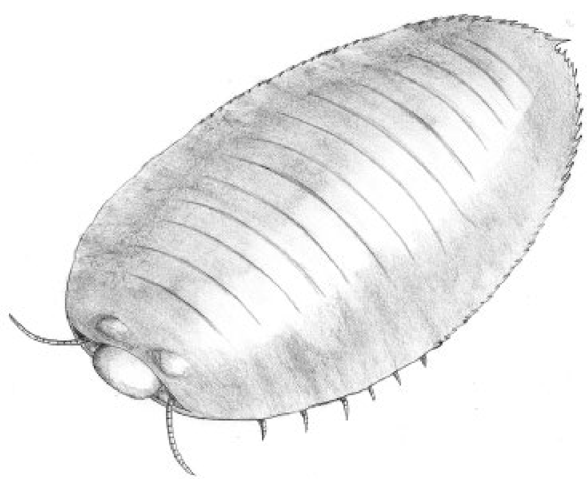


Figure 20.40 Reconstruction of ***Skioldia aldna*** (modified from Hou *et al*. 2004a). The morphology of the endopods is hypothetical.

Figure 20.41 ***Skioldia aldna***. RCCBYU 10287, ×2.3; Maotianshan, Chengjiang.

Genus *Saperion* Hou, Ramsköld & Bergström, 1991

Saperion glumaceum Hou, Ramsköld & Bergström, 1991

Saperion glumaceum is rare, known from only about four specimens. The exoskeletons range to about 12 cm long and are thin and have little relief.

The exoskeleton is fairly plain, elongate, gently convex axially, and slightly turned up marginally, with rounded margins to the head and tail. The effacement of segmental boundaries, producing what seems to be a single fused shield, is a feature also seen in related genera. Remnants of tergites are indicated in the central regions of the putative thorax and tail, but become weaker laterally and are lost at the margins of the exoskeleton. The head is smooth and lacks segmentation. Anteriorly in the head there is an anterior sclerite (rostral plate) and a hypostome that are flanked by a pair of antennae that recline backwards and lie under the shield (Edgecombe & Ramsköld 1999b). Weak exoskeletal swellings mark the position of ventral eyes, which are interpreted as homologous to the lateral facetted eyes in other arthropods. The biramous appendages of the trunk have a well-developed basipod from which stems the endopod (walking branch) consisting of at least six simple podomeres and an exopod consisting of two lobes with many long lamellar setae on the proximal lobe. Setae of similar proportions occur in the head and perhaps also the pygidium.

Analysis resolves *Saperion* as a member of Conciliterga (within Trilobitomorpha *sensu stricto*, a clade of Cambrian stem chelicerates) (Hou & Bergström 1997; Edgecombe & Ramsköld 1999b; Paterson *et al.* 2012; Legg *et al.* 2013; Zhao Fang-chen *et al.* 2014b). Other representatives of Conciliterga include *Kuamaia*, *Skioldia*, and *Haifengella* from Chengjiang, *Helmetia* and *Tegopelte* from British Columbia, and *Australimicola* from Australia. In these genera the boundaries of the anterior trunk segments are reflexed anteriorly. *Saperion* has a more elongate outline than both *Kuamaia* and *Skioldia* and it lacks marginal spines.

As in species of *Kuamaia* and *Skioldia,* the flat exoskeleton of *S. glumaceum* may be an adaptation for living on the sea bottom. One view is that it was a highly flexible animal, capable of enrollment along its longitudinal axis.

S. glumaceum is the only known species of *Saperion.* It has not been recorded outside the Chengjiang biota.

Key references

Hou *et al.* 1991, 1999, 2004a; Ramsköld *et al.* 1996; Chen Jun-yuan *et al.* 1996; Hou & Bergström 1997; Chen Jun-yuan & Zhou 1997, Edgecombe & Ramsköld 1999b; Chen Jun-yuan 2004; Paterson *et al.* 2012; Legg *et al.* 2013.

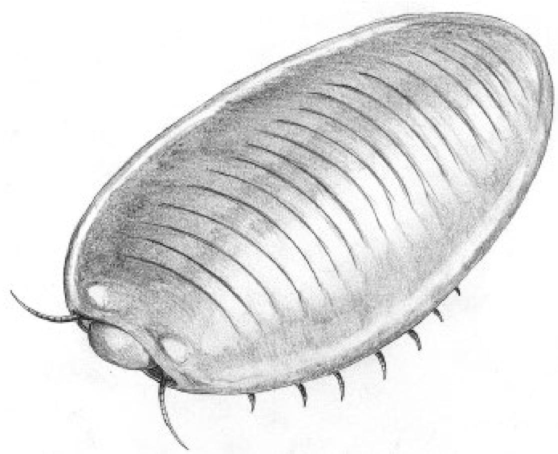
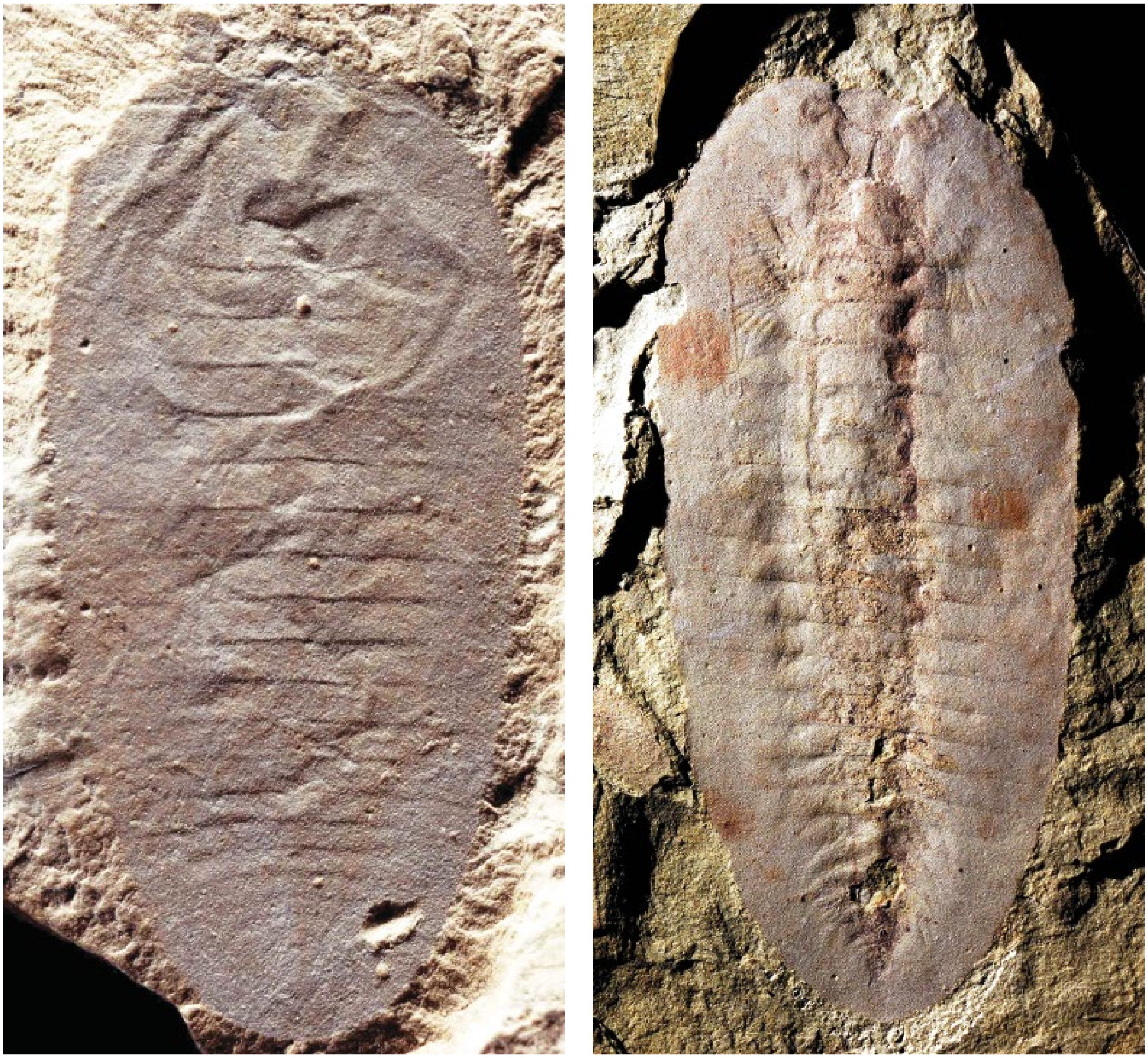


Figure 20.42 Reconstruction of ***Saperion glumaceum*** (modified from Hou *et al.* 2004a).

Figure 20.43 ***Saperion glumaceum*. (a)** NIGPAS 115289, ×6.0; Jianbaobaoshan, near Dapotou, Chengjiang. **(b)** YKLP 13940, ×5.1; Mafang, Haikou, Kunming.



(a) (b)

Genus *Kuamaia* Hou, 1987

Kuamaia lata Hou, 1987

The exoskeleton of *Kuamaia lata* is typically preserved as a thin, white or purplish-red film and appears to be unmineralized. Many tens of specimens are known, the largest exoskeleton being at least 10 cm long excluding appendages.

The broadly oval-shaped dorsal exoskeleton slopes gently from a weakly convex axially region. The head shield has a prominent sclerite ventrally, the thorax consists of seven tergites that overlap axially, and the tail shield bears an axial spine and two pairs of lateral spines. Parts of the exoskeleton are fused, though opinions vary on features affected and the extent of the fusion (see Hou & Bergström 1997; Edgecombe & Ramsköld 1999b). Tear-shaped eyes originate ventrally and are evident on the head shield as a pair of low-relief anterior swellings. The tiny segments of the antennae bear long setae. The head shield may, in addition, bear at least three pairs of biramous limbs. A pair of biramous limbs occurs on each thoracic tergite and possibly also on the five(?) segments in the tail. The basal part of the limb is large and spinose. The endopod consists of simple spinose podomeres. The exopod has a petal-shaped, lobe-like proximal element with long lamellar setae extending from its outer edge and a broad bipartite element along the inner edge. The gut is identified as a narrow dark band.

Conventional consensus identifies the near relatives of *Kuamaia* as the Chengjiang genera *Saparion* and *Skioldia* and *Helmetia* and *Tegopelte* from the Burgess Shale (Hou & Bergström 1997; Edgecombe & Ramsköld 1999b). This view has been endorsed in recent analyses that have added *Australimicola* from the Cambrian of Australia and *Haifengella* from Chengjiang to this list of Conciliterga (Trilobitomorpha *sensu stricto*) arthropods, a clade characterized by having the boundaries of the anterior trunk tergites reflexed anteriorly (Paterson *et al.* 2012; Legg *et al.* 2013; Zhao Fang-chen *et al.* 2014b). The monospecific *Rhombicalvaria* from Chengjiang is possibly a synonym of *Kuamaia*.

The dorsoventrally flat exoskeleton of *K. lata* is in keeping with a possible benthic mode of life. The spiny inner edge of its legs may have functioned in tearing food.

K. lata is unknown outside the Chengjiang Lagerstätte, which also has yielded a rare congeneric species, *Kuamaia muricata* Hou & Bergström, 1997.

Key references

Hou 1987b; Chen Jun-yuan *et al.* 1996; Hou & Bergström 1997; Chen Jun-yuan & Zhou 1997; Bergström & Hou 1998; Edgecombe & Ramsköld 1999b; Hou *et al.* 1999, 2004a; Chen Jun-yuan 2004; Paterson *et al.* 2012; Legg *et al.* 2013.

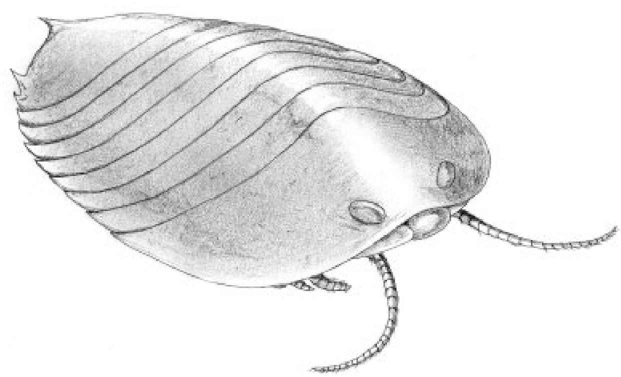
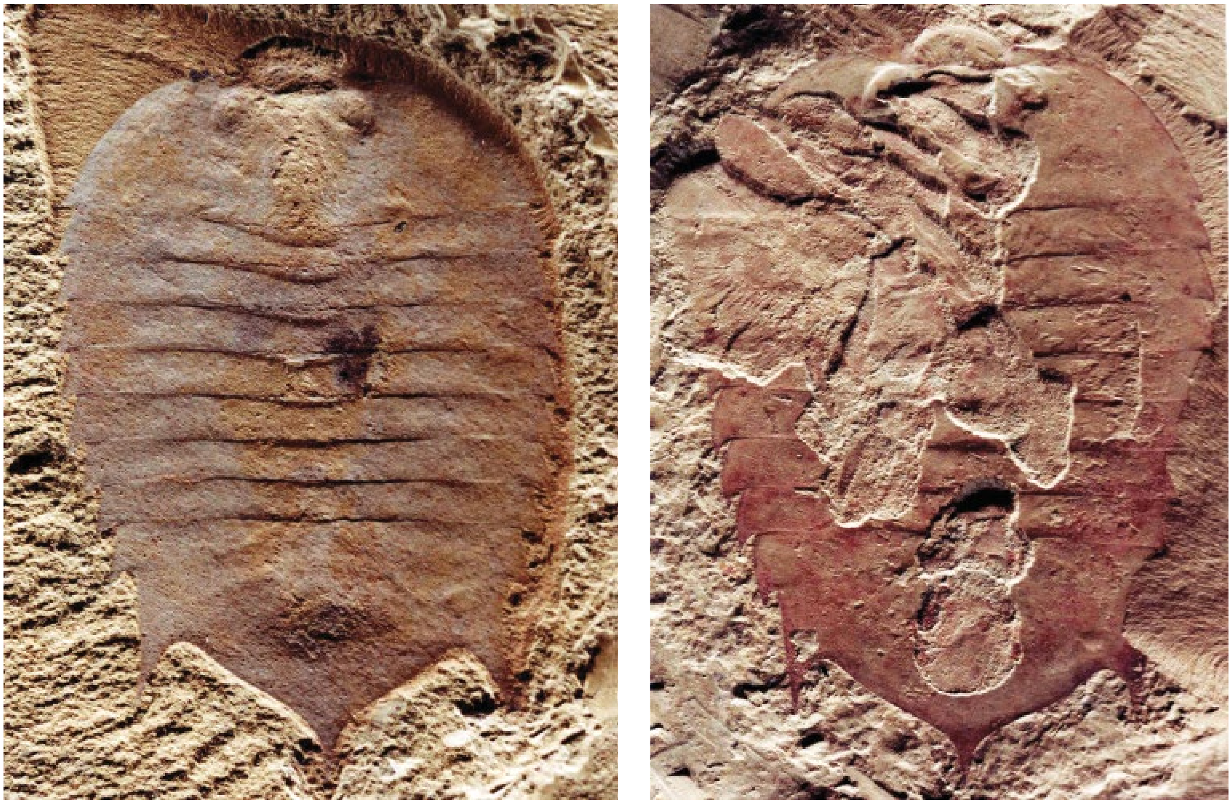


Figure 20.44 Reconstruction of ***Kuamaia lata*** (modified from Hou & Bergström 1997).

Figure 20.45 ***Kuamaia lata***. **(a)** NIGPAS 115400, ×2.5; Maotianshan, Chengjiang. **(b)** NIGPAS 115318, ×2.1; Maotianshan, Chengjiang.



(a) (b)

Genus *Naraoia* Walcott, 1912

Naraoia spinosa Zhang & Hou, 1985

Naraoia spinosa is known from at least 1500 specimens. Dimorphism has been identified in the most recent study of the species (Zhang Xing-liang *et al.* 2007), on which this description is based. 'Morph A' bears marginal spines: a pair of genal spines in the head shield, and 10 or 11 pairs of lateral spines and one pair of posterior spines in the trunk shield; 'morph B' lacks marginal spines. Both morphs carry identical appendages and digestive tract. All specimens assigned to the species have a maximum length of about 5 cm, when the head shield is about 3 cm long, and the trunk shield about 2 cm.

Paired antennae, often directed more laterally than anteriorly in front of the head shield, consist of up to at least 30 articles. A hypostome with a medial and two lateral bulges has been recognized. Post-antennal appendages are biramous, of which there are possibly four pairs under the head shield and 14 pairs in the trunk shield. Each limb comprises a basis, endopod, and exopod. A distally expanding, flap-like exopod shows a convex outer margin that bears long, closely spaced lamellae. Seven podomeres, including a terminal claw, make up the endopod; the more proximal bear endites with spines on their inner margins. The gut extends from the center of the head shield to the posterior margin of the trunk shield; two anterolaterally directed minor ducts come off it anteriorly. The anterior-most diverticula, originating immediately posterior to the minor ducts, each divides into antero- and postero-lateral branches that ramify extensively into the cheeks. The succeeding diverticula are more simple and confined to the axial region; four are in the head region, and six in anterior part of (or the whole of; Vannier & Chen 2002) the trunk region.

Naraoiids are characterized in part by an unmineralized cuticle, and they are now widely regarded as nektaspidid trilobitomorphs that are very closely related to trilobites, rather than being considered to be trilobites (Hou & Bergström 1997; Wills 1998; Edgecombe & Ramsköld 1999b; Paterson *et al.* 2010; Ortega-Hernández *et al.* 2013; Legg *et al.* 2013).

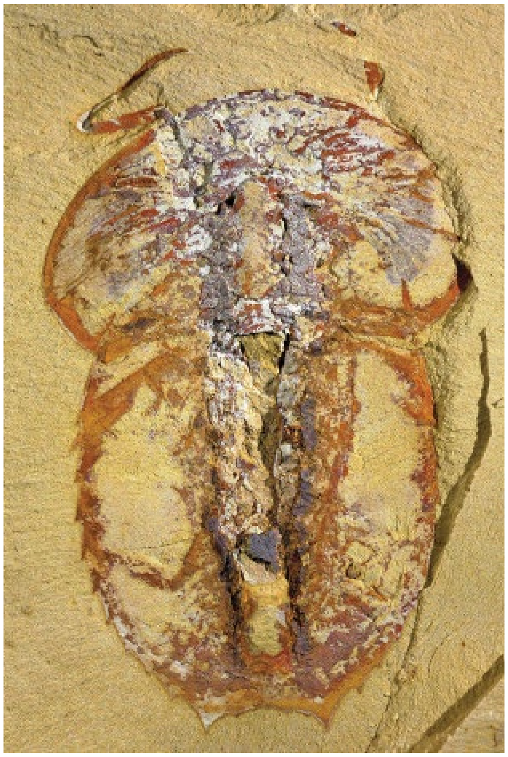
The feeding strategy of *N. spinosa* has been interpreted as that of either a sediment-ingesting deposit feeder, or that of a scavenger/predator, as for the naraoiid *Misszhouia longicaudata* (see discussion of that species). The different arrangement of the diverticula of the head region in *N. spinosa* compared to that in *M. longicaudata* has been taken to indicate a more intermittent and opportunistic feeding habit in the former compared with the latter (Vannier & Chen 2002).

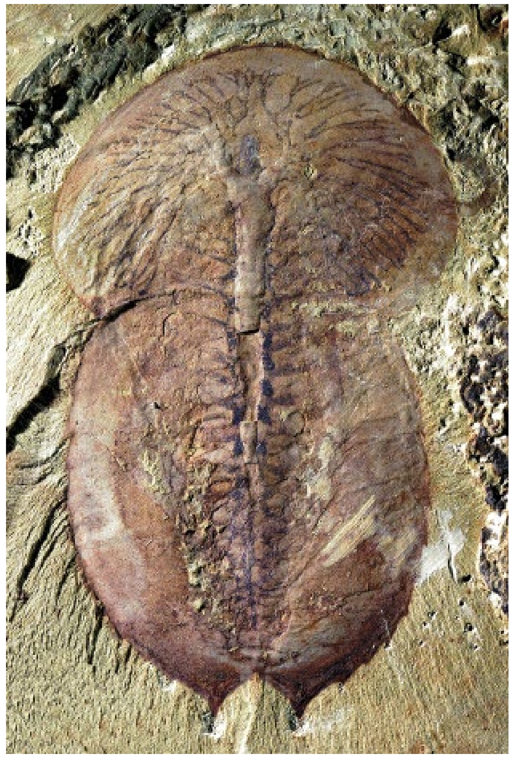
In addition to the occurrence of *N. spinosa* in the Chengjiang fauna, it has also been identified from the lower Cambrian of Guizhou Province (Steiner *et al.* 2005; Zhang Xing-liang *et al.* 2007). Other *Naraoia* species recorded from China are *Naraoia halia*, a species originally described from the Burgess Shale in Canada (Simonetta & Delle Cave 1975), which has now been reported from the Chengjiang Lagerstätte (Zhang Xing-liang *et al.* 2007), and *Naraoia taijiangensis* from the lower Cambrian of Guizhou (Peng *et al.* 2012). The genus also occurs in the middle Cambrian of the Kaili Lagerstätte, Guizhou (Zhao Yuan-long *et al.* 1999b). Outside China, *Naraoia* ranges into the Silurian, through *N. bertiensis* from Ontario, Canada (Caron *et al.* 2004).

Key references

Zhang Wen-tang & Hou 1985; Chen Jun-yuan & Zhou 1997; Chen Jun-yuan *et al.* 1997; Hou & Bergström 1997; Hou *et al.* 1999; Butterfield 2002; Vannier & Chen 2002; Bergström *et al.* 2007; Zhang Xing-liang *et al.* 2007.

Figure 20.46 ***Naraoia spinosa***. **(a)** YKLP 13941, ×4.1; Ercaicun, Haikou, Kunming. **(b)** RCCBYU 10413, ×3.3; Ercaicun, Haikou, Kunming. **(c)** YKLP 13803, ×1.2; Ercaicun, Haikou, Kunming. **(d)** YKLP 13942, ×11.0; Xiaolantian, Chengjiang.


(a)


(b)


(c)


(d)

Genus *Misszhouia* Chen, Edgecombe & Ramsköld, 1997

Misszhouia longicaudata (Zhang & Hou, 1985)

Misszhouia longicaudata is represented by at least 1500 specimens. It has a long, smoothly outlined trunk shield. The shorter and wider head shield is subsemicircular in outline, with a rounded posterolateral cheek margin. Both the head and trunk shields are dorsally effaced.

Specimens can reach up to 6.5 cm in length exclusive of a pair of long uniramous antennae. A pair of small rounded structures between the antennae may represent ventral eyes. A hypostome, with a medial and two lateral bulges anteriorly, is apparently connected to the ventral cuticle of the head shield by a suture. The number of biramous appendages identified in the head varies from three to four; the number beneath the posterior shield is from 19 to 26, with juveniles carrying from 16 to 18 (Hou & Bergström 1997; Edgecombe & Ramsköld 1999b; Zhang Xing-liang *et al.* 2007). A large basis bearing spines on its inner margin connects dorsally to arthrodial membrane. The endopod consists of seven podomeres, the two most proximal of which each bears an endite with spines, and the most distal is a claw. The exopod is attached to the basis and apparently the proximal part of the first podomere of the endopod. It comprises a long, slender proximal segment with long, flat (lamellar) setae, and a narrow distal lobe with bristles. Gut diverticulae are relatively short and restricted to the axial region; they comprise numerous tubules and minute granules.

M. longicaudata is the only species assigned to *Misszhouia*, which is a nektaspidid trilobitomorph closely related to *Naraoia* (Legg *et al.* 2013). The very long trunk and simplified anterior-most pair of gut diverticulae of *Misszhouia* readily distinguish it from *Naraoia* species (Zhang Xing-liang *et al.* 2007).

M. longicaudata is widely regarded as a benthic predator or scavenger. However, arguments have been put forward to suggest that it had a mud-ingesting deposit-feeding strategy. The basis of such contentions has been disputed by taphonomic studies that indicate that mud within its gut originated from the weathering of phosphate permineralizations of mid-gut glands (Chen Jun-yuan *et al.* 1997; Edgecombe & Ramsköld 1999b; Hou & Bergström 1997; Butterfield 2002; Vannier & Chen 2002; Bergström *et al.* 2007; Zhang Xing-liang *et al.* 2007).

M. longicaudata is known with certainty only from the lower Cambrian of Yunnan Province. Material that has been compared with this species has been recorded from strata of this age from Guizhou (Steiner *et al.* 2005), though it has subsequently been referred to *Naraoia spinosa* (Zhang Xing-liang *et al.* 2007).

Key references

Zhang Wen-tang & Hou 1985, Chen Juan-yuan *et al.* 1997, Hou & Bergström 1997, Edgecombe & Ramsköld 1999b, Butterfield 2002, Vannier & Chen 2002, Bergström *et al.* 2007, Zhang Xing-liang *et al.* 2007.

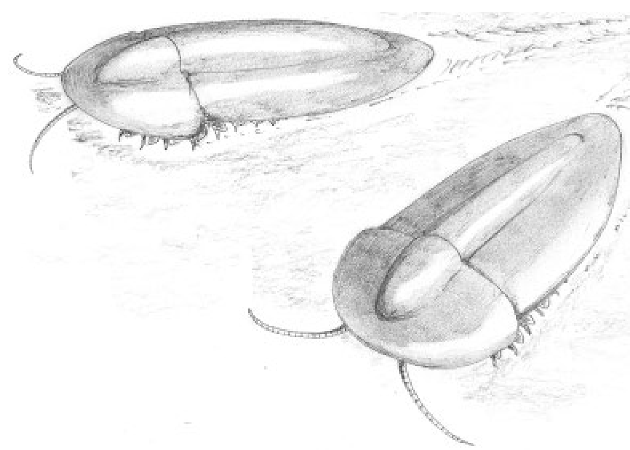
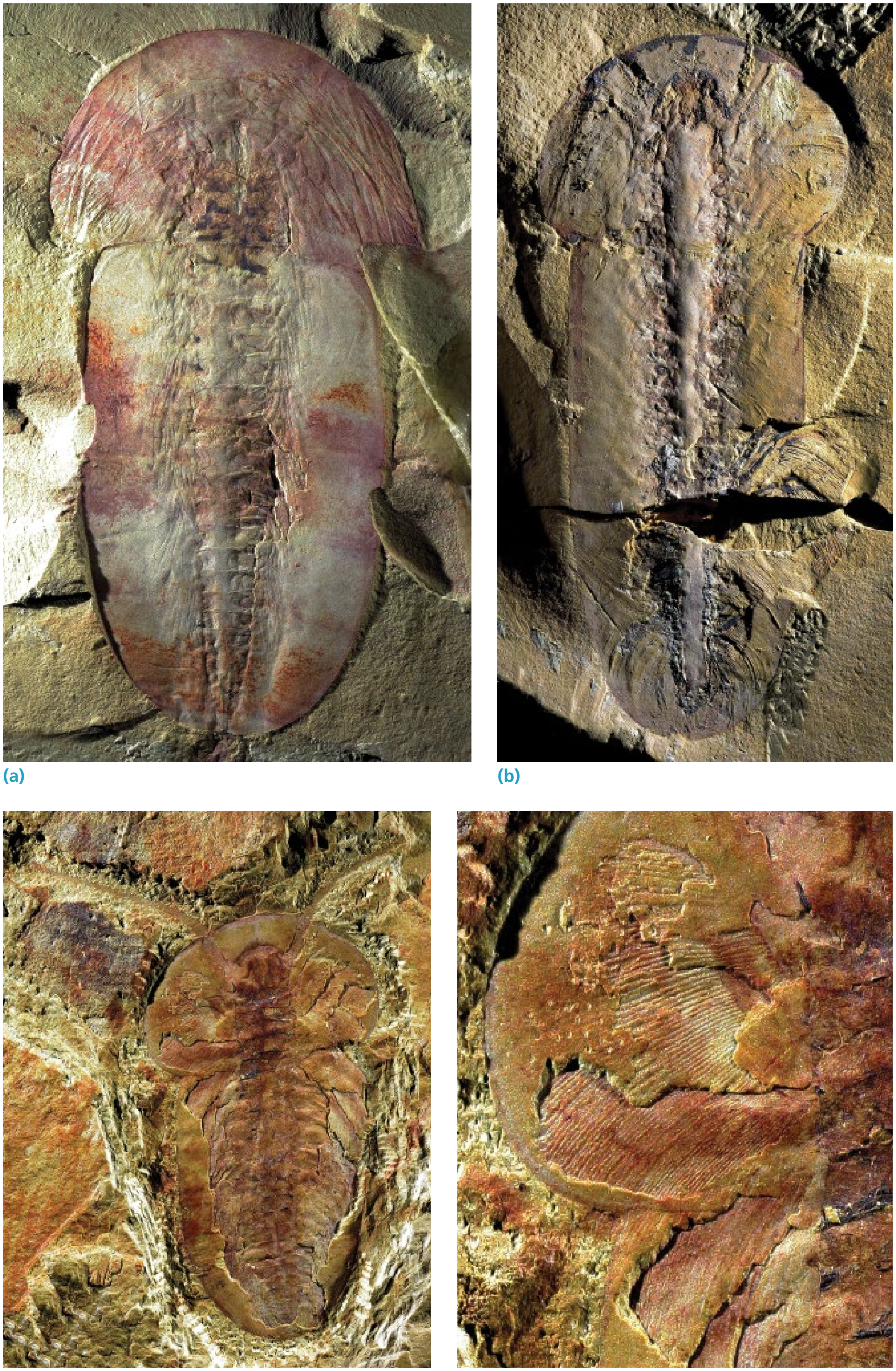


Figure 20.47 Reconstruction of ***Misszhouia longicaudata*** (modified from Hou *et al.* 2004a).

Figure 20.48 ***Misszhouia longicaudata*.** **(a)** YKLP 13943, ×2.2; Maotianshan, Chengjiang. **(b)** YKLP 13944, ×2.1; Mafang, Haikou, Kunming. **(c), (d)** RCCBYU 10275, ×2.2, ×7.2; Maotianshan, Chengjiang.



(a) (b) (c) (d)

Genus *Eoredlichia* Zhang, 1951

Eoredlichia intermedia (Lu, 1940)

Over 500 specimens of *Eoredlichia intermedia* have been collected from the Chengjiang biota, at least 25 of which have their appendages preserved. *Eoredlichia* lends its name to the *Eoredlichia-Wutingaspis* trilobite biozone, in which the biota occurs. Antennae, biramous appendages, and features of the digestive system are known for this species.

Long, uniramous antennae diverge anteriorly from underneath the head shield; each consists of 46–50 short, spine-bearing articles. Post-antennal appendages are biramous, with three pairs beneath the head shield, one pair underneath each of the 15 thoracic segments, and probably three pairs under the tail shield. Each biramous limb is associated proximally with a stout basal unit, the basis. The endopod consists of seven podomeres, the most distal of which is divided into three claws. The basis bears short, spinose endites on its inner margin, together with more sparse long ventral spines, and the endopod podomeres also support spines. The exopod consists of a blade-like shaft that bears some 40 long filaments, and a distal lobe fringed with short bristles. The proximal part of the exopod is attached to the basis by a hinge joint, and the proximal part of the first podomere of the endopod is also attached to it. The gut is straight, only weakly expanding beneath the glabella; it is associated with four pairs of glabellar gut diverticula, and five thoracic pairs up to the rear margin of the fourth axial ring, posterior to which it apparently lacks them (Hou *et al*. 2009a).

The head shield has a forwardly tapering glabella that is well rounded anteriorly. In front of the neck (occipital) ring, which is longest medially and which shows weak lateral lobes, the first glabellar furrow runs backward and inward before turning transversely across the central glabellar area; the second glabellar furrow is weaker. The preglabellar field and the anterior border are subequally long. A long, moderately curved cheek spine extends to at least the posterior part of the thorax. The facial sutures diverge at about 80 degrees, with the posterior suture meeting the posterior margin. The hypostome and rostral plate (two ventral sclerites) attach beneath the anterior glabellar margin (conterminant mode; Fortey 1990). Large crescentic eyes reach posteriorly to the neck furrow. Fifteen segments comprise the thorax; they are laterally spinose, and the ninth axial ring supports a very long posteriorly directed spine. A very small tail shield is made up of two axial rings and a weak third, and the flank area shows two fused segments and associated furrows. Fine pustules cover various parts of the cuticle.

Redlichioids, such as *Eoredlichia*, have been considered to be the sister group of a group comprising all higher (non-olenelloid) trilobites (Fortey 1990). Trilobites as a whole resolve as stem chelicerates (artiopodan arthropods) closely related to nektaspidids such as *Naraoia* (Legg *et al*. 2013).

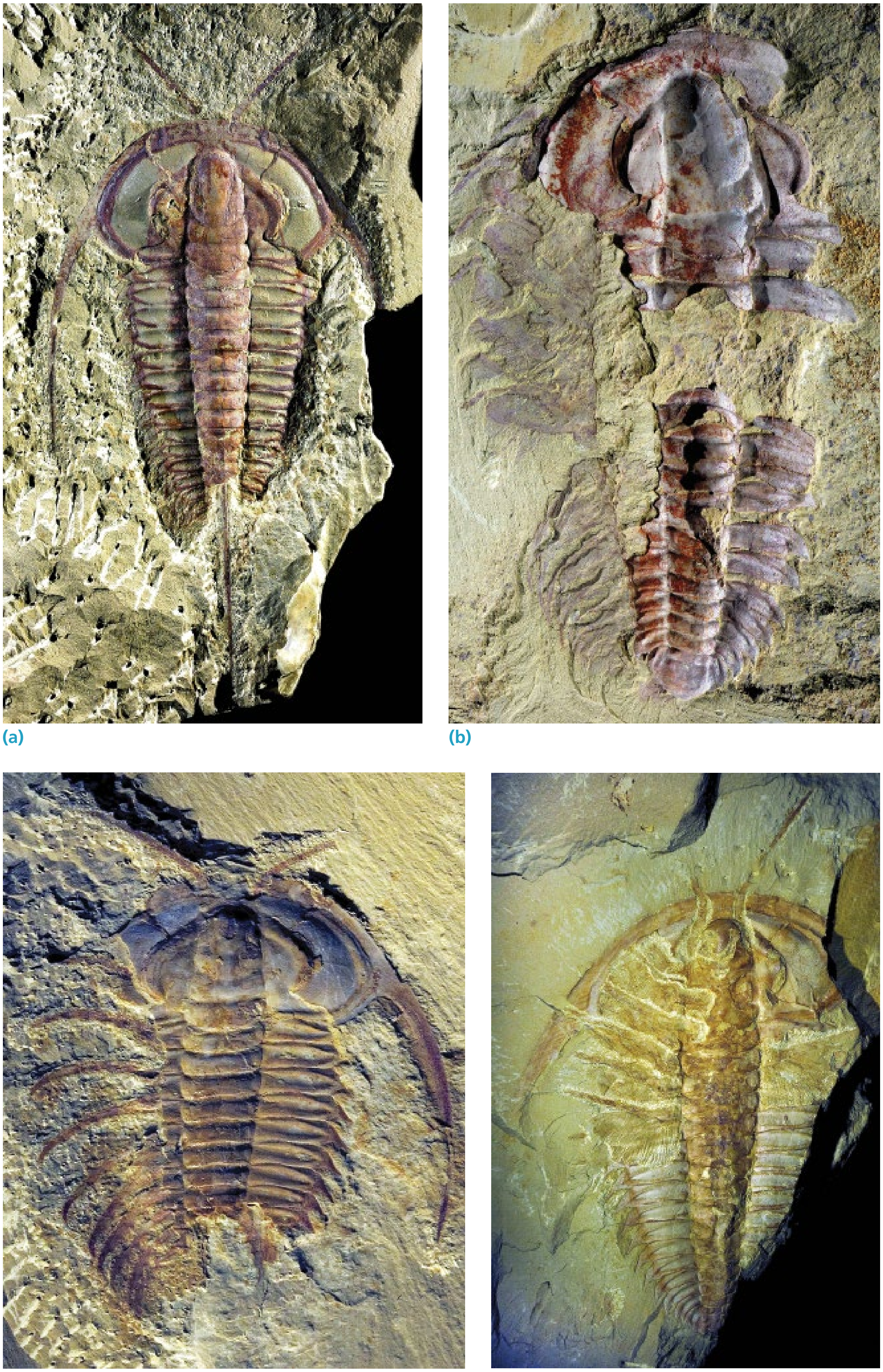
Eoredlichia intermedia lived on or close to the sea floor. A study that assessed trilobite feeding habits argued for *Eoredlichia* being a predator, based on the nature of its stout spinose limb bases and its braced hypostome (Fortey & Owens 1999), and a predator/scavenger feeding mode has been accepted for it on the basis of current evidence (Hou *et al*. 2009a). Another analysis suggested that the long setae on the proximal part of the exopod were used for filtering food (Shu *et al.* 1995a).

Various lower Cambrian localities in Yunnan Province have yielded specimens of *E. intermedia*.

Key references

Lu 1940; Zhang Wen-tang 1951; Fortey 1990; Shu *et al.* 1995a; Ramsköld & Edgecombe 1996; Hou *et al*. 2009a; Legg *et al.* 2013.

Figure 20.49 ***Eoredlichia intermedia***. **(a)** YKLP 13945, ×2.3; Mafang, Haikou, Kunming. **(b)** YKLP 13946, ×2.6; Mafang, Haikou, Kunming. **(c)** YKLP 10972, ×1.9; Mafang, Haikou, Kunming. **(d)** YKLP 10964, ×1.0; Mafang, Haikou, Kunming.



(a) (b) (c) (d)

Genus *Kuanyangia* Hupé, 1953

Kuanyangia sp. of Hou & Bergström, 1997

Specimens of *Kuanyangia* are relatively uncommon in the Chengjiang biota by comparison with those of other trilobites. They have been referred to five species, at least several if not all of which may be conspecific (Hou & Bergström 1997); the first published, *Redlichia pustulosa* Lu, 1941, is the type species of *Kuanyangia*. The material commented on here is therefore described under open nomenclature pending revision of this species group. Antennae and biramous appendages are known for *Kuanyangia*.

The uniramous antennae attach under the frontal lobe of the glabella; each is stout proximally, beyond which there are about 20 short articles, though the most distal part of the antenna is unknown. Four exopods of the head region have been identified, together with, in head and thoracic limbs, a large basis that is finely serrated medially and ventrally. At least five or six cylindrical podomeres have been identified in the endopod, the terminal one bearing a few short spines. Two segments form the large, blade-like main shaft of the exopod, which is fringed with narrow, flat setae posteriorly and distally.

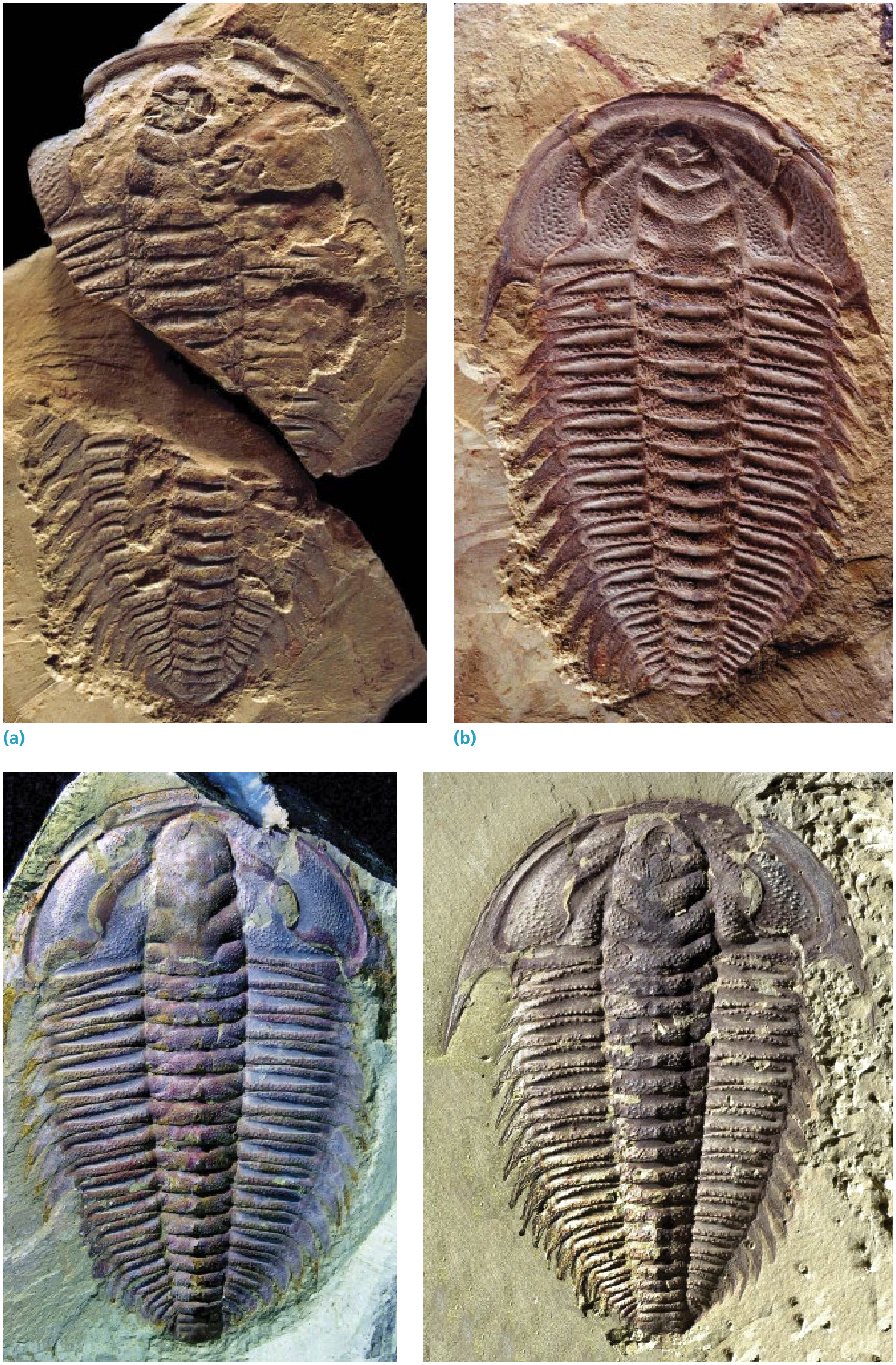
The head shield has a subsemicircular outline. The glabella is conical; it has three distinct furrows, all of which are deepest as they run obliquely backward from the axial furrow before they continue more weakly across the central glabellar area. The neck (occipital) ring bends forward laterally into a small occipital lobe, in front of which the occipital furrow is deepest. There is a short preglabellar field posterior to a convex anterior border. A medium-sized eye lobe lies opposite the mid-length of the glabella, and the eye ridge is strong. Facial sutures diverge anteriorly and run outward and backward posteriorly. There is a short cheek spine. The thorax comprises 16 segments, the axial rings of which have a median node and a lateral lobe, and there are short spines laterally on the thoracic segments. The tail shield is very small with two or three axial rings. Pustules cover much of the cuticle.

Kuanyangia is a redlichioid trilobite, benthic in habit, and it occurs in the *Eoredlichia-Wutingaspis* trilobite biozone of Yunnan.

Key references

Lu 1941; Hupé 1953; Hou & Bergström 1997.

Figure 20.50 ***Kuanyangia* sp.** **(a)** NIGPAS 115407a, ×1.6; Maiotianshan, Chengjiang. **(b)** NIGPAS 115407b, ×1.5; Maiotianshan, Chengjiang. **(c)** YKLP 13947, ×0.8; Ercaicun, Haikou, Kunming. **(d)** YKLP 13948, ×2.2; Mafang, Haikou, Kunming.



(a) **(b)** **(c)** **(d)**

Genus *Yunnanocephalus* Kobayashi, 1936

Yunnanocephalus yunnanensis (Mansuy, 1912)

Yunnanocephalus yunnanensis is a fairly common trilobite of the Chengjiang biota. Antennae and biramous appendages have been prepared out in a few specimens. Genal diverticula, reflecting an underlying network of vessels or nerves, are also known. The antennae are subparallel proximally from their origins to the margin of the head shield, in front of which they diverge strongly and taper. Biramous appendages are known from both the head and the thorax, but their preservation precludes detailed morphological interpretation.

The head shield is well rounded in outline. The glabella tapers anteriorly and has straight sides, a bluntly rounded frontal lobe, and weak or very weak furrows. The neck ring comprises a broad band. The preglabellar field is slightly longer than the anterior border, and the anterior margin may project forward medially. The eye is relatively small, situated anterior to the mid-length of the glabella to which it is connected by a slightly curved and weakly forwardly projecting eye ridge. Facial sutures are subparallel to gently converging anteriorly; posteriorly they run obliquely backward to a rounded cheek margin. The hypostome has a conterminant attachment style (Fortey 1990), and has been inferred to connect to the ventral continuation of the anterior border by means of a plectrum-like rostral plate. Fourteen segments make up the thorax, with the axial rings showing lateral lobes, and with short, stout lateral marginal spines. A median node is present on most axial rings. The tail shield is very small and largely consists of a subquadrate axis that has two incomplete axial rings and a boss below its posterior tip. The flank area is tiny and subtriangular.

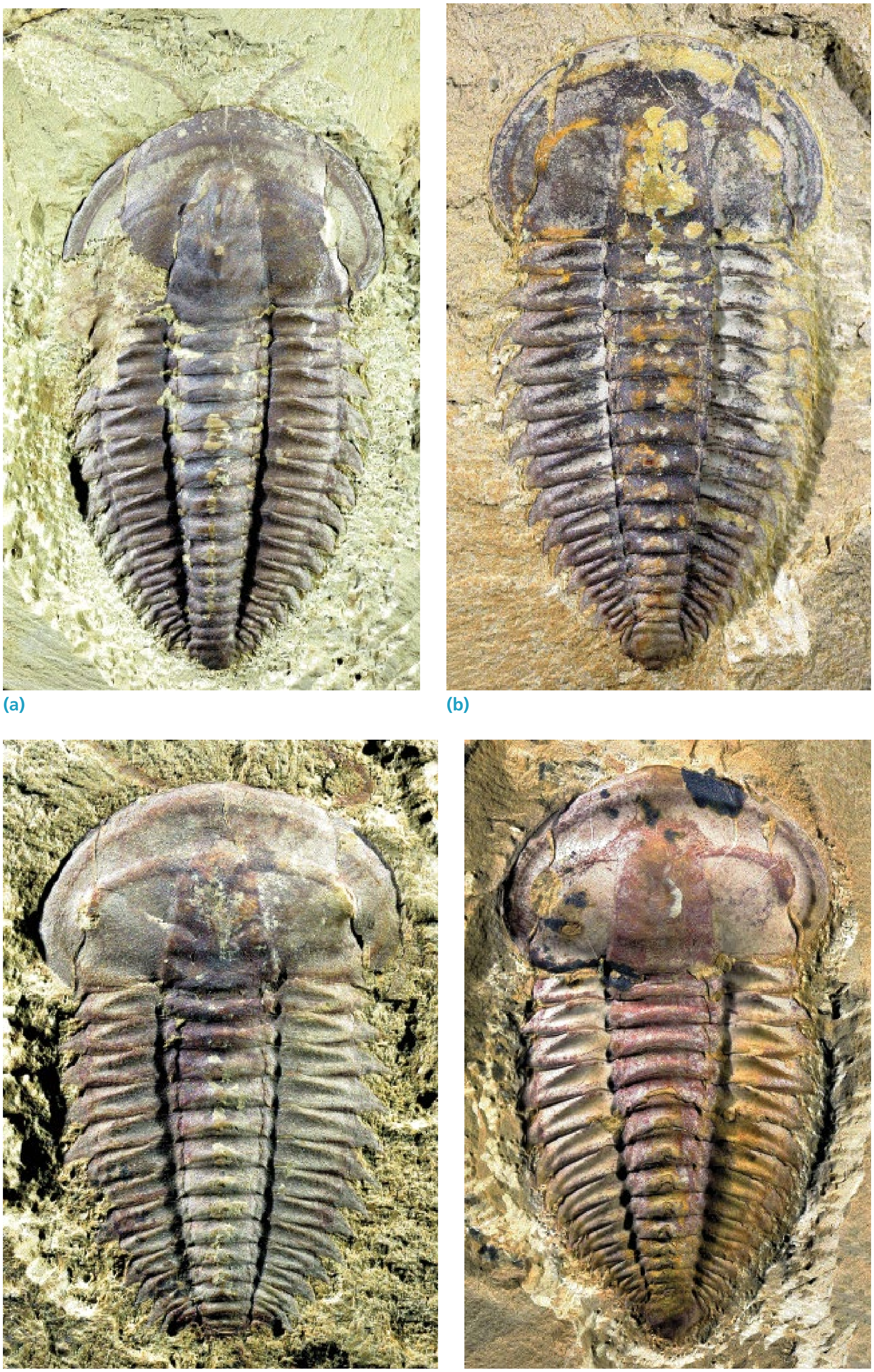
Y. yunnanensis, like the Chengjiang species *Eoredlichia intermedia* and *Kunyangia pustulosa*, belongs to the Redlichioidea, a phylogenetically relatively basal group of trilobites. All probably lived on or near the sediment/water interface.

Yunnanocephalus is known from various localities in Yunnan Province.

Key references

Mansuy 1912; Kobayashi 1936; Shu *et al*. 1995a.

Figure 20.51 ***Yunnanocephalus yunnanensis***. **(a)** YKLP 13949, ×4.3; Mafang, Haikou, Kunming. **(b)** YKLP 13950, ×4.8; Mafang, Haikou, Kunming. **(c)** YKLP 13951, ×2.7; Ercaicun, Haikou, Kunming. **(d)** YKLP 13952, ×4.3; Mafang, Haikou, Kunming.



(a) (b) (c) (d)

Genus *Parapaleomerus* Hou, Bergström, Wang, Feng & Chen, 1999

Parapaleomerus sinensis Hou, Bergström, Wang, Feng & Chen, 1999

Specimens of *Parapaleomerus sinensis* are typically dorsoventrally compressed. In addition to the three specimens mentioned by Hou *et al*. (2004a), several others have been identified that may be referable to *Parapaleomerus*. As these have variable exoskeleton shapes their exact affinity to *P. sinensis* (Hou *et al*. 1999, fig. 201) remains uncertain: one of these specimens bears trunk appendages.

The exoskeleton of *P. sinensis* has a semi-elliptical head shield that lacks any indication of the presence of dorsal eyes. The trunk appears to have 11 tergites, and its overall shape narrows posteriorly. The presence of a telson is uncertain. The largest specimen described by Hou *et al*. (2004a) is recorded as 9.2 cm long, with a maximum width of 9 cm.

Parapaleomerus has been suggested to show similarities to three other early Paleozoic arthropods, namely *Paleomerus* Størmer, 1956 from the early Cambrian of Sweden, and the late Cambrian *Strabops* Beecher, 1901 and late Ordovician *Neostrabops* Caster & Macke, 1952 from the USA. *Parapaleomerus* has been suggested to be a synonym of *Paleomerus* (Hou *et al*. 2004a) but it shows no evidence for dorsal eyes and the morphology of the posterior end of its exoskeleton needs to be resolved. In *Paleomerus* the posterior end of the exoskeleton terminates in a large telson (Tetlie & Moore 2004).

The ecology of *Parapaleomerus* cannot be discerned until its soft anatomy is known. *P. sinensis* is known only from the Chengjiang biota.

Key references

Hou *et al*. 1999; Hou *et al*. 2004a.

Figure 20.52 ***Parapaleomerus sinensis***. NIGPAS 115439, ×1.8; Xiaolantian, Chengjiang.

Genus *Kwanyinaspis* Zhang & Shu, 2005

Kwanyinaspis maotianshanensis Zhang & Shu, 2005

Kwanyinaspsis maotianshanensis was originally described from a single specimen preserved with some soft parts. Only a few additional specimens have subsequently been found.

The unmineralized exoskeleton is preserved in dorsoventral aspect and is about 6 cm long. Its semicircular head shield has two bulges either side of a weakly defined central region that is outlined by concentric wrinkles. The broad trunk, which is composed of 12 tergites, widens to the level of the third tergite, thereafter narrowing towards the 12th. Pleural spines are weakly developed in the first four tergites, but become much longer and are projected posteriorly in tergites 5 to 9. Tergites 10 to 12 are small, but relative to their size have long posterior projecting pleural spines. The trunk terminates in a blade-like tail-spine.

The presence of stalked ventral eyes has been inferred (Zhang Xing-liang & Shu 2005), equating in their position to the two bulges on the head shield. The occurrence of antennae could not be confirmed, but the presence of biramous appendages in the head has been noted. The appendages of the trunk show a large basipod, a large flap-like exopod, and an endopod composed of six podomeres and a terminal spine.

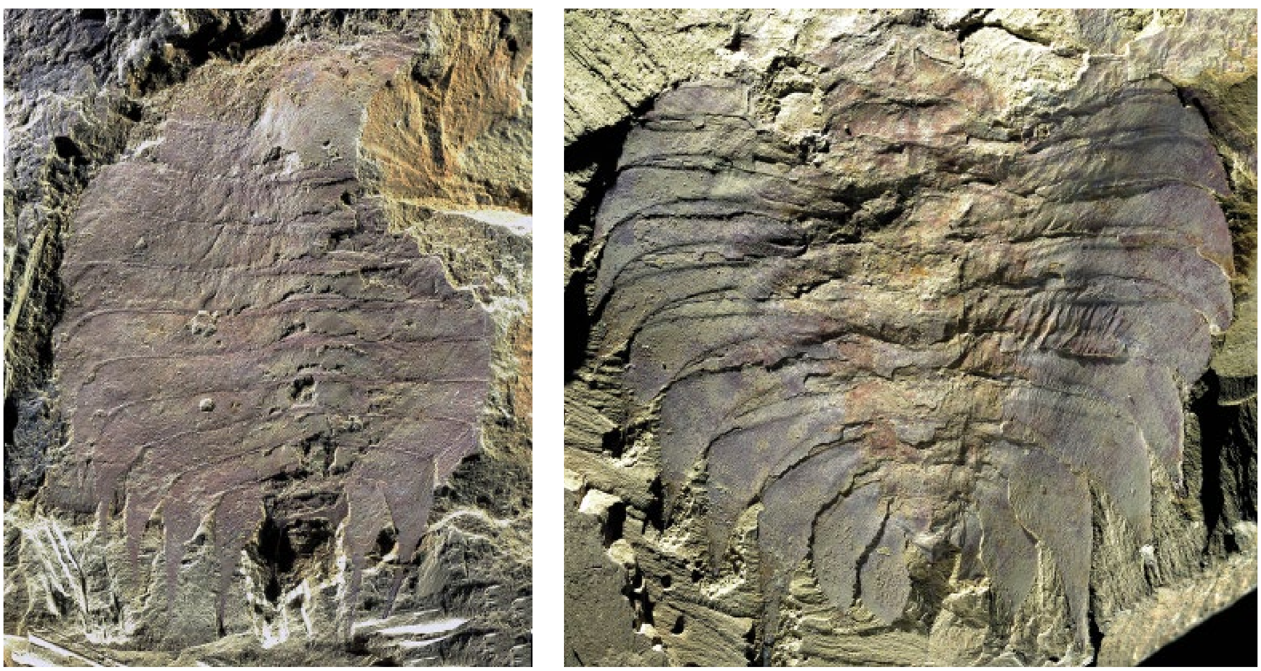
This taxon has been assigned to the Aglaspidida based on its exoskeleton morphology (Zhang Xing-liang & Shu 2005), especially its elongate pleural spines and tail spine. An aglaspidid affinity was also recovered in a comprehensive phylogenetic analysis of arthropods (Legg *et al.* 2013), with *Kwanyinaspis* resolved, among other aglaspids, as a stem chelicerate.

The morphology of *Kwanyinaspis* suggests it functioned as a benthic predator or scavenger.

K. maotianshanesis is know only from the Chengjiang biota.

Key references

Zhang Xing-liang & Shu 2005; Legg *et al.* 2013.



(a) (b)

Figure 20.53 ***Kwanyinaspis maotianshanensis*****.** **(a)** YKLP 13956, ×1.5; Mafang, Haikou, Kunming. **(b)** YKLP 13957, ×1.6; Ercaicun, Haikou, Kunming.

Genus *Kunmingella* Huo, 1956

Kunmingella douvillei (Mansuy, 1912)

This bivalved arthropod is the most abundant of the many bradoriid species in the Chengjiang biota. Thousands of its thin, weakly mineralized carapaces occur at many horizons, accounting for a high percentage of recovered individuals from the biota. Conjoined valves of the carapace of *Kunmingella douvillei*, preserved in articulated so-called butterfly orientation on bedding planes, are common. Soft parts are known from several tens of specimens.

Adult valves are generally smooth, about 5 mm long, with a tapering posterior lobe, an anterodorsal node, and a narrow marginal ridge. The body has 10 narrow appendage-bearing segments, five on the head and five on the trunk: the distinction between the head and trunk is given by the orientation of these appendages, the head appendages pointing forward, whilst the trunk appendages point backward (Hou *et al.* 2010). A pair of lateral eyes occur just in front of the insertion point of the first appendages on either side of the head. The first appendage is a pair of uniramous, presumed sensory antennae that project beyond the anterior margin of the carapace. Behind the antennae, body segments 2 to 8 each have a pair of biramous appendages. The exopods are leaf-shaped, fringed with marginal spines, and may have had a respiratory function; each endopod of these appendages is elongate, consisting of at least five podomeres, and was probably used for walking. The ninth and tenth pairs of appendages are uniramous. The ninth appendage trails well beyond the posterior margin of the carapace and possesses a terminal claw-like structure. The trunk end of the body is terminated by a narrow triangular tail-piece flanked by the short 10th appendages. This tail-piece and parts of several of the posterior appendages are preserved projecting beyond the posterior margin of the carapace in some specimens.

Bradoriids were traditionally regarded as ostracod crustaceans. However, the soft parts of *Kunmingella* (Hou *et al.*, 1996, 2010) indicate that some bradoriids belong outside the Crustacea *sensu stricto* and are basal crown euarthropods (Legg *et al.* 2013). Bradoriids are just one of several groups of Cambrian arthropods that developed bivalved carapaces through convergent evolution.

K. douvillei probably crawled on, and swam near, the seabed, protected by its carapace. Eggs preserved within the carapace of several *K. douvillei* indicate brooding (Shu *et al.* 1999c; Duan *et al.* 2014), a reproductive strategy that may have contributed to the numerical abundance of bradoriids in the Chengjiang biota. The occurrence of supposed coprolites rich in *Kunmingella* indicates that bradoriids were a food source for larger predators.

K. douvillei is known from early Cambrian strata of Shaanxi, Sichuan, and Yunnan provinces of China, the country that contains the richest bradoriid faunas globally (Hou *et al.* 2002b).

Key references

Mansuy 1912; Huo 1956; Hou *et al.* 1996, 1999, 2002b, 2004a, 2010; Shu *et al.* 1999c; Duan *et al.* 2014.

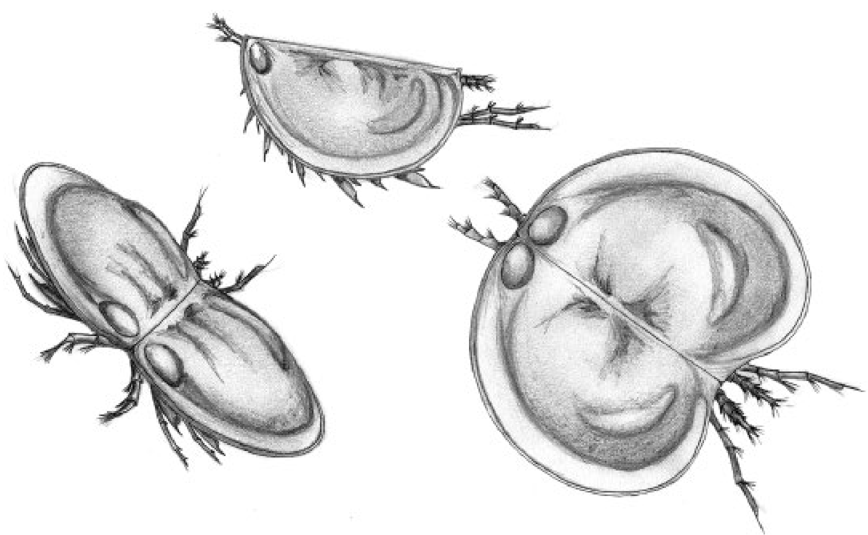
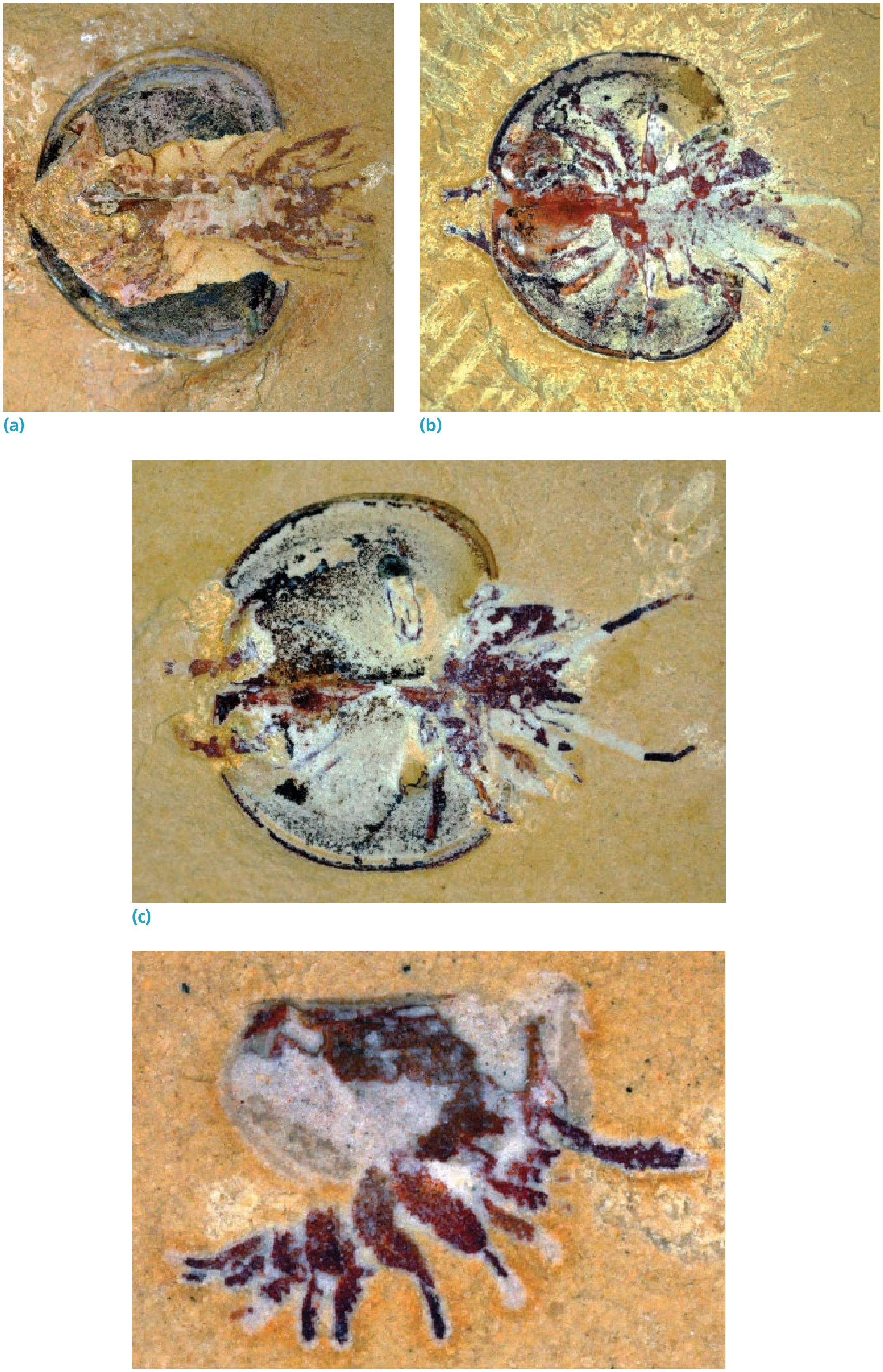


Figure 20.54 Reconstruction of ***Kunmingella douvillei*** (based on Shu *et al.* 1999c and Hou *et al.* 2010).

Figure 20.55 ***Kunmingella douvillei***. **(a)** YKLP 10988b, ×6.5; Xiaolantian, Chengjiang. **(b)** YKLP 10994, ×9.8; Ercaicun, Haikou, Kunming. **(c)** YKLP 10998, ×13.4; Ercaicun, Haikou, Kunming. **(d)** YKLP 11001a, ×37.5; Ercaicun, Haikou, Kunming.



(a) (b) (c) (d)

Genus *Kunyangella* Huo, 1965

Kunyangella cheni Huo, 1965

Despite the abundance of bradoriid arthropods in the Chengjiang biota, *Kunyangella cheni* is only the second species known with preserved soft parts. It is known from a few hundred specimens, but only two of these have traces of appendages.

Adult bivalved carapaces are a little over 2 mm long and have a bulbous, elongate to arched mid-dorsal node and a weakly developed marginal ridge on each valve. There is evidence for five pairs of appendages, three on the head pointing forward, and two pointing backward, presumably on the trunk (Hou *et al*. 2010). The first pair of appendages protrude anteriorly from the carapace and may have served a sensory function analogous to the first appendages of the bradoriid *Kunmingella douvillei*. More posteriorly are the remnants of the endopods of two appendage pairs on the head that protrude beyond the edge of the carapace, and which possess paired claw-like setae at their terminations. Broader, presumed endopods of two trunk appendages protrude beyond the edge of the carapace posteroventrally.

K. cheni is significantly different from the other Chengjiang bradoriid with soft part preservation, *K. douvillei*, and this may support the hypothesis that bradoriids are a polyphyletic group of arthropods that acquired bivalved carapaces through convergence (Hou *et al*. 2010). However, Legg *et al*. (2013) grouped *Kunyangella* with *Kunmingella* in their phylogenetic analysis and regarded *K. cheni* as a basal euarthropod.

K. cheni probably crawled and swam near the seabed, protected by its carapace. This species is known only from early Cambrian strata of Yunnan province, China (Hou *et al.* 2002b).

Key references

Huo 1965; Hou *et al*. 2002b, 2010.

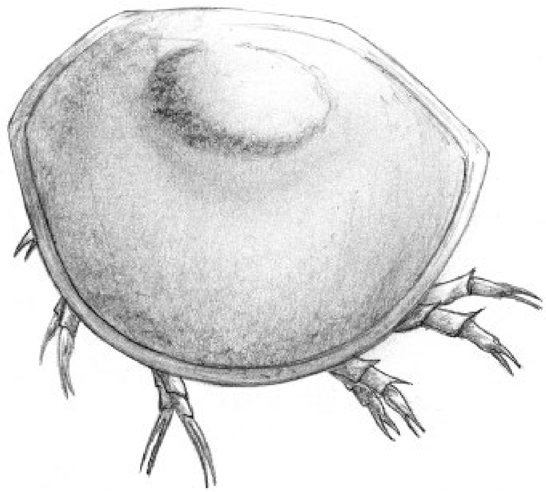
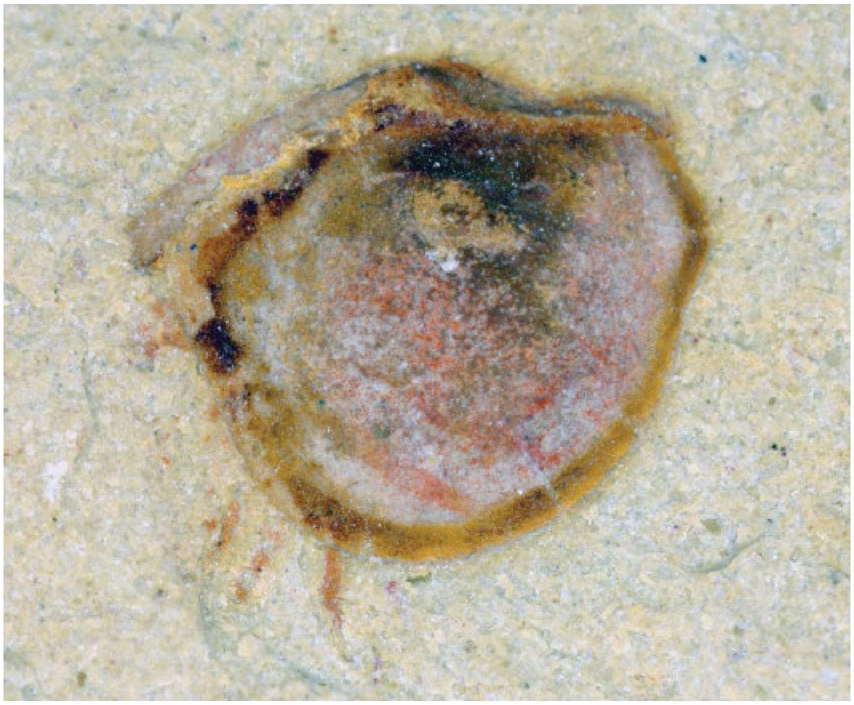
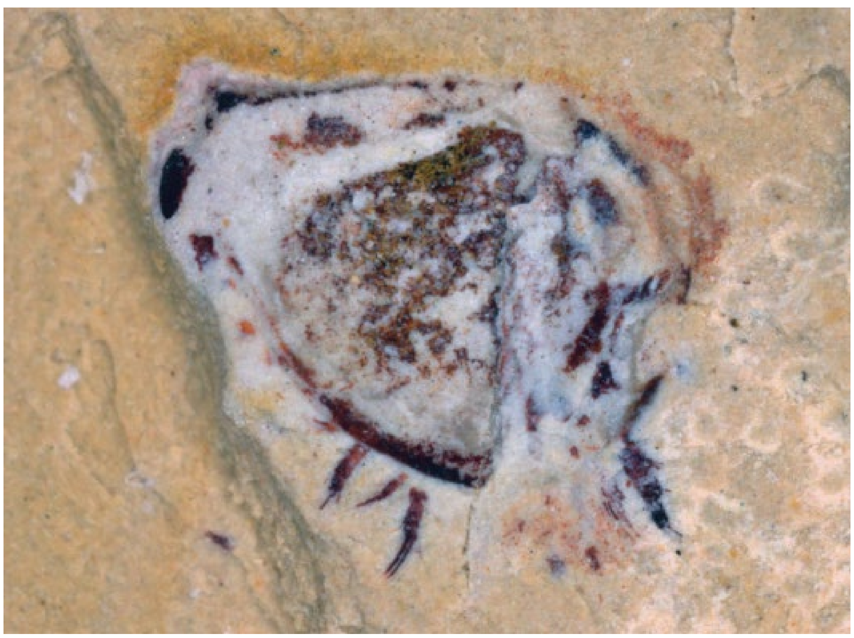


Figure 20.56 Reconstruction of ***Kunyangella cheni***.

Figure 20.57 ***Kunyangella cheni***. **(a)** YKLP 11003, ×35.3; Mafang, Haikou, Kunming. **(b)** YKLP 11002, ×36.2; Ercaicun, Haikou, Kunming.



(a)



(b)

Genus *Primicaris* Zhang, Han, Zhang, Liu & Shu, 2003

Primicaris larvaformis Zhang, Han, Zhang, Liu & Shu, 2003

Many thousands of specimens are known of *Primicaris larvaformis*, including several hundred well-preserved examples. Typically they are dorsoventrally compressed parallel to the bedding plane. Ventral morphological structures are observable directly or through the flattened dorsal shield, indicating that such specimens represent carcasses rather than molts (Zhang Xing-liang *et al*. 2003).

This species has a larva-like morphology overall. The maximum length of complete specimens ranges from about 2 to 6 mm. The dorsal exoskeleton shows convexity in the axial region but otherwise seems undivided, without a distinct separation of head and trunk regions. It has marginal ridges anteriorly, 10 pairs of small spines laterally, and a pair of spines posteriorly. Ventrally, a pair of uniramous, multi-annulate antennae project anterolaterally from either side of a large hypostome that is about a quarter of the length of the exoskeleton. There are at least 10 other pairs of appendages, each biramous with a flagelliform outer branch that bears setae distally (Zhang Xing-liang *et al.* 2003; Chen Jun-yuan 2004).

Specimens of this small species were originally considered by many authors to represent a large, possibly protaspid larval stage of development of a Chengjiang naraoiid arthropod (e.g., Hou *et al*. 1991, 1999; Chen Jun-yuan *et al*. 1996; Hou & Bergström 1997). Based on much additional Chengjiang material, it was subsequently reinterpreted as not a small growth stage of a naraoiid (the juvenile stages of which are smaller), or a trilobite species, but as a separate taxon, and its larva-like morphology is thought to have resulted from paedomorphic evolutionary processes (Zhang Xing-liang *et al*. 2003; Chen Jun-yuan 2004; Zhang Xing-liang *et al*. 2007; Paterson *et al*. 2010). Recent phylogenetic analysis resolves *Primicaris* as a marellomorph, a euarthropod group positioned at the base of the mandibulate stem (Legg *et al*. 2013). In particular, it stands closest to the similarly small, skaniid marrellomorph species.

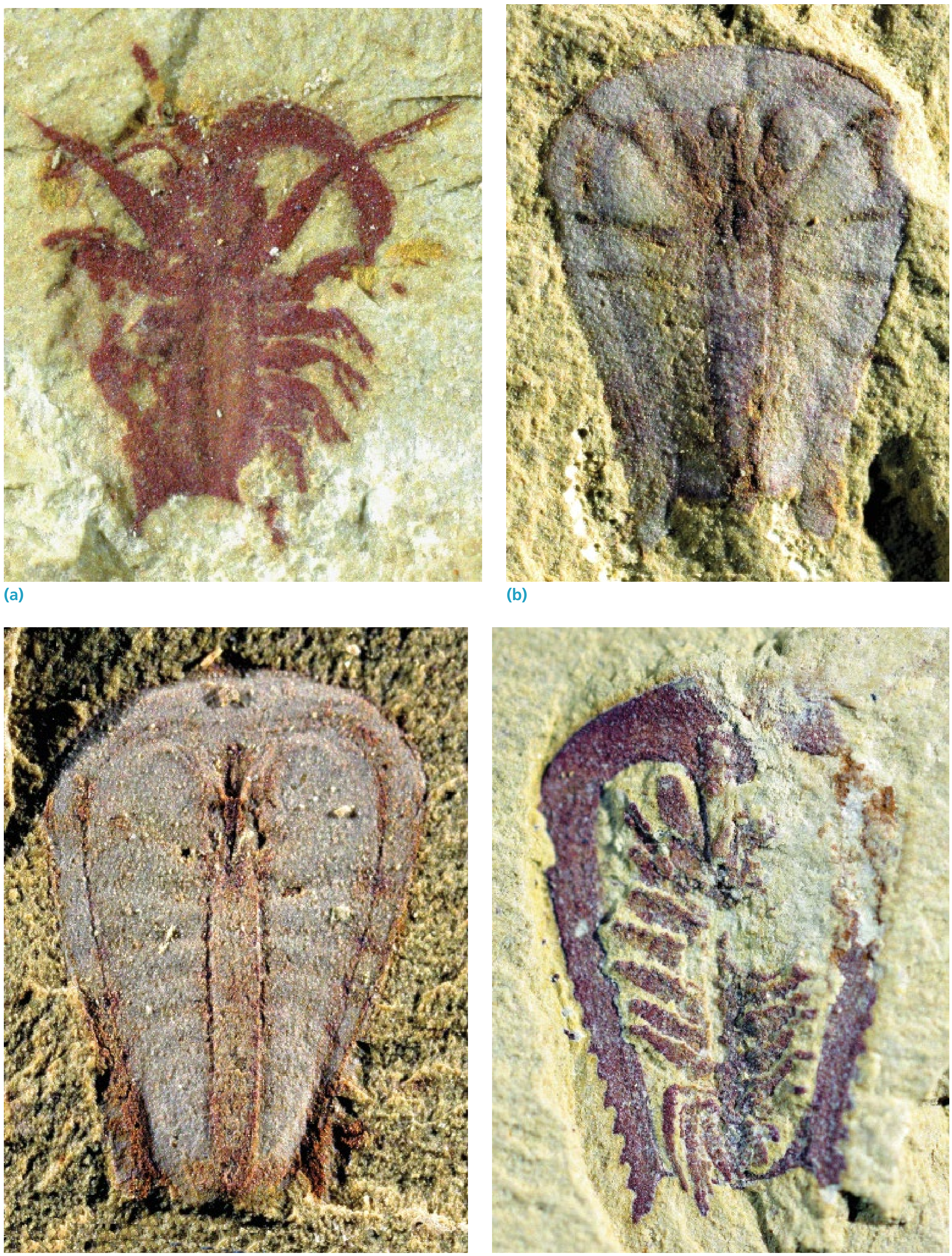
Vannier (2007) suggested that *Primicaris* possibly represented part of the early Cambrian interstitial (meio) fauna.

This species is known from many localities in both the Chengjiang and Haikou areas, especially the sections at Ercaicun and Mafang. Zhang Xing-liang *et al*. (2003) considered that a similar or the same species is present in the middle Cambrian Kaili biota of Guizhou Province, China (Zhao Yuan-long *et al*. 1999b).

Key references

Hou *et al*. 1991, 1999; Chen Jun-yuan *et al*. 1996; Hou & Bergström 1997; Zhang Xing-liang *et al*. 2003, 2007; Chen Jun-yuan 2004.

Figure 20.58 ***Primicaris larvaformis***. **(a)** YKLP 13958, ×27.0; Mafang, Haikou, Kunming. **(b)** YKLP 13959, ×17.8; Ercaicun, Haikou, Kunming. **(c)** YKLP 13960, ×19.0; Ercaicun, Haikou, Kunming. **(d)** YKLP 13961, ×17.3; Ercaicun, Haikou, Kunming.



(a) (b) (c) (d)

Genus *Branchiocaris* Briggs, 1976

Branchiocaris? *yunnanensis* Hou, 1987

This is a fairly common species, but only the bivalved carapace is known and its assignment to *Branchiocaris* is questionable. Valves are wrinkled, presumably as a result of compaction.

The carapace has a straight dorsal margin to an otherwise subcircular valve outline, and can be more than 5 cm long and 4 cm high. The anterodorsal and posterodorsal corners of the valves are projected into small processes.

Phylogenetic analysis resolved the Burgess Shale type species *Branchiocaris pretiosa* (Resser, 1929), for which detailed soft anatomy is known (Briggs 1976), as a stem euarthropod (Legg *et al*. 2013). However, the affinity of *B*.? *yunnanensis* to the type species is uncertain.

B.? *yunnanensis* is known from the Chengjiang biota and from the slightly younger Guanshan biota of Yunnan Province (Hu *et al*. 2013).

Key references

Hou 1987c; Hou *et al*. 1999, 2004a; Hu *et al*. 2013.

Figure 20.59 ***Branchiocaris*? *yunnanensis***. **(a)** YKLP 13962, ×1.6; Mafang, Haikou, Kunming. **(b)** YKLP 13963, ×1.5; Ercaicun, Haikou, Kunming. **(c)** YKLP 13964, ×2.0; Ercaicun, Haikou, Kunming.

(a)

(b)

(c)

Genus Uncertain

‘*Canadaspis*’ *laevigata* (Hou & Bergström, 1991)

This is a relatively common bivalved species that is usually preserved in lateral aspect. It has a carapace covering the head and part of the trunk. The carapace is less than 2 cm long, and the entire animal is less than 3 cm long.

The head bears a pair of stalked eyes and a pair of uniramous antennae, both of which project anteriorly beyond the carapace. Behind the antennae there are at least 10 pairs of uniform, biramous appendages that shorten in length posteriorly. The stout, multisegmented endopod of these appendages terminates in a set of spines; the exopod is a large, flat blade with a wrinkled appearance in places. The abdomen comprises 10 segments, nine of which are limbless whilst the terminal segment carries spines. The body terminates in a comparatively long telson.

‘*Canadaspis*’ *laevigata* was originally assigned to *Perspicaris* (Hou 1987c; Hou & Bergström 1991) and later to *Canadaspis* (Hou & Bergström 1997). Legg and Caron (2014) consider that it lacks diagnostic characters of either of these taxa, and as currently understood ‘*C.*’ *laevigata* is not referable with conviction to any known genus of Cambrian bivalved arthropod.

The Chengjiang species *Canadaspis eucalla* Chen & Zhou, 1997 is thought (Hou *et al.* 1999) to be synonymous with C. *laevigata*. The poorly known *Yiliangocaris ellipticus* Luo & Hu, 1999 from Yunnan Province is possibly another junior synonym.

‘*C.*’ *laevigata* seems to lack appendages specialized for feeding. The occurrence of what has been identified as silt in its gut suggests to some authors that its food supply might have been the organic contents of ingested sediment (Hou & Bergström 1997).

‘*C.*’ *laevigata* is known from the Chengjiang biota at Maotianshan, Xiaolantian, and Fengkoushao.

Key references

Hou 1987c; Hou & Bergström 1991, 1997; Chen Jun-yuan & Zhou 1997; Bergström & Hou 1998; Hou *et al.* 1999, 2004a.

Figure 20.60 ***'Canadaspis' laevigata*.** **(a)** NIGPAS 115361b, ×3.4; Maotianshan, Chengjiang. **(b)** NIGPAS 115361a, ×3.0; Maotianshan, Chengjiang. **(c)** YKLP 13965, ×6.6; Mafang, Haikou, Kunming. **(d)** YKLP 13966, ×5.2; Maotianshan, Chengjiang.


(a)


(b)


(c)


(d)

Genus *Chuandianella* Hou & Bergström 1991

Chuandianella ovata (Lee, 1975)

This is a common species, known mostly from the wrinkled remains of its carapace. Some carapaces are found in clusters.

The carapace is folded about a median line, is up to 1.4 cm long, and may have covered as many as 13 head and thoracic segments (Liu Hu-qin & Shu 2008). Projecting beyond the anterior end of the carapace are a pair of compound eyes and a pair of elongate uniramous antennae. Segments covered by the carapace are also reported to bear biramous appendages, each consisting of a narrow, filamentous comb-shaped exopod and a segmented endopod (Taylor, R. 2002). Extending beyond the posterior end of the carapace are seven limbless segments of the trunk (the abdomen), ending in a flattened, bilobed telson.

This species was originally assigned to the bradoriid genus *Mononotella* (Lee 1975), but later it was referred to the new genus *Chuandianella* by Hou and Bergström (1991), and subsequently (Chen Jun-yuan 2004) to the North American taxon *Waptia* Walcott, 1912. Most recently, after investigation of over 100 such *Waptia*-like Chinese specimens and a literature-based comparison with *Waptia fieldensis*, material of the Chinese species has been reassigned (Liu Hu-qin & Shu 2004, 2008) back to *Chuandianella*. In that latest study *C. ovata* specimens were distinguished from those of *Waptia fieldensis* from the Burgess Shale by the wide oval shape, larger size and greater height to length ratio of the carapace, and by differences in the number of head and abdominal segments.

The affinities of *Chuandianella ovata* remain speculative, including its similarity to *Waptia*. A recent analysis of the appendages and overall morphology of *W. fieldensis* suggest that it differs both from crown and stem crustaceans (Vannier *et al*. 2012).

Chuandianella specimens are known from supposed coprolites found in the Chengjiang Lagerstätte (Chen Jun-yuan & Zhou 1997; Vannier & Chen 2005). The biramous appendages of *C. ovata* might have been adapted for swimming in a nekto-benthic environment (Liu Hu-qin & Shu 2008).

C. ovata has been reported from the lower Cambrian of Yunnan, Sichuan, Ghizhou, and southern Shaanxi provinces, China, but only the material from the Chengjiang biota contains soft parts.

Key references

Hou & Bergström 1991, 1997; Chen Jun-yuan & Zhou 1997; Hou *et al*. 1999, 2009b; Liu Hu-qin & Shu 2004, 2008.

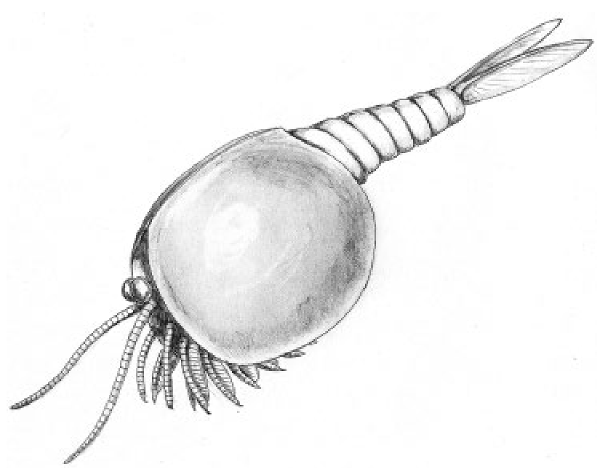
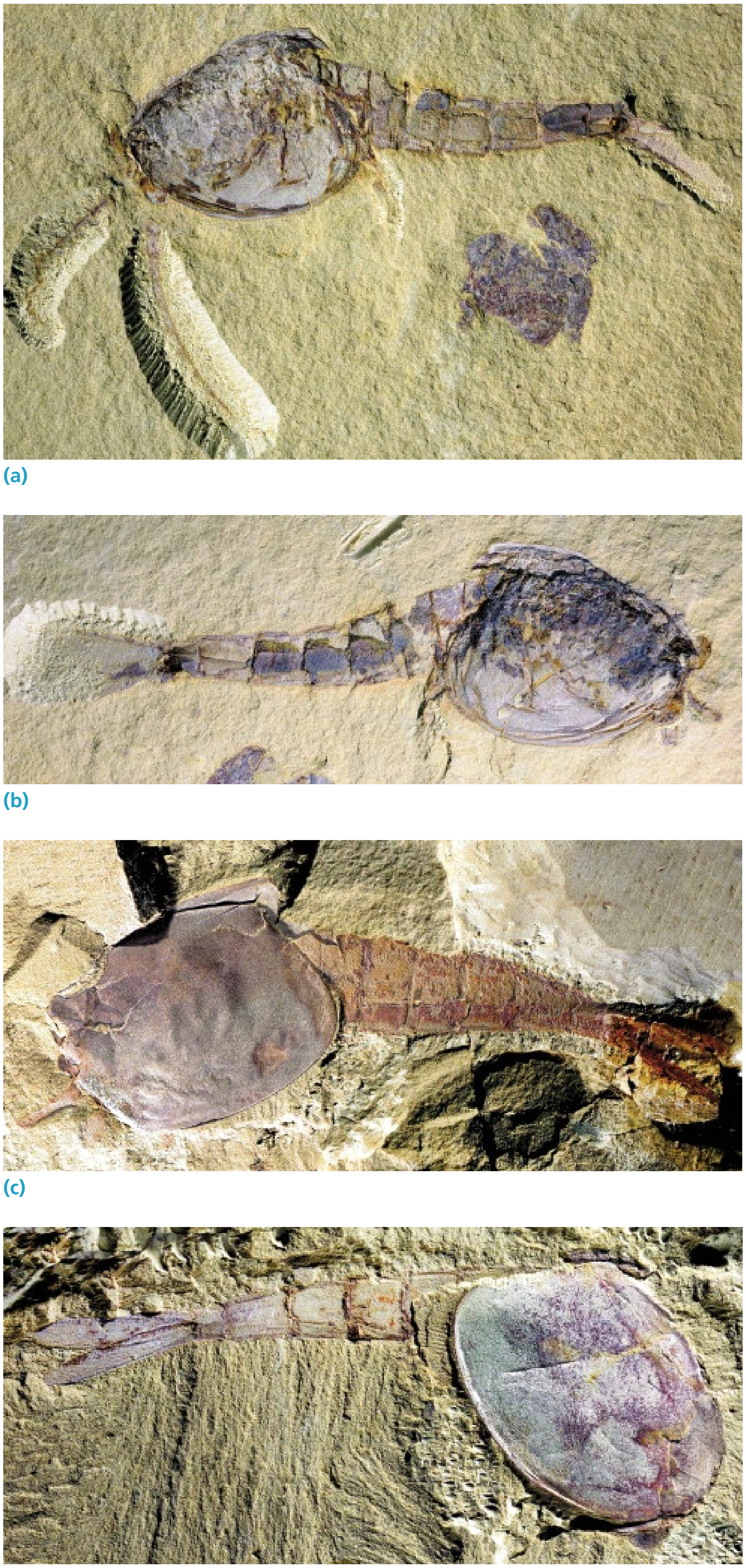


Figure 20.61 Reconstruction of ***Chuandianella ovata*** (based on Hou *et al*. 2004a). The post-antennal appendages are not known in detail and their reconstruction is tentative.

Figure 20.62 ***Chuandianella ovata***. **(a)** YKLP 13967a, ×3.5; Mafang, Haikou, Kunming. **(b)** YKLP 13968b, ×3.7; Ercaicun, Haikou, Kunming. **(c)** NIGPAS 115376, ×3.3; Maotianshan, Chengjiang. **(d)** RCCBYU 10272, ×5.1; Mafang, Haikou, Kunming.



(a)

(b)

(c)

(d)

Genus *Clypecaris* Hou, 1999

Clypecaris pteroidea Hou, 1999

This species was originally described from only one specimen. More material, including soft parts of this species is known, but awaits detailed study.

The thin, unmineralized bivalved carapace, about 5 mm long in the type specimen, covers the head and anterior part of the body. As originally described, paired stalked eyes and annulate antennae project anteriorly from under the carapace (Hou 1999). The number of post-antennal head appendages is uncertain, but considering the length of the head it is likely that there are several pairs. Behind the presumed head region there are about 19 segments, about eight of which are covered by the carapace. All but the last three of these segments appear to bear a pair of biramous appendages. The details of these appendages are unclear, although the supposed exopods seem to be slender and have setae along the margin (Hou 1999). At the posterior terminus of the body, the telson has a pair of wing-like rami. The gut can be clearly traced, in many cases in relief, from the anterior head region to the last segment of the trunk.

Clypecaris was erected as the only member of the Family Clypecarididae. The detailed morphology of the head appendages of *Clypecaris pteroidea* is unclear (Hou 1999) and therefore judgment on its affinity is uncertain. It has been compared to the Burgess Shale genus *Waptia* Walcott, 1912 and the Chengjiang genus *Chuandianella* Hou & Bergström, 1991 based on the shape of its carapace, but it differs in the morphology of its trunk and disposition of its appendages (Hou 1999). *Clypecaris* has been considered as a stem euarthropod (Budd 2002) and as a stem crustacean (Chen Jun-yuan *et al.* 2001), but such assignments require detailed re-evaluation when more evidence is available for the head appendages. The Chengjiang arthropod *Ercaicunia multinodosa* Luo & Hu (*in* Luo *et al.* 1999) may be a synonym of *C. pteroidea*.

The gut of *C. pteroidea* is reported as filled with fine sediment (Bergström & Hou 2005) and the species has been considered to be a deposit feeder (Hou 1999). Its large, flat terminal rami and many biramous appendages hint that it may also have been adapted for swimming.

The species is rare in the Chengjiang area but is more common near Haikou, Yunnan Province.

Key references

Hou 1999; Hou *et al.* 1999, 2004a; Chen Jun-yuan *et al.* 2001; Budd 2002; Bergström & Hou 2005.

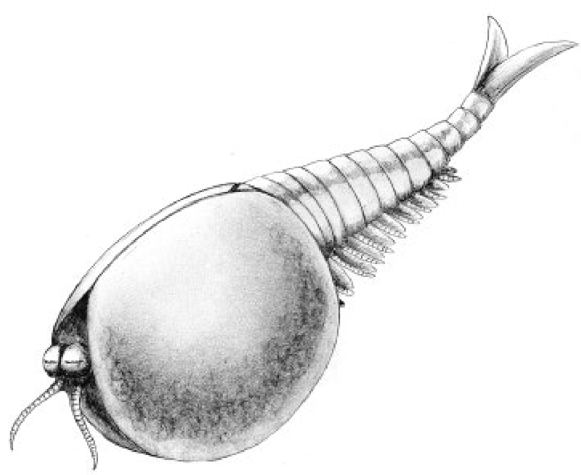


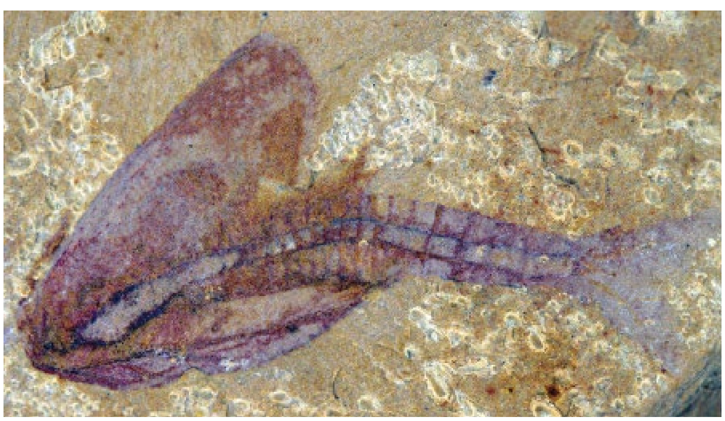
Figure 20.63 Reconstruction of ***Clypecaris pteroidea*** (modified from Hou *et al.* 2004a).

Figure 20.64 ***Clypecaris pteroidea*****.** **(a)** YKLP 13969, ×5.8; Mafang, Haikou, Kunming. **(b)** YKLP 13970, ×7.0; Mafang, Haikou, Kunming. **(c)** NIGPAS 115413, ×7.8; Xiaolantian, Chengjiang. **(d)** RCCBYU 10273, ×9.1; Mafang, Haikou, Kunming.

(a)

(b)

(c)



(d)

Genus *Combinivalvula* Hou, 1987

Combinivalvula chengjiangensis Hou, 1987

This species is known from several specimens, typically preserved with a little relief and in dorsal aspect. The compacted carapace is usually strongly wrinkled, indicating that in life it was probably thin and unmineralized.

The carapace is elongate, up to about 1.5 cm long and vaulted. A furrow marks the dorsal junction of the two sides of the carapace, but is developed only posteriorly: this feature facilitates identification of this species even if the fossil is strongly distorted and also implies that the carapace was not designed to open and close. Little is known of the soft parts, but dark patches mark the position of large, possibly pedunculate paired eyes that project just beyond the front of the carapace. A third dark patch between the paired eyes has been interpreted as a median eye (Zhang Xing-liang & Shu 2007). The body is poorly preserved, but appears to taper to a point immediately beyond the posterior margin of the carapace. Zhang Xing-liang and Shu (2007) estimated there to be between 15 and 20 body segments, though the evidence for this is unclear. Head appendages are not preserved, but the flap-like exopods of the trunk appendages decrease in size from the anterior to posterior (Zhang Xing-liang & Shu 2007). A dark, broad, elongate structure at the midline of the posterior of the animal has been interpreted as the gut (Zhang Xing-liang & Shu 2007).

Although *Combinivalvula* has carapace features that seem comparable to *Isoxys* and some bradoriids, the absence of detailed information about its soft anatomy, particularly about the morphology of its head and trunk appendages, means that the affinities of *Combinivalvula* are imperfectly known. Likewise, its ecology is uncertain.

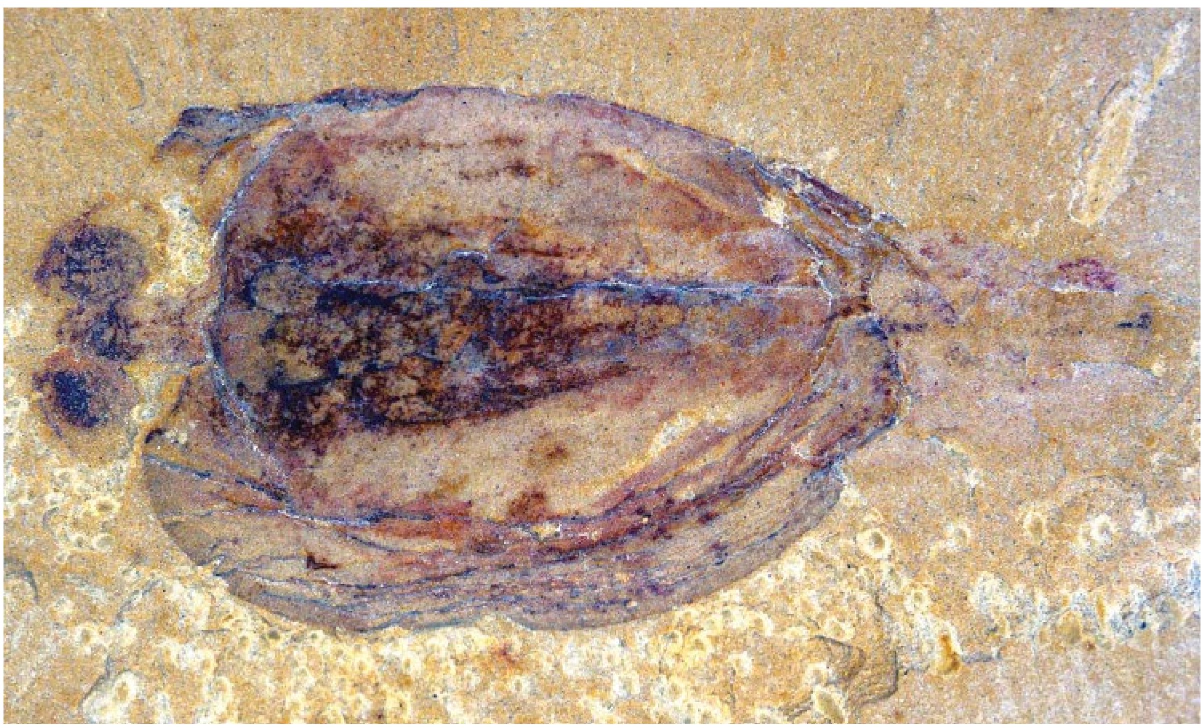
C. chengjiangensis is known only from the Chengjiang biota.

Key references

Hou 1987c; Hou *et al.* 1999, 2004a; Zhang Xing-liang & Shu 2007.

Figure 20.65 ***Combinivalvula chengjiangensis***. **(a)** NIGPAS 100156, ×5.5; Maotianshan, Chengjiang. **(b)** NIGPAS 115416, ×15.7; Xiaolantian, Chengjiang.

(a)



(b)

Genus *Synophalos* Hou, Siveter, Aldridge & Siveter, 2009

Synophalos xynos Hou, Siveter, Aldridge & Siveter, 2009

Synophalos xynos is preserved in unusual fashion, as a series of straight to twisted chains of two to some twenty linked individuals. There are 22 such chain-like associations known. The type specimen, alone, is preserved as a solitary individual. The name *Synophalos,* meaning "to journey in company under the sea," alludes to the activity shown by the type and only species.

Each individual consists of a simple carapace anterior to the exposed abdomen. Crumpling of the carapace and distortion of the abdomen indicate that the cuticle was thin and flexible. Appendages are unknown. The carapace is subovoid in lateral outline and is dorsomedially folded and apparently lacks a true hinge. Ventral overlap of the sides of the carapace is pervasive and presumably post-mortem as both right over left and vice versa modes occur. The abdomen comprises six or possibly seven presumably apodous segments that gradually taper in width and increase in length posteriorly. There is a short telson bearing a horizontal caudal furca with unsegmented, spatula-like rami. Excluding the telson and caudal furca the holotype is 2.38 cm long. The carapaces of individuals in the chains range from about 5 to 9 mm long.

The affinity of *Synophalos* is problematic, particularly as appendages are unknown. It most resembles species that have been assigned to the Waptidae, such as the type species *Waptia fieldensis* from the Burgess Shale of British Columbia and specimens assigned to *Chuandianella ovata* from the lower Cambrian of south-west China (Hou *et al*. 2009b). The taxonomic affinity of *Waptia* is unclear, but it has traditionally been regarded as a putative crustacean.

The individuals in each chain all point in the same direction and are linked by the insertion of at least the telson and caudal furca into the carapace of the individual behind. Individuals in some of the chains are variously stretched, bent, twisted, or telescoped together, but each chain maintains its integrity. This pattern is possibly the result of the chain being pelagic in life and falling to the sediment on death (Hou *et al*. 2009b). The configuration of these chains – robustly integrated and strictly linear aggregations of individuals – is seemingly unique for any fossil or living arthropod. It suggests a collective behavioral strategy, the earliest known amongst animals and a rare example from the fossil record (Hou *et al*. 2008, 2009b).

S. xynos is known only from the lower Cambrian type locality, near Haikou, in Yunnan Province.

Key references

Hou *et al*. 2008, 2009b.

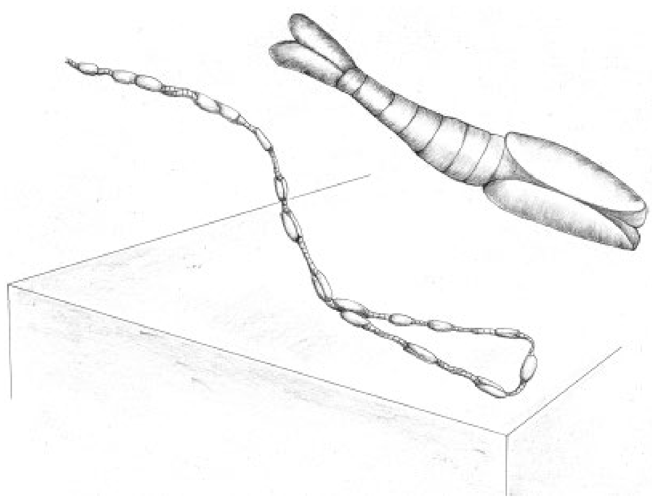
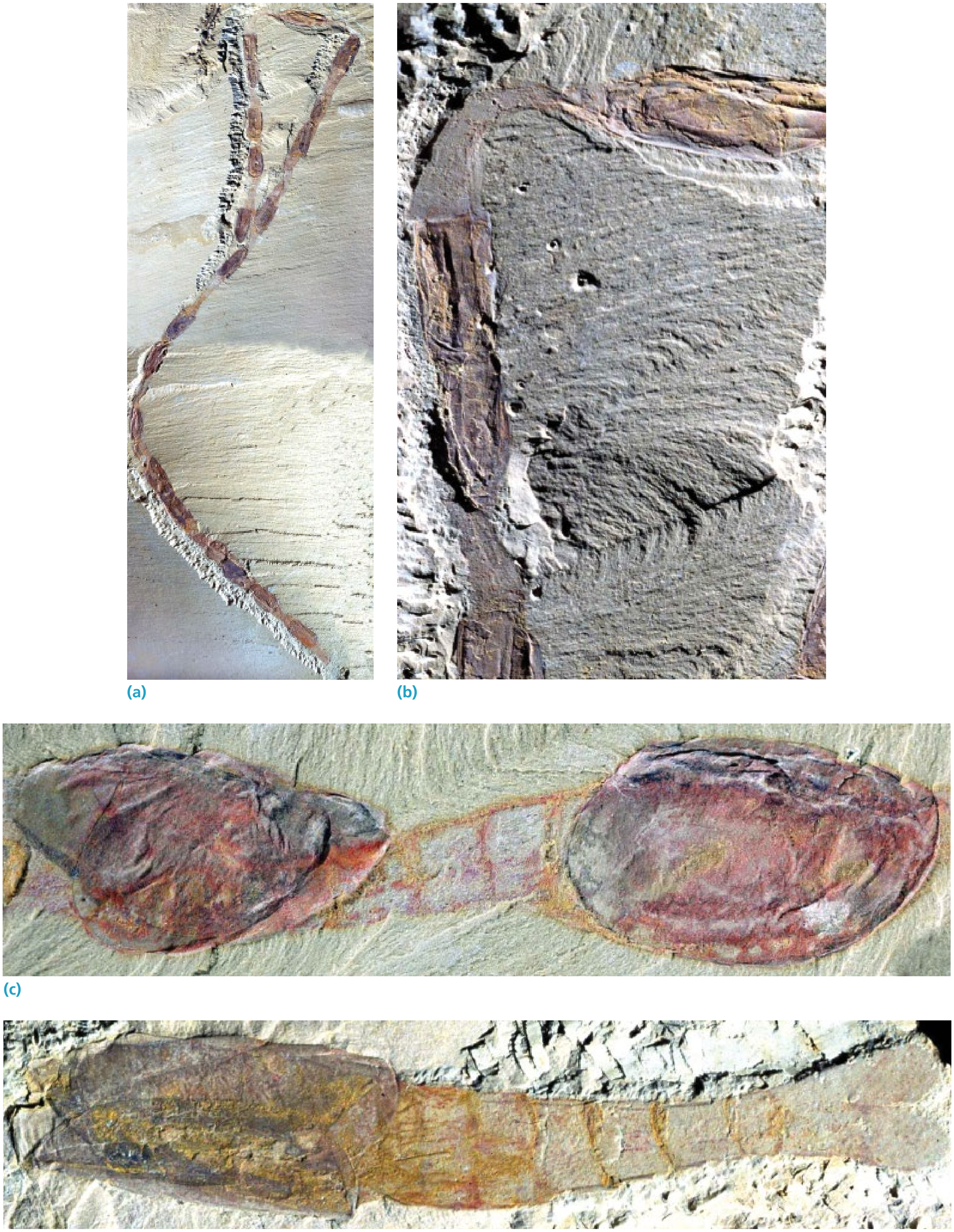


Figure 20.66 Reconstruction of ***Synophalos xynos***; a single specimen in ventral view and a chain of specimens (modified from Hou *et al*. 2008 and Hou *et al*. 2009b).

Figure 20.67 ***Synophalos xynos*. (a)** Composite image of YKLP 11020a and YKLP 11020b, ×1.0; Aa'shan section, Mafang, Haikou, Kunming. **(b)** Part of YKLP 11020a, ×4.3; Aa'shan section, Mafang, Haikou, Kunming. **(c)** YKLP 11021, ×6.5; Aa'shan section, Mafang, Haikou, Kunming. **(d)** YKLP 11019, ×7.4; Aa'shan section, Mafang, Haikou, Kunming.



(a) **(b)** **(c)** **(d)**

Genus *Yunnanocaris* Hou, 1999

Yunnanocaris megista Hou, 1999

This arthropod is known from only a few bivalved carapaces that show modest relief.

Each valve of the carapace of *Yunnanocaris megista* is large and suboval, rounded both anteriorly and posteriorly, and has a relatively straight and short dorsal margin measuring about half the length of the valve. The most complete carapace is 7.1 cm long and 5.3 cm high; the holotype specimen is broken posteriorly and is 5.5 cm long and 4.4 cm high. In lateral view the valves show a marked backward swing. The valve surface lacks ornament but has concentric wrinkles and irregular ridges and depressions that result from compaction of the convex valves (Vannier *et al*. 2006). No appendages or other soft parts of *Y. megista* are known.

The overall carapace shape of *Y. megista* is similar to the Chengjiang species *Chuandianella ovata* (Lee, 1975), from which it differs in being much larger (Hou 1999).

In the absence of knowledge of its soft parts the affinities and mode of life of *Y. megista* are unclear.

Yunnanocaris is known from only a single, Chengjiang biota species recorded from the Xiaolantian and Maotianshan localities.

Key references

Hou 1999; Hou *et al*. 1999, 2004a.

Figure 20.68 ***Yunnanocaris megista***. NIGPAS 115415, ×2.2; Maotianshan, Chengjiang.

21 Chaetognatha

Chaetognaths (arrow worms) are very abundant, tiny, streamlined predators numbering more than 120 species today. Their position within the plexus of major bilaterian groups is uncertain. Most Recent chaetognaths live permanently in the water column. They are ecologically important because they provide a large proportion of the marine biomass, and are a key part of the food web both as consumers and as a food source for larger animals (Vannier *et al*. 2007). The fossil record of body fossils of chaetognaths is extremely sparse. Their only hard parts with high preservation potential are chitinous circumoral grasping spines and teeth. Small spine-like fossils known as protoconodonts, which are common in the Cambrian, are widely accepted as the possible elements of the grasping apparatuses of chaetognaths (Vannier *et al*. 2007).

Genus *Protosagitta* Hu *in* Chen, Luo, Hu, Yin, Jiang, Wu, Li & Chen, 2002

Protosagitta spinosa Hu *in* Chen, Luo, Hu, Yin, Jiang, Wu, Li & Chen, 2002

Protosagitta spinosa is known with certainty from just one specimen, which is some 3.5 cm long. It is well preserved, showing the entire soft body with external and internal features.

The general morphology of *P. spinosa* is similar to Recent chaetognaths, indicating that the body plan of the group was already established by the early Cambrian (Hu 2005; Vannier *et al*. 2007). The head is short and bears two symmetrical sets of lateral grasping spines around the area of the mouth. It is separated by a constriction from a cylindrical trunk, and then a more slender tail whose distal part is mostly missing. A narrow, axial digestive tract terminates at the presumed anus located at the boundary between trunk and tail. Possible muscles, ovaries, and at least one pair of lateral fins and a caudal fin are also evident.

The systematic position of chaetognaths is problematical. The group has traditionally been assigned to the deuterostomes but molecular phylogenetics has indicated an affinity with protostomes (Dunn *et al*. 2014). The Chengjiang taxon *Eognathacantha ercainella* Chen & Huang, 2002, from the same locality as *P. spinosa,* is possibly the same species.

Like living chaetognaths, *P. spinosa* is presumed to have been a predator, swimming and passively sinking in the water column, perhaps close to the sea bottom (Vannier 2007; Vannier *et al*. 2007; Hu *et al*. 2007). The grasping spines of the circumoral apparatus almost certainly had a raptorial function, which places Cambrian chaetognaths amongst the earliest active predator metazoans.

The single specimen of *P. spinosa* is from Ercaicun, Haikou, Kunming, and represents the earliest record of the group.

Key references

Chen Liang-zhong *et al.* 2002; Hu 2005; Vannier *et al*. 2007; Hu *et al*. 2007.

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Figure 21.1 ***Protosagitta spinosa***. YIGS CHE-f-1001, ×47.8; Ercaicun, Haikou, Kunming.

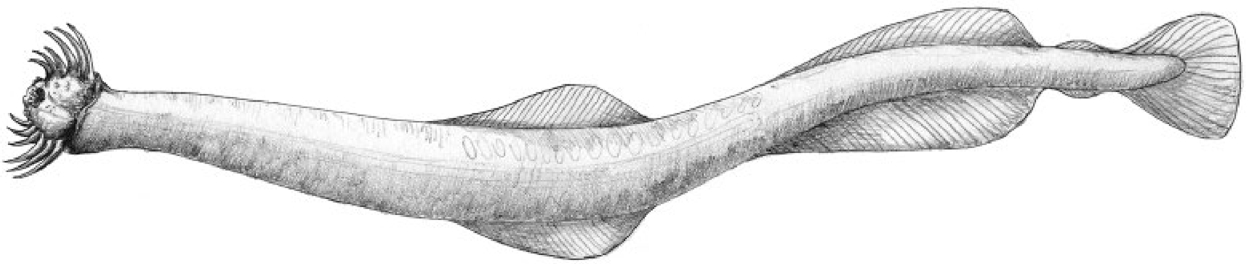

Figure 21.2 Reconstruction of the Recent chaetognath ***Sagitta*** (modified from Vannier 2007 and Vannier *et al*. 2007).

22 Hemichordata

Hemichordates are the sister group to the echinoderms and comprise animals with a tripartite body plan. There are two main classes within the phylum, the enteropneusts (acorn worms) and the pterobranchs. The Chengjiang fossil *Yunnanozoon lividum* has been interpreted to be an enteropneust (Shu *et al.* 1996b), but there are several alternative views regarding the nature of this enigmatic animal. More recently, the species *Galeaplumosus abilus* from the Chengjiang biota has been described as a pterobranch (Hou *et al.* 2011). Pterobranchs have a muscular cephalic shield, one or more pairs of tentacular arms, and a trunk that houses the digestive system and the gonads and extends into a stalk that may connect with other individuals to form a colony; each zooid is usually housed within a secreted tube. Apart from the graptolites, which are common in lower to middle Paleozoic strata, hemichordates are very rare in the fossil record.

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Genus *Galeaplumosus* Hou, Aldridge, Siveter, Siveter, Williams, Zalasiewicz & Ma, 2011

Galeaplumosus abilus Hou, Aldridge, Siveter, Siveter, Williams, Zalasiewicz & Ma, 2011

This species is known from a single specimen from the Chengjiang biota. It comprises a conical tube, 1.4 cm long, from which two arms extend. The tube expands from about 0.5 mm to 4 mm and narrows slightly at the presumed apertural margin. Fine, transverse, subparallel lines, approximately 100 μm apart, are evident on parts of the tube and have been interpreted to be fusellar rings similar to those in the tubes of graptolites. Within the tube is a weakly three-dimensional longitudinal structure that projects toward the arms; this has been interpreted as a putative contractile stalk.

Only the most proximal part of one of the arms is preserved in the specimen, but the other is 2.25 cm long and bears at least 36 pairs of annulated tentacles. The tentacles are regularly spaced, approximately equal in size, and up to 2.5 mm long; each tapers gradually, and some show annulation, a central linear structure, and probable cilia.

That *Galeaplumosus* is a hemichordate is not universally accepted. It has been suggested that the arm and the tube may be fragments of separate organisms that have become accidentally superposed (Maletz 2014). It is difficult to refute this speculation unequivocally on the basis of a single specimen, but it seems unlikely that two fragments have become so fortuitously associated as to mimic so precisely the expected anatomy of an early pterobranch zooid.

Galeaplumosus abilus was probably benthic with the tentaculate arms used in filter feeding.

Key references

Hou *et al.* 2011; Maletz 2014.

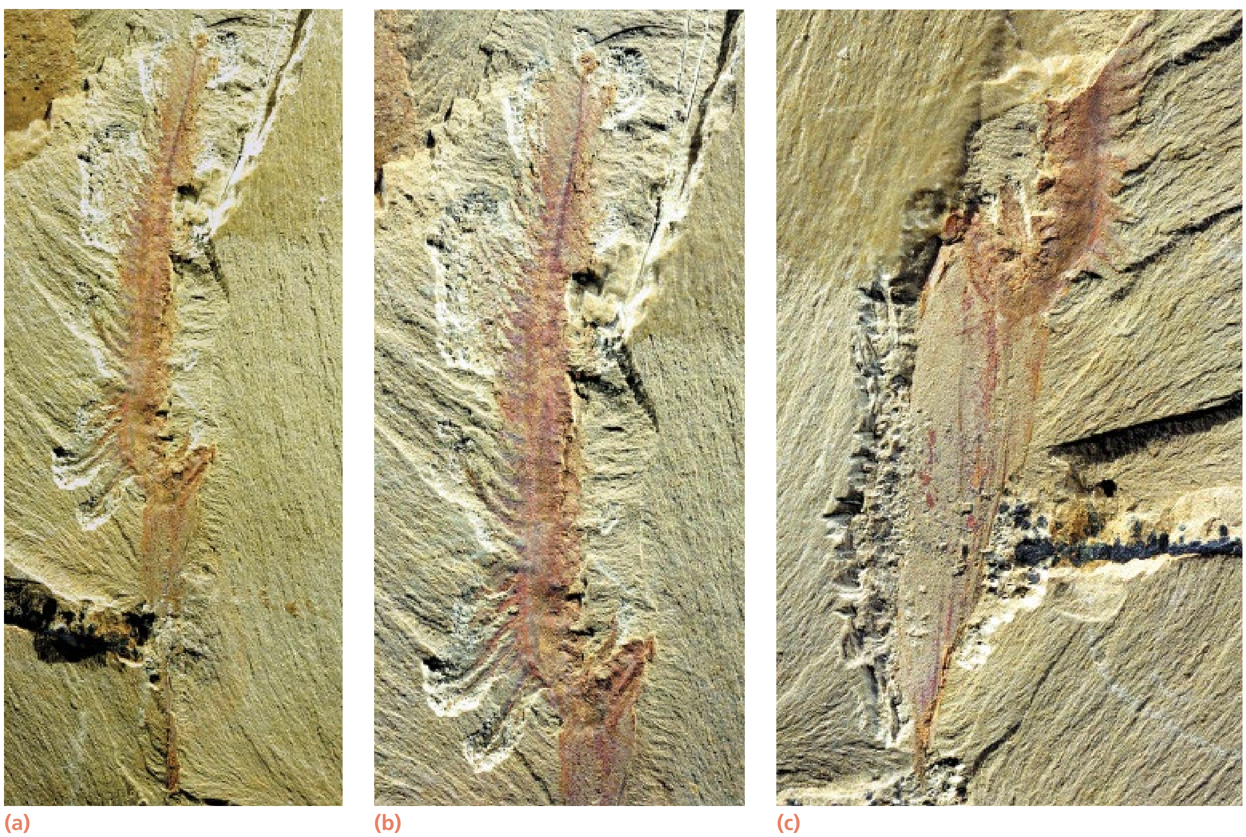

Figure 22.1 ***Galeaplumosus abilus***. **(a), (b)** YKLP 11042a, ×2.5, ×4.8; Mafang, Haikou, Kunming. **(c)** YKLP 11042b, ×3.9; Mafang, Haikou, Kunming.

23 Ambulacraria of Uncertain Affinity

Ambulacraria comprises the Echinodermata – including starfish, brittle stars, sea urchins, and crinoids – and the less familiar hemichordates (pterobranchs and acorn worms). Three taxa are considered here. *Phlogites*, *Eldonia*, and *Rotadiscus* were originally considered to be quite different animals because of the differences in their gross body shape, but they are now generally recognized as a clade. Similarities in their sclerotized organic outer covering and guts (Hou *et al*. 2006a), and evidence from the Burgess Shale genus *Herpetogaster,* have led to a working hypothesis that these taxa form a clade (Caron *et al*. 2010). Members of this clade, informally referred to as cambroernids, share a distinct and identifiable body plan diagnosed on the basis of prominent feeding tentacles and a coiled sac, housing a conspicuous gut.

Speculation about the affinities of *Eldonia*, *Rotadiscus*, and *Phlogites* has ranged widely. *Eldonia* was originally thought to be a pelagic holothurian (sea cucumber) (Walcott 1911a), and thus a member of the Echinodermata. That idea was subsequently supported by several authors, but others assigned *Eldonia* to the cnidarians. A holothurian affinity is difficult to support because *Eldonia* preserves no evidence of pentameral symmetry or of a mesodermal calcitic skeleton (Dzik 1991), and that study concluded that *Eldonia* and similar animals possessed a lophophore and were therefore related to brachiopods and bryozoans. *Rotadiscus* (previously interpreted as a medusoid) and *Dinomischus* were also considered to be part of this grouping (Dzik 1991). Others have speculated that *Eldonia* and *Rotadiscus* evolved through heterochronic retention of the larval stage of a *Facivermis*-like ancestor (Chen Jun-yuan & Zhou 1997).

Phlogites (under the name *Cheungkongella)* has been interpreted as a tunicate (Shu *et al*. 2001a), or a lophophorate with a particular resemblance to, but questionable relationship with, bryozoans (Luo *et al*. 1999; Chen Jun-yuan *et al.* 2003). *Phlogites* was also invoked as part of a scenario for the origin of tentaculate phyla from worm-like ancestors by heterochronic retention of ciliary feeding into adult life stages (Hou *et al.* 2006a); according to this *Phlogites* lay somewhere among the Spiralia on the stem of the Gnathifera (a clade including the phyla Gnathostomulida, Micrognathozoa, and Rotifera).

Taken together as cambroernids (Caron *et al*. 2010), *Phlogites*, *Eldonia*, and *Rotadiscus* were compared to tentaculate lophotrochozoans and ecdysozoans, but ultimately these hypotheses were rejected in favor of a relationship with deuterostomes. Three possible affinities within deuterostomes were considered: that cambroernids are stem echinoderms, stem hemichordates, or lie on the stem of the clade that combines the two, the Ambulacraria. This is reminiscent of earlier discussions of *Phlogites* (Smith, A.B. 2004; Swalla & Smith 2008). Although somewhat tentative and not without critics (Maletz 2014), the hypothesis that cambroernids are stem ambulacrarians or possibly stem hemichordates has gained some currency (e.g., Erwin & Valentine 2013).

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Genus *Rotadiscus* Sun & Hou, 1987

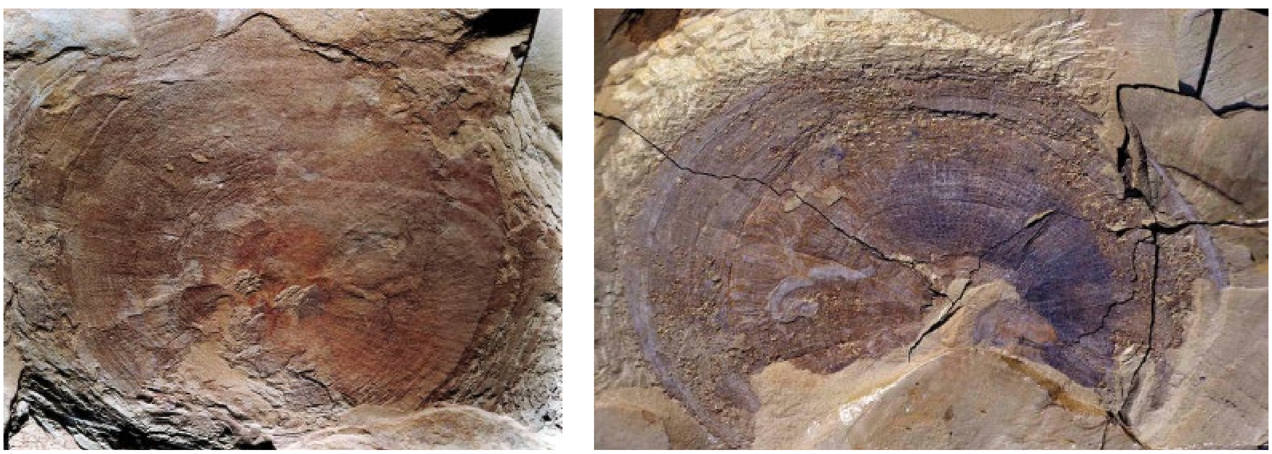
Rotadiscus grandis Sun & Hou, 1987

Several tens of specimens are known of this large discoidal animal, up to 15 cm in diameter, preserved as flat impressions with little relief. The fossil has two distinct surfaces. One surface, or disk, is sclerotized and covered with numerous fine radial lines and closely spaced concentric rings, with spots arranged radially between the radial lines. The other surface is separate and has a number (88 according to Zhu *et al.* 2002) of paired radial structures. A coiled structure between the two surfaces is interpreted as the gut. The tentacles, of which there is a single pair, bifurcate once at their base (Zhu *et al.* 2002).

Some specimens in the Chengjiang biota have been found with juvenile individuals of the lingulate brachiopod *Lingulellotreta malongensis* attached to them (Chen Jun-yuan & Zhou 1997). A closely similar species, *Pararotadiscus guizhouensis,* has been reported from the Middle Cambrian Kaili fauna of Guizhou Province (Zhao Yuan-long & Zhu 1994), and some of these specimens are encrusted by shelled epizoans of unknown affinities (Dzik *et al.* 1997). This evidence of epibiont encrustation supports an interpretation of *Rotadiscus* as a sedentary epibenthic animal, which lay on the sea floor with the convex side of the disk facing downwards (Dzik *et al.* 1997). The ecology of *Rotadiscus* is considered in more detail under discussion of the related genus *Eldonia*.

Key references

Sun & Hou 1987a; Chen Jun-yuan & Zhou 1997; Dzik *et al.* 1997; Zhu *et al.* 2002.



(a) (b)

Figure 23.1 ***Rotadiscus grandis***. (a) RCCBYU 10308, ×1.0; Maotianshan, Chengjiang. (b) RCCBYU 10309, ×0.8; Xiaolantian, Chengjiang.

Genus *Eldonia* Walcott, 1911

Eldonia eumorpha (Sun & Hou, 1987)

This is one of the most frequently found fossils in the Chengjiang biota and often occurs in associations of several individuals. It is preserved as nearly flat discoidal impressions, but with a low relief defining the margin and picking out some internal structures.

The fossils are large, up to over 10 cm in diameter, with a circular outline; the presence of concentric lines is either evidence of marginal accretion, or is an artifact of compression of a bell-shaped disk (Zhu *et al.* 2002). Distinct strands radiate from the center to the margin: there are about 80 dorsal so-called canals, which have been interpreted as a fluid-filled hydrostatic skeleton, or part of a water vascular system or internal support structures (Zhu *et al.* 2002); the ventral canals, about 40 in number, do not show three-dimensional preservation, and have been interpreted as mesenteries separating radiating lobes (Zhu *et al.* 2002). A U-shaped or dextrally coiled structure, sometimes darkened in color, surrounds the center of the disk at about two-thirds of the distance from the margin. This is considered to be the gut, with the oral and anal ends situated close to each other. A pair of tentacular structures surround the mouth, each set ramifying distally. Evidence of decay of tentacles suggests that they are less resistant to decay than the disk (Caron *et al.* 2010).

Eldonia eumorpha was originally described under the name of *Stellostomites eumorphus* (Sun & Hou 1987a), but was subsequently considered to be a species of *Eldonia*. As well as being common in the Chengjiang biota, *Eldonia* is a well-known component of the fauna of the Burgess Shale. The differences between the Chengjiang and Burgess Shale specimens are considered by some authors to warrant generic separation (Zhu *et al.* 2002).

The ecology of *Eldonia* and the related *Rotadiscus* is controversial. For many years their medusoid shape led to interpretations that they were pelagic (e.g., Chen Jun-yuan *et al.* 1995e; Chen Jun-yuan & Zhou 1997), and the sometimes close association of *Eldonia* with *Microdictyon* or *Paucipodia* led some to conclude that these lobopodians were pseudopelagic riders on their pelagic host (Chen Jun-yuan & Zhou 1997). Others argued that *Eldonia* and *Rotadiscus* were benthic epifaunal deposit feeders, lying passively on the mud surface with tentacles raised (Dzik *et al.* 1997). Alternatively, the tentacles could have swept across the sea floor, and although there is no evidence of gas-filled chambers to confer buoyancy it is possible that eldoniids were semivagrant rather than completely sedentary (Dzik *et al.* 1997; Caron *et al.* 2010).

E. eumorpha has been recorded only from the Chengjiang biota.

Key references

Sun & Hou 1987a; Chen Jun-yuan *et al.* 1995e; Chen Jun-yuan & Zhou 1997; Dzik *et al.* 1997; Zhu *et al.* 2002.

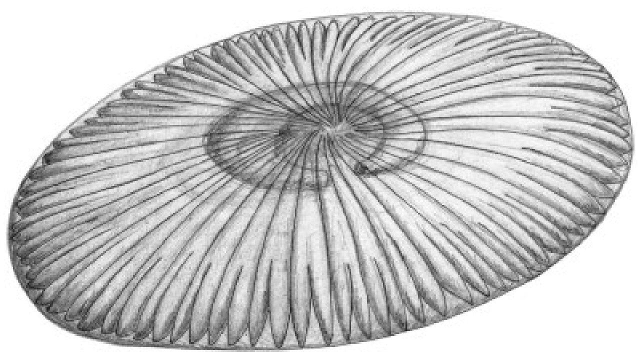


Figure 23.2 Reconstruction of ***Eldonia eumorpha***.

Figure 23.3 ***Eldonia eumorpha***. **(a)** RCCBYU 10304a, ×1.5; Maotianshan, Chengjiang. **(b)** RCCBYU 10304b, ×1.4; Maotianshan, Chengjiang.

(a)

(b)

Genus *Phlogites* Luo & Hu *in* Luo, Hu, Chen, Zhang & Tao, 1999

Phlogites longus Luo & Hu *in* Luo, Hu, Chen, Zhang & Tao, 1999

This chalice-shaped animal is known from a few tens of specimens, ranging in size between 1 cm and 5 cm long.

Phlogites longus had a body comprising a basal stalk or stolon, an expanded, bell-shaped theca or calyx, and a number of tentacles. Wrinkled preservation indicates that the calyx was stiffened but was not mineralized. The calyx contains a twisted tube interpreted as a gut, and, toward the distal part of the calyx, two to three ovate structures with some relief, possibly the remains of reproductive structures of some sort. A slightly expanding upper collar-like region is divided from the main body of the calyx by a slight constriction, and attached to this collar are the tentacles. Like the calyx, the tentacles were stiffened; they show dichotomous branching with simple terminations, and preserve internal strands that extend into the distal part of the calyx. These strands might be the remains of blood vessels and/or coelomic cavities. The basal stalk is effectively continuous with the body, and preserves fine longitudinal and transverse strands and lineations. In many specimens with a complete stalk it is seen to be attached to a hard substrate, such as trilobite fragments.

The Chengjiang genus *Cheungkongella* Shu *et al*., 2001 (type species *Cheungkongella ancestralis*), was originally interpreted as a tunicate. Other authors argue convincingly that the single specimen of *C. ancestralis*, from the same horizon and locality as *P. longus*, is simply a taphonomic variant of the latter taxon, in which the tentacles are either unpreserved or unexposed (Chen Jun-yuan *et al.* 2003; Hou *et al.* 2006a). Shu *et al*. (2010) maintain that it is a separate taxon. *Phlogites brevis* Luo & Hu *in* Luo *et al*., 1999 is also considered to be conspecific with *P. longus*.

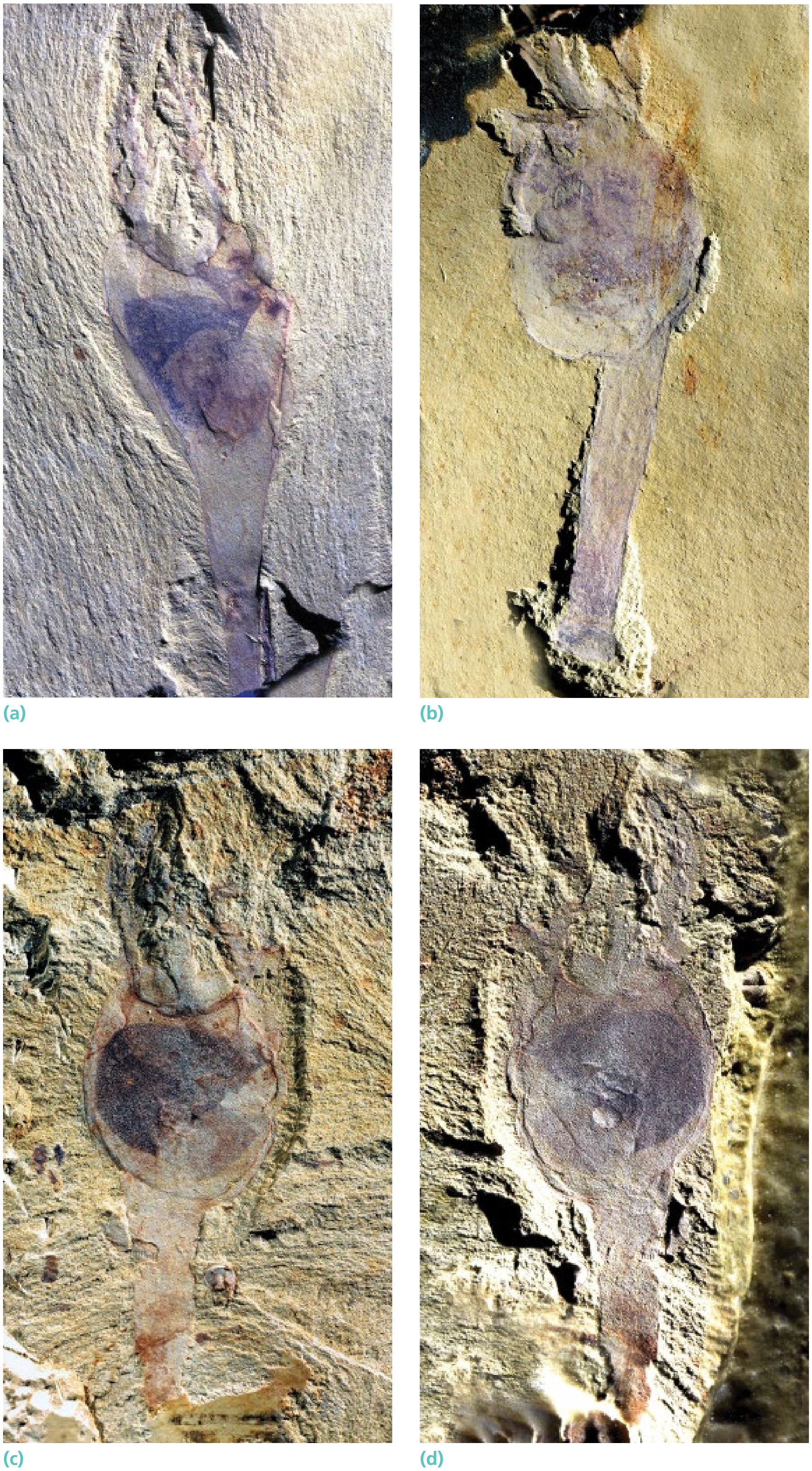
Compared to other cambroernids, the mode of life of *Phlogites*, with its stalk and basal attachment, is less controversial. It is presumed to have been a suspension feeder, using its ciliated tentacles to capture food particles, while attached to the sea floor (Hou *et al.* 2006a; Caron *et al.* 2010).

P. longus is known only from the Ercaicun section, at Haikou, Kunming, Yunnan Province.

Key references

Luo *et al.* 1999; Chen Jun-yuan *et al.* 2003; Hou *et al.* 2006a; Caron *et al.* 2010.

Figure 23.4 ***Phlogites longus***. **(a)** YKLP 13204b, ×2.7; Erjie, Jinning. **(b)** YKLP 10398a, ×2.3; Ercaicun, Haikou, Kunming. **(c)** YKLP 13206a, ×3.5; Ercaicun, Haikou, Kunming. **(d)** YKLP 13206b, ×3.1; Ercaicun, Haikou, Kunming.


(a)
(b)
(c)
(d)

24 Chordata

Chordates comprise three clades of anatomically disparate organisms – Cephalochordata, Urochordata, and Vertebrata – each commonly recognized as a phylum or subphylum. Fossils interpreted as representatives of each of these clades are recorded in the Chengjiang biota, although some are extremely rare, and only a handful of species are known; phylogenetic placement of most of them is not uncontroversial.

As a range of Chengjiang organisms attest, interpretation and phylogenetic placement of exceptionally preserved fossil remains of organisms that lack character-rich, decay-resistant body parts can be problematic (Donoghue & Purnell 2009), but these difficulties are compounded in chordates because the anatomical features that are most informative regarding correct phylogenetic placement within chordates are also the features that are soonest lost to decay (Sansom *et al.* 2010b). Fortunately, important chordate characteristics, such as the notochord and myomeres, are relatively decay resistant, so although the degree to which they can be accurately placed in the tree of life varies, a number of taxa are securely identified as chordates. Herein the following Chengjiang taxa are considered to be chordates: *Shankouclava* as Urochordata; *Haikouichthys*, *Myllokunmingia*, *Zhongjianichthys*, and *Zhongxiniscus* (some of which might be synonyms) as Vertebrata; and *Cathaymyrus* as a chordate of uncertain affinity. Yunnanozoa, the range of suggested affinities of which includes chordates, are discussed elsewhere, as Bilateria of uncertain affinity (Chapter 25).

Of the various fossils interpreted as deuterostomes and chordates in the Chengjiang biota, the vertebrates are the most securely placed phylogenetically. They thus provide important calibration points for molecular clock analyses of the origins of crown group deuterostomes, crown group chordates, and total group vertebrates (Benton & Donoghue 2007; Benton *et al.* 2015). Furthermore, the vertebrate taxa from the Chengjiang biota provide the oldest fossil evidence of the ecology and anatomy of the common ancestor we share with all other vertebrates. As such, these fossils are widely cited in various hypotheses and scenarios concerning the evolutionary history of vertebrates, including the evolution of body size, vision, central nervous system, and even consciousness (Albert & Johnson 2012; Northcutt 2012; Feinberg & Mallatt 2013; Lamb 2013).

Nevertheless, the number of species of vertebrate present in the Chengjiang biota is uncertain. Four monotypic species have been named: *Myllokunmingia fengjiaoa* Shu, Zhang & Han (*in* Shu *et al.* 1999b), *Haikouichthys ercaicunensis* Luo, Hu & Shu (*in* Shu *et al.* 1999b), *Zhongxiniscus intermedius* Luo & Hu (*in* Luo *et al.* 2001), and *Zhongjianichthys rostratus* Shu, 2003. *Z. intermedius* is dealt with below; the other three species have many features in common, with the vast majority, more than 500 specimens, assigned to *H. ercaicunensis*. It is possible that this species, *M. fengjiaoa*, and *Z. rostratus* are taphonomic variants, and Hou *et al.* (2002a) suggested synonymy, selecting *M. fengjiaoa* as the name for all specimens known at that time. Most subsequent authors have not followed this, with some arguing that the body proportions, the presence of dorsal fin radials and branchial basket, and the number of gill pouches differ between the three species (Shu *et al.* 2003a, 2010). Nevertheless, uncertainty remains regarding the reliability of these characters for distinguishing between these taxa, and the opinion of Hou *et al.* (2002a) is followed herein: the name *Myllokunmingia fengjiaoa* is used.

Genus *Shankouclava* Chen, Huang, Peng, Chi, Wang & Feng, 2003

Shankouclava anningense Chen, Huang, Peng, Chi, Wang & Feng, 2003

Shankouclava anningense, also mistakenly referred to as *Shankouclava shankouense* in Chen Jun-yuan *et al.* (2003), is known from eight specimens from Shankou village, Anning County, after which it is named. A possible ninth

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specimen, described as a shankouclavid, is from the same locality (Shu *et al.* 2010). *S. anningense* is widely accepted and cited as the earliest fossil tunicate.

The bilaterally symmetrical, club-shaped, and originally sac-like body comprises a larger, barrel-shaped part, considered to be anterior, and an elongated, posterior part. The anterior part preserves a gray-colored outer organic layer, within which lies another organic layer and numerous rods or ribs oriented transversely to the long axis of the body; in some specimens these form a network with rectangular openings. These structures are interpreted as a tunic, mantle, and branchial basket, respectively, comparable to the anatomy of tunicates. Structures interpreted as an endostyle, atrial pore, and an oral siphon have also been observed (Chen Jun-yuan *et al.* 2003). The posterior part of the fossils contains dark stains that are interpreted as a U-shaped gut, with a stomach. Traces of transverse banding are considered to be evidence of dorsal segmentation, and structures toward the posterior end of the body are interpreted as stolons. The complete body length of specimens of *S. anningense* is estimated to range from 2 to 4 cm.

Based on these anatomical interpretations *Shankouclava* bears a striking resemblance to single zooids of modern colonial aplousobranch tunicates such as *Clavelina* (Chen Jun-yuan *et al.* 2003). Particular attention was drawn to the similarity of the "tunic and mantle, the large perforated pharyngeal region, with numerous transversely oriented structure/branchial bars, the sac-like peri-pharyngeal atrium, the oral siphon, with what appear to be oral tentacles at its base, the dorsal atrial pore, and the elongated endostyle band on the mid-ventral part of the pharynx" (Chen Jun-yuan *et al.* 2003, p. 8315). That *Shankouclava* is a tunicate is widely accepted (e.g., Smith, A.B. 2004; Schubert *et al.* 2006; Erwin & Valentine 2013), and the striking similarity to aplousobranch ascidians hints that crown-group tunicate divergence may have already occurred by the early Cambrian (Swalla & Smith 2008). However, it has been suggested that this view might need to be reconsidered because of a new (but as yet undescribed) shankouclavid specimen preserving an almost identical body but with anterior tentacles (Shu *et al.* 2010).

The attaching stolons and large branchial basket are taken to indicate that *Shankouclava* was a sessile, rooted solitary suspension feeder resembling, both anatomically and ecologically, individual zooids of modern, colonial, aplousobranch tunicates (Chen Jun-yuan *et al.* 2003).

S. anningense is known only from the lower Cambrian type locality, near Shankou, in Yunnan Province.

Key references

Chen Jun-yuan *et al.* 2003; Swalla & Smith 2008; Shu *et al.* 2010.

Figure 24.1 ***Shankouclava anningense*****.** **(a)** ELCC SK01001b, ×4.5; Shankou, Anning, Kunming. **(b)** ELCC SK01001a, ×3.5; Shankou, Anning, Kunming.

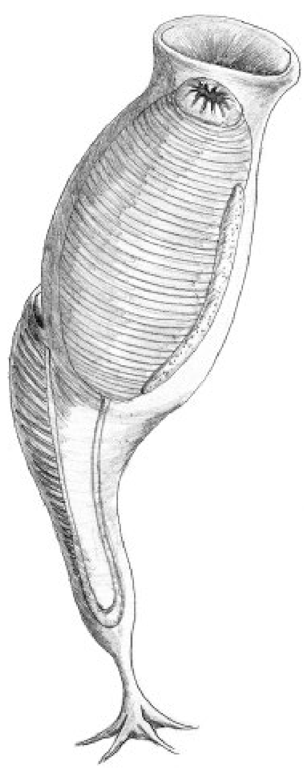


Figure 24.2 Reconstruction of ***Shankouclava anningense*** (modified from Chen Jun-yuan *et al.* 2003).

Myllokunmingia Shu, Zhang & Han *in* Shu *et al.*, 1999

Myllokunmingia fengjiaoa Shu, Zhang & Han *in* Shu *et al.*, 1999

Most specimens of this species (which include those commonly referred to as *Haikouichthys ercaicunensis*) are preserved in lateral aspect, and like many fossil jawless vertebrates they are incompletely preserved posteriorly. A number of specimens preserve the head in dorsoventral aspect, illustrating clearly the bilaterally paired nature of anterior spots interpreted as sensory structures.

The anterior end of the body is differentiated as an area of darker preservation, probably iron oxides after sulfides, with patches of differential coloring and relief interpreted as the remains of cartilages. Many specimens show paired eyes and other possible sensory structures. Ventrally, a set of up to eight gill pouches is preserved, associated in some specimens with gill arches and feathery gill filaments. Behind the head lies a series of arched structures, which are either aligned to form a dorsal row or extend across the entire height of the body and are more complex in shape. The former arrangement has been interpreted as the remains of arcualia associated with a notochord (Shu *et al.* 2003a), but the latter pattern, if it represents the same structures, would make this interpretation unlikely (Hou *et al.* 2002a). A feature interpreted as a possible pericardial cavity is evident above the ventral margin behind the gill pouches. The trunk is characterized by a series of zigzag muscle blocks, the more ventral inflection point of which is associated with a row of depressions that might be the remains of metameric gonads. Along the dorsal margin there is a distinct dorsal fin, in some specimens preserving what appear to be anteriorly inclined radials. Along the ventral margin of the trunk there is a single, or possibly paired, smooth, narrower ventral fin. A trace of the gut has been identified in some specimens and although no specimens are well preserved in the caudal region, there may be a subterminal anus.

There seems to be universal agreement that *Myllokunmingia* (and *Haikouichthys*, if they are distinct species) is a jawless fish sitting somewhere in the total group Vertebrata. This is based on the possession of zigzag muscle blocks, a dorsal fin, filamentous gills, paired sensory structures in the head and, more equivocally, arcualia. Yet phylogenetic analyses have produced a range of results regarding its precise position among vertebrates (e.g., Hou *et al.* 2002a; Shu *et al.* 2003a; Sansom *et al.* 2010a; Conway Morris & Caron 2014). These results partly depend on whether extant hagfish and lamprey are considered to be a clade (Cyclostomata), and in analyses that recognize this, *Myllokunmingia* is resolved as a basal branch on the vertebrate stem lineage (Sansom *et al.* 2010a; Conway Morris & Caron 2014).

With its fins and axial musculature it seems highly likely that *Myllokunmingia* swam by lateral undulations of the body, possibly with an escape response involving powerful tail flips (Lacalli 2012). It has been asserted that *Myllokunmingia* was a suspension feeder (García-Bellido *et al.* 2014), but this appears to be based on a general scenario of chordate origins rather than direct evidence.

Myllokunmingia is known only from the Chengjiang biota, and all Chengjiang vertebrates come from localities around Haikou, including Ercaicun and Mafang, in Yunnan Province.

Key references

Shu *et al.* 2003a, 2010; Hou *et al.* 2002a.

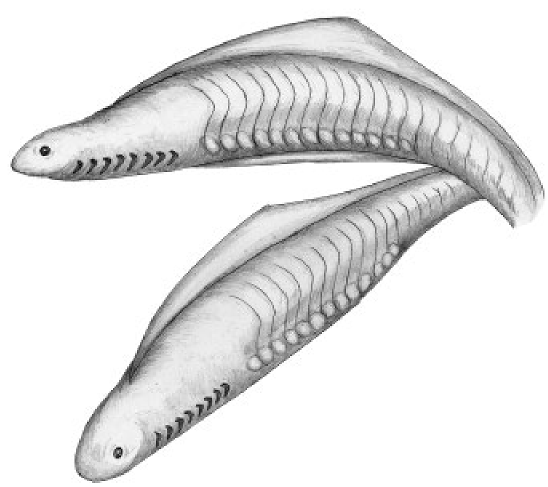


Figure 24.3 Reconstruction of ***Myllokunmingia fengjiaoa***.

Figure 24.4 ***Myllokunmingia fengjiaoa***. **(a)** RCCBYU 10200a, ×3.7; Mafang, Haikou, Kunming. **(b)** RCCBYU 10200b, ×5.7; Ercaicun, Haikou, Kunming. **(c)** Two specimens, YKLP 13608a; ×6.8; Mafang, Haikou, Kunming. **(d)** Putative eyes. YKLP 13608a, ×60.0; Mafang, Haikou, Kunming.

(a)

(b)

(c)

(d)

Genus *Zhongxiniscus* Luo & Hu *in* Luo, Hu & Chen, 2001

Zhongxiniscus intermedius Luo & Hu *in* Luo, Hu & Chen, 2001

Although known only from one specimen, *Zhongxiniscus intermedius* is widely cited among the chordates and vertebrates of the Chengjiang biota (e.g., Shu 2003; Li *et al.* 2007; Zhao Fang-chen *et al.* 2010; Conway Morris & Caron 2012; Donoghue & Keating 2014).

The preserved body outline is spindle-shaped, tapering more posteriorly than anteriorly, with supposedly two triangular fins along the dorsal margin (Luo *et al.* 2001). The specimen is 1.1 cm long. The trunk preserves clear sigmoidal bands (7 per mm) interpreted as myomeres and anterior structures interpreted as the remains of a pharynx (Luo *et al.* 2001).

Largely on the basis of the complexity of the myomeres *Z. intermedius* was considered to be anatomically and phylogenetically intermediate between *Cathaymyrus* and *Myllokunmingia* (*Haikouichthys*) (Luo *et al.* 2001). An alternative but similar interpretation is that *Zhongxiniscus* might be somewhat more advanced than *Cathaymyrus*: the myomeres are not simple chevrons, but their precise disposition is unclear (Conway Morris & Caron 2012). Others have commented that *Zhongxiniscus* and *Cathaymyrus* might be conspecific (Shu 2003), and even that both *Cathaymyrus haikouensis* and *Z. intermedius* might be the poorly preserved remains of the worm *Cricocosmia* (Hou *et al.* 2004a). Unlike *Cathaymyrus*, the possibility that the anatomy of *Zhongxiniscus* reflects decay of a more complex vertebrate (Sansom *et al.* 2010b) has not been investigated.

Current anatomical interpretations suggest that *Zhongxiniscus* is likely to have been an active swimmer. As with *Cathaymyrus*, the extreme rarity of chordates in the Chengjiang biota might be because they avoided burial in benthic sediment flows by swimming away (Shu *et al.* 1999b).

The single specimen is from Ercaicun, near Haikou, Yunnan Province.

Key reference

Luo *et al.* 2001.

Figure 24.5 ***Zhongxiniscus intermedius***. YIGS He-f-6-4-682, ×13.1; Ercaicun, Haikou, Kunming.

Genus *Cathaymyrus* Shu, Conway Morris & Zhang, 1996

Cathaymyrus haikouensis Luo & Hu *in* Luo, Hu & Chen, 2001

Cathaymyrus haikouensis is considered here as a chordate of uncertain affinity. The genus *Cathaymyrus* was erected on the basis of a single specimen, named as *Cathaymyrus diadexus* Shu *et al.*, 1996. A second specimen was assigned to the genus but described as a different species, *C. haikouensis* Luo & Hu, 2001, although whether the differences between the two known specimens are enough to warrant them being assigned to separate species has been questioned (Conway Morris & Caron 2012). The possibility that *Cathaymyrus* is a dorsoventrally collapsed specimen of *Yunnanozoon* (Chen Jun-yuan & Li 1997; Chen Jun-yuan 2011) is not supported by the configuration of myomeres in *Cathaymyrus* and the differences in the nature of the anterior filamentous arches/pharynx (Smith, M.P. *et al.* 2001; Shu *et al.* 2010; Cong *et al.* 2015).

Neither of the specimens assigned to *Cathaymyrus* preserves anything more than a few anatomical features. The body is anguilliform and tapers posteriorly, with sigmoidal bands interpreted as myomeres; their shape and disposition is unclear but they may have been more complex than the simple V-shaped myomeres of extant cephalochordates. Neither specimen preserves evidence of tail fins. Luo *et al.* (2001) identified a distinct dorsal notochord and an intermittent dark ventral line representing the gut. Although the trunk expands anteriorly, the anterior end of *C. haikouensis* is not preserved, so the presence of a large pharynx with closely spaced gill slits, like that interpreted from the anterior striated area in *C. diadexus*, is inferred.

There is a suggestion that *C. haikouensis* might be a poorly preserved specimen of the worm *Cricocosmia* (Hou *et al*. 2004a). Nevertheless, *Cathaymyrus* was originally described as a cephalochordate (Shu *et al.* 1996a), and the view that it represents a chordate of cephalochordate grade seems widely accepted (e.g., Shu *et al.* 1999b, 2010; Conway Morris & Caron 2012). However, *Cathaymyrus* lacks any clear derived characters to unite it with crown group cephalochordates (Budd & Jensen 2000; Donoghue & Purnell 2005), making its precise phylogenetic placement uncertain. The preserved anatomical characters are known to be among the most resistant to decay in non-biomineralized chordates (Sansom *et al.* 2010b), thus the absence of apomorphies could be the result of their non-preservation. According to this view, *Cathaymyrus* specimens are a good example of the phenomenon of stemward slippage, and could be the decayed remains of any non-biomineralized, total-group chordate (Sansom *et al.* 2010b). This interpretation has been contested (Conway Morris & Caron 2012), but only on the basis of erroneous assertions that Sansom *et al*. (2010b) did not mention the pharyngeal structures of *Cathaymyrus* and that there was no counterpart to this in decayed amphioxus. In fact the compelling resemblance of the *Cathaymyrus diadexus* specimen to a decayed cephalochordate, and the pharyngeal structures in particular, was noted and illustrated (Sansom *et al.* 2010b).

The anguilliform body and myomeres of *Cathaymyrus* suggest that it could have been an active swimmer. This has been invoked as the reason for the extreme rarity of chordates in the Chengjiang biota: by swimming away they were able to avoid being buried in benthic sediment flows (Shu *et al.* 1999b).

C. diadexus and *C. haikouensis* are known only from Ma'anshan and Ercaicun respectively, Yunnan Province.

Key references

Shu *et al.* 1996a, Luo *et al*. 2001.

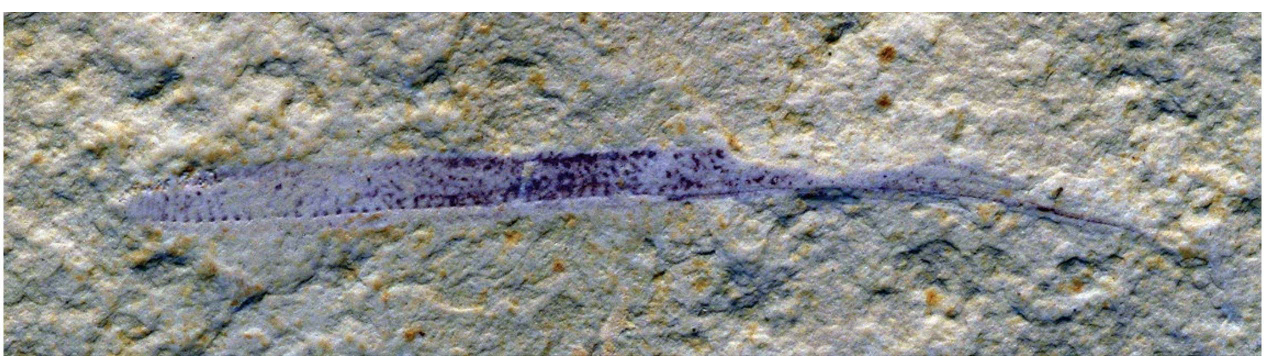


Figure 24.6 ***Cathaymyrus haikouensis***. YIGS Hz-f-12-129, ×9.3; Ercaicun, Haikou, Kunming.

25 Bilateria of Uncertain Affinity

Dinomischus, *Facivermis*, *Vetulocystis*, and *Yunnanozoon* are controversial taxa for which a consensus regarding phylogenetic placement within Bilateria remains elusive. *Dinomischus* has been compared with a range of spiralian clades and putative deuterostomes, and vetulocystids have been interpreted as basal echinoderms, but for neither taxon has any hypotheses of phylogenetic placement met with universal acceptance. The proposed affinities of yunnanozoans have ranged perhaps more widely than any other taxon in the Chengjiang biota. The morphological interpretations and biological affinities proposed for *Facivermis* are also very diverse. The inclusion of these taxa in the same chapter should not be taken to imply a relationship. Vetulicolians would also be at home in this chapter but in view of the much greater taxonomic diversity and anatomical disparity within what is widely accepted as a clade and is thought by some to be a phylum, they are considered in a separate chapter.

Genus *Dinomischus* Conway Morris, 1977

Dinomischus venustus Chen, Hou & Lu, 1989

This species is known from dozens of specimens. Its generic name refers to its fancied resemblance to a wine glass. Specimens can exceed 10 cm in height. Although some are preserved as impressions with low relief, many are more three-dimensional.

Dinomischus venustus is reconstructed as being goblet-shaped, with a tall, slender stem supporting a cone-shaped calyx, the upper margin of which was fringed by a circlet of plate-like structures, termed bracts. The calyx appears to be formed of two parts, one inside the other, together supporting about 18 rigid, plate-like bracts, about 1.2 cm in length. The inner surfaces of the bracts are wrinkled, and outer surfaces are divided into three smooth fields by longitudinal ridges. A single, tall, apparently tubular structure, about 0.8 mm across, extends for some 4.4 cm above the bracts and may represent an excretory tube (Chen Jun-yuan *et al.* 1989c) or a rudder for orientating the bract apparatus against the current (Chen Jun-yuan & Zhou 1997). A large curved sac has been identified within the calyx. The stem is tubular, terminating abruptly where it connects to the base of the calyx, which is noticeably wider than the top of the stem.

Dinomischus was originally described from the Burgess Shale, where it is one of the rare components of the biota. The preservation of the Chengjiang material is generally better: the so-called excretory tube, for example, has not been recognized in the Burgess Shale material. However, the latter specimens do reveal a structure interpreted as a U-shaped gut, a sac-like putative stomach, and also a bulbous swelling at the bottom of the stem that appears to be a holdfast that anchored the animal in the sediment (Conway Morris 1977c). *Dinomischus* shows broad resemblances to a number of other stalked fossils in the Chengjiang biota, such as *Phlogites* and *Cotyledion*, like which it has been compared to entoprocts. This hypothesis, however, is considered doubtful because *Dinomischus* lacks the pliable and foldable tentacles characteristic of extant entoprocts and other morphological details supporting an entoproct affinity (Todd & Taylor 1992; Nielsen 2012). It is also an order of magnitude larger than extant entoprocts, although this is also true of *Cotyledion*, which is considered to be an entoproct. *Dinomischus* has been allied with *Eldonia* and *Rotadiscus* (cambroernids, also present in the Chengjiang biota) and an affinity has been proposed with brachiopods

The Cambrian Fossils of Chengjiang, China: The Flowering of Early Animal Life, Second Edition. Hou Xian-guang, David J. Siveter, Derek J. Siveter, Richard J. Aldridge, Cong Pei-yun, Sarah E. Gabbott, Ma Xiao-ya, Mark A. Purnell, Mark Williams.

and bryozoans on the basis that they possessed a homologous lophophore (Dzik 1991). Neither the relationship with eldoniids nor that with brachiopods and bryozoans has found much subsequent support. Although superficially radial, the body of *Dinomischus* is bilaterally symmetrical (Conway Morris 1977c), and at present it seems prudent to consider *Dinomischus* as a bilaterian animal of uncertain affinity.

Dinomischus probably lived on the sea floor with most of the stem clear of the sediment, holding the calyx above the sea bed. The bracts were probably feeding devices, although their rigidity means that they were not true tentacles; it is possible that they were ciliated and swept suspended food into the mouth, which was situated on the upper surface of the conical calyx (Conway Morris 1977c). A specimen preserved with the bracts spread radially on the sediment surface indicates that they could have been spread in life to form a feeding bowl (Chen Jun-yuan & Zhou 1997).

Although *Dinomischus* is known from the Burgess Shale and the Cambrian Kaili Lagerstätte of China, *D. venustus* has been reported only from the Chengjiang biota of Yunnan Province.

Key references

Conway Morris 1977c; Chen Jun-yuan *et al.* 1989c; Chen Jun-yuan & Zhou 1997; Hou *et al.* 1999, 2004a.

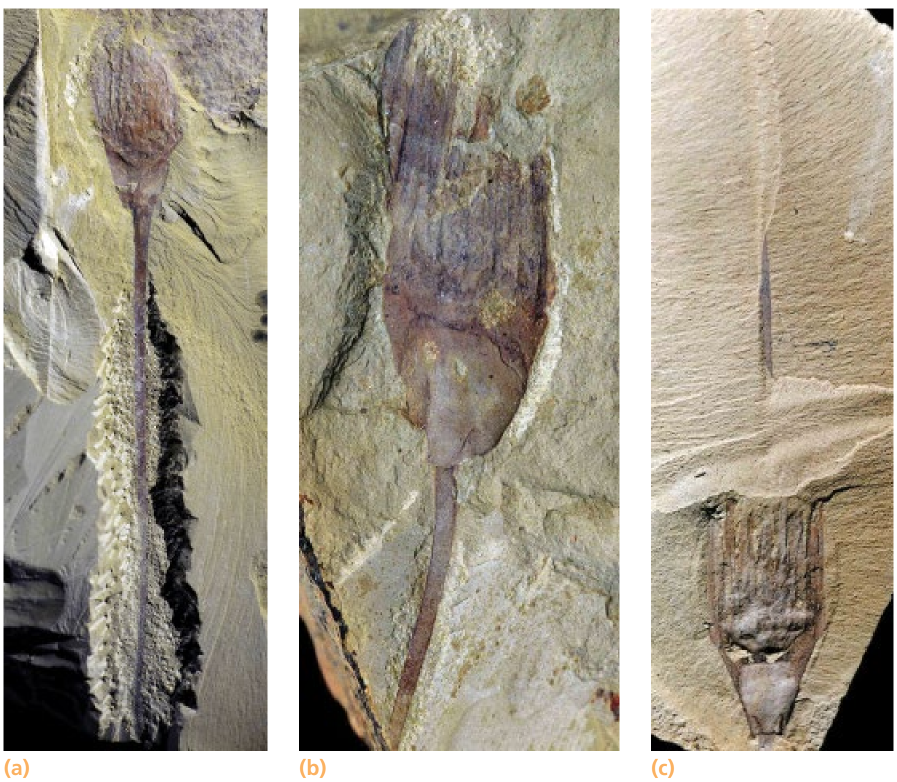


Figure 25.1 ***Dinomischus venustus***. (a) YKLP 13893, ×1.3; Mafang, Haikou, Kunming. (b) RCCBYU 10303, ×2.6; Maotianshan, Chengjiang. (c) NIGPAS 108478a, ×1.4; Maotianshan, Chengjiang.

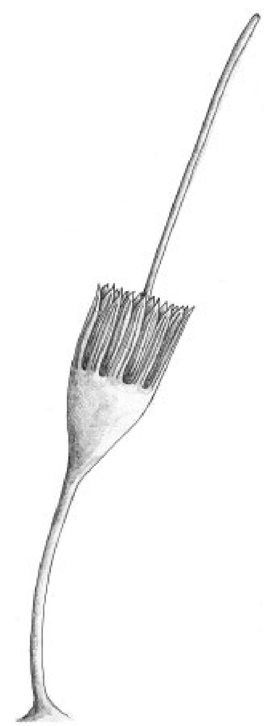


Figure 25.2 Reconstruction of ***Dinomischus venustus*** (modified from Hou *et al.* 2004a).

Genus *Facivermis* Hou & Chen, 1989

Facivermis yunnanicus Hou & Chen, 1989

This is a bilaterally symmetrical animal with a worm-like appearance. The holotype is ×2.4 cm long in its preserved portion, but specimens occur up to ×7 cm in length.

The body of *Facivermis yunnanicus* is interpreted to comprise three portions, with approximate ratios of 1 to 5 to 1 (Liu *et al*. 2006a). Five pairs of annulated lobe-like appendages protrude laterally from the tapered anterior portion of the body. Two rows of setae occur on the anterior and posterior margin of the appendages. The middle, trunk-like portion of the body is elongate, with no appendages (or parapodia). The trunk shows clear annulations or segments, spaced with a density of 50–60 per centimetre. A straight gut running medially in the trunk is preserved as a line of raised relief or as a black organic film. The posterior portion of the body is expanded, and has up to three circlets of hooks.

The morphological interpretations and biological affinities proposed for *Facivermis* are diverse (Hou *et al*. 2004a). Initially it was suggested that it might be related to the annelids, with attention drawn to the fact that the number of appendages (tentacles) in the head region is identical to that of the extant nereid polychaetes. A relationship to lobopodians was subsequently suggested (Hou *et al.* 1991; Delle Cave & Simonetta 1991). Based on more recent interpretation of the appendages, especially their lobe-like morphology and strong attachment with the trunk, and possession of a fine canal running centrally through the entire length of each appendage, a lobopodian relationship was also favored (Liu *et al*. 2006a; Dzik 2011). In a more radical interpretation, Chen Jun-yuan and Zhou (1997) proposed that the tentacles are homologous to the lophophore and designated *Facivermis* as a member of the superphylum Lophophorata. A contrasting idea envisages a possible distant relationship to the pentastomids, an enigmatic group of parasitic arthropods (Delle Cave *et al.* 1998).

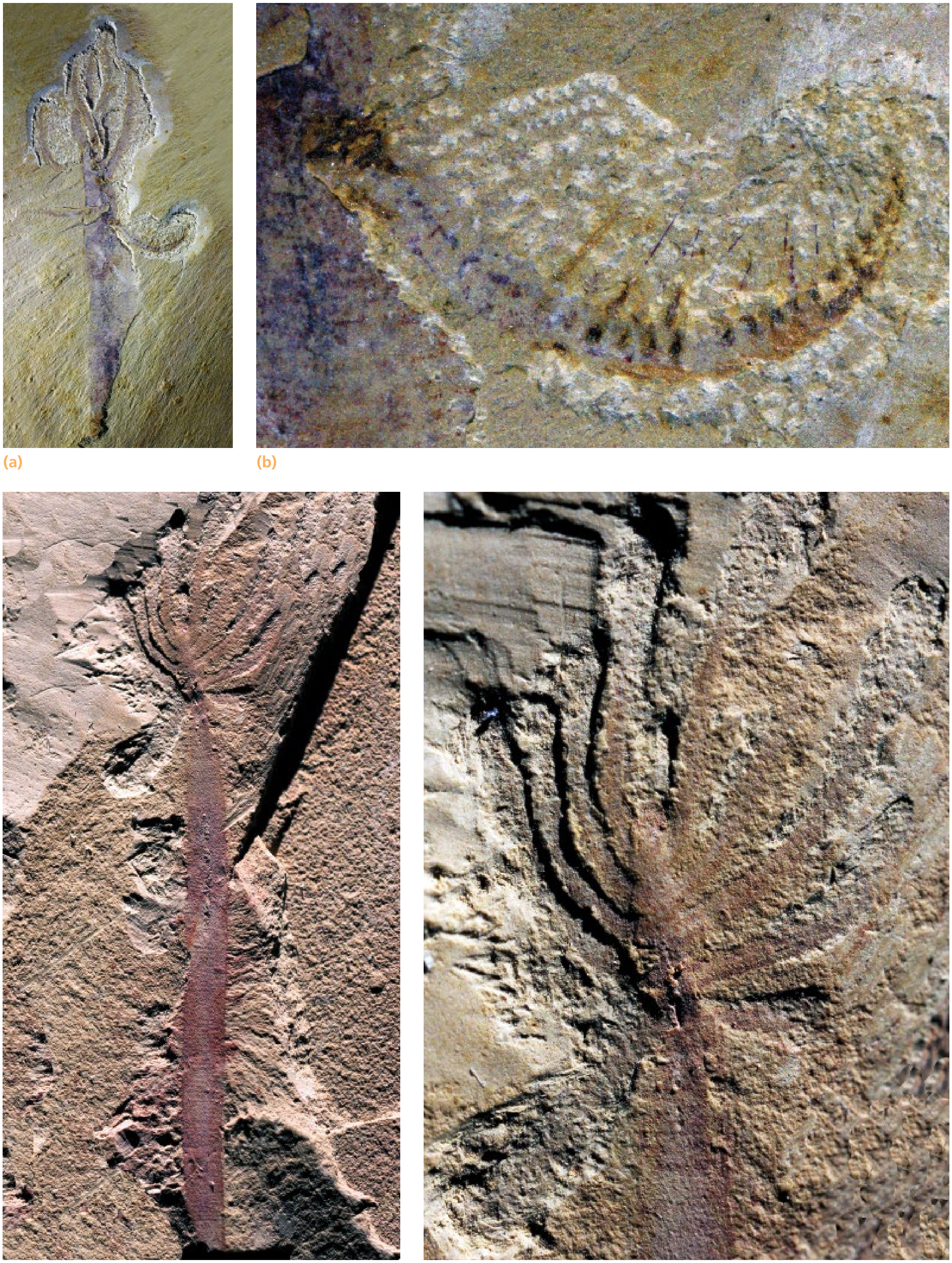
Facivermis is generally considered to have been a burrower (Hou & Chen 1989a), and possibly fixed in the sediment by means of the circlets of spines on the posterior part of the body (Liu *et al*. 2006a). Its appendages may have been used to collect food from above the burrow opening.

F. yunnanicus is only known from the Chengjiang biota. A second species, *Xishania longiscula* Hu *in* Chen *et al*. 2002, was referred to this genus by Huang *et al*. (2012), but may represent incomplete material of *F. yunnanicus* (see Liu *et al*. 2006a).

Key references

Hou & Chen 1989a; Chen Jun-yuan & Zhou 1997; Hou *et al*. 2004a; Liu *et al*. 2006a.

Figure 25.3 ***Facivermis yunnanicus***. **(a), (b)** RCCBYU 10306, ×2.2, ×14.2; Maotianshan, Chengjiang. **(c), (d)** NIGPAS 108720, ×4.3, ×11.6; Maotianshan, Chengjiang.



(a) (b) (c) (d)

Genus *Vetulocystis* Shu, Conway Morris, Han, Zhang & Liu, 2004

Vetulocystis catenata Shu, Conway Morris, Han, Zhang & Liu, 2004

In the original description, only two specimens were assigned to this species. Additional vetulocystid material was described as another newly erected species, *Dianchicystis jianshanensis* Shu *et al.*, 2004 (four specimens), along with two poorly preserved forms. All are door knob-shaped in general form, and although there are differences between the two named taxa and they come from different localities, the possibility remains that they are variants of a single species. Very few specimens have subsequently been discovered.

In the absence of clear indicators of biological orientation, describing the body plan of vetulocystids is challenging. The body consists of an inflated ball-like sheath or theca and a shorter tail-like structure that is assumed to be posterior. A median strand in the holotype of *V. catenata* was interpreted as a possible intestine. The theca is longer than it is wide, but there appears to have been some flexibility. After death, specimens collapse into two dimensions, creating marked wrinkles over the surface of the theca and tail. The nature of the wrinkles and the absence of evidence that the surface was brittle suggest that the theca was not biomineralized. One surface of the collapsed theca bears two cones exhibiting clear radial ribs that converge on a central opening; one of these is interpreted as a mouth. The theca also has an additional ribbed structure, close to the junction with the tail. Because in some specimens this structure seems to have internal folds or lamellae, it has been interpreted as a respiratory organ (Shu *et al.* 2004). All known specimens are less than 1 cm in size.

The vetulocystid body plan, with its bipartite body and internal cavity connected externally by conical thecal openings, has been compared (Shu *et al.* 2004) to tunicates and vetulicolians, with the arrangement of mouth, respiratory organ, and anus interpreted as being similar to homalozoan echinoderms. This interpretation was linked to a tentative phylogenetic hypothesis placing vetulocystids as the basal branch of echinoderms, intermediate between vetulicolians (interpreted as active stem deuterostomes) and semi-sessile, homalozoan-like organisms. Many authors note the general similarity to vetulicolians, supporting the hypothesis that the two fossil groups are related, but the similarities to echinoderms and placement within ambulacraria have been strongly questioned (Smith, A.B. 2004; Swalla & Smith 2008). The hypothesis that vetulocystids were "pre-echinoderms" has been defended on the basis of interpretations of aspects of their anatomy as ancestral to key innovations in the echinoderm body plan (Shu *et al.* 2010). However, it is difficult to evaluate scientifically a hypothesis that proposes a phylogenetic placement that is not supported by any shared derived characters (Clausen *et al.* 2010); a similar type of argument could be used to support a relationship with almost any metazoan group.

Interpretation of the functional morphology of the vetulocystid body suggests they probably spent most of their time with their tail embedded in sediment to anchor the theca on the sea floor, possibly with some form of slow locomotion brought about by sideways movement of the tail (Shu *et al.* 2004). According to this view, vetulocystids were filter feeders.

Vetulocystids are unique to the Chengjiang biota. *V. catenata* is known only from the Shankou section near Anning. Specimens assigned by Shu *et al.* (2004) to *D. jianshanensis* are from Jianshan, near Haikou, in Yunnan Province.

Key references

Shu *et al.* 2004, 2010; Swalla & Smith 2008; Clausen *et al.* 2010.

Figure 25.4 ***Vetulocystis catenata*****.** **(a)** YKLP 13895a, ×6.0; Jianshan, Haikou, Kunming. **(b)** YKLP 13895b, ×8.4; Jianshan, Haikou, Kunming.

(a)

(b)

Genus *Yunnanozoon* Hou, Ramsköld & Bergström, 1991

Yunnanozoon lividum Hou, Ramsköld & Bergström, 1991

Three species have been recognized within the higher taxon Yunnanozoa: *Yunnanozoon lividium*, *Haikouella lanceolata* Chen *et al*., 1999, and *Haikouella jianshanensis* Shu *et al*., 2003, but the differences between these supposed species, which tend to occur at different localities, are probably the result of taphonomic processes and they are likely synonymous (Cong *et al*. 2015). Hundreds of specimens are known, including slabs containing mass accumulations. Body length ranges between 2 and 6 cm. Almost all specimens of *Yunnanozoon* are preserved as thin, carbon-rich films, a mode of preservation unusual for the Chengjiang Lagerstätte (Cong *et al*. 2015).

Descriptions of yunnanozoans are difficult to compare because different authors have applied different anatomical terminology (e.g., Chen Jun-yuan *et al.* 1995a, 1999; Shu *et al.* 1996b, 2003b; Mallatt & Chen 2003; Donoghue & Purnell 2009; Cong *et al*. 2015). However, there is considerable agreement on the general features and orientation of this enigmatic animal. The anterior part of the body comprises paired filamentous arches that are attached at their dorsal and ventral ends to anteroposteriorly oriented dorsal and ventral rods. Each rod exhibits at least one linear structure. Where the filamentous arches attach to the ventral rod small circular structures are present; sac-like structures lie exterior to the arches, with openings to the exterior between them (this feature is seen only in the most complete specimens). The dominant feature of the posterior part of the body, termed the dorsal repetitive units, is an elongate, semi-circular structure made up of subrectangular subunits. The posterior-most subunit of this structure bears a small posterior projection; the anterior-most subunit has a distinctive triangular morphology. Ventral to the dorsal repetitive units is an anteroposteriorly oriented axial zone exhibiting transverse stripes. At approximately mid-length, close to the ventral margin, a series of four, paired circular structures occurs. The ventral side of the body, from mid-length posteriorly, also bears a ventral tube that in some specimens appears coiled.

Yunnanozoon might well hold a record for the range of hypotheses of affinity that have been proposed. This includes stem cephalochordates (Chen Jun-yuan *et al.* 1995a), stem-chordates (Dzik 1995), crown or stem hemichordates (Shu *et al.* 1996b, 2004), craniates (Holland & Chen 2001; Mallatt & Chen 2003), stem ambulacrarians (Shu *et al.* 2003b), stem deuterostomes (Budd & Jensen 2000; Shu *et al.* 2001b, 2004; Shu 2003), Ecdysozoa (Bergström 2010), and even stem bilaterians (Dewell 2000). Yunnanozoans have been implicated in debates concerning the emergence of neural crest (Holland & Holland 2001; Holland & Chen 2001; Meulemans & Bronner-Fraser 2007), vertebrate brain and sensory systems (Northcutt 2002; Butler 2006), origin of the vertebrate eye (Lamb 2013), myosepta (Gemballa *et al.* 2003), the diagnostically chordate myomere-notochord locomotory system (Conway Morris & Caron 2012), jaws (Kuratani 2004), and the evolution of cognition (Heeren 2003). Neither of the two most widely debated hypotheses of affinity is without difficulties. The suggestion that yunnanozoans are cephalochordates or stem chordates is based largely on interpretation of the dorsal repetitive unit as myomeres, and axial structures as a notochord. These are better interpreted as features of a cuticular exoskeleton and a body cavity, respectively, and without evidence of myomeres and notochord, there is no basis for assigning yunnanozoans to the chordates (Conway Morris & Caron 2012; Cong *et al.* 2015). The hypothesis that yunnanozoans might represent more basal deuterostomes derives primarily from interpretations of the filamentous arches as exterior gills with homologies to deuterostome pharyngeal slits (e.g., Shu *et al.* 2003b, 2004). Evidence of external sac-like structures (Cong *et al.* 2015) does not necessarily refute the hypothesis that yunnanozoans possess structures that are homologous with deuterostome phayngeal slits, but there is little other evidence to place yunnanozoans within the deuterostome total group. Currently it seems prudent to consider *Yunnanozoon*, like the vetulicolians, as a bilaterian of uncertain affinity. Indeed, a relationship between the two has been suggested (e.g., Shu *et al.* 1999a, 2001b; Ou *et al.* 2012a), but this would require the yunnanozoans to be nested among more derived vetulicolians (Cong *et al.* 2015).

The ecology of *Yunnanozoon* is as enigmatic as its affinities, and will remain so until the nature of its locomotory and feeding apparatus is resolved. Cong *et al.* (2015) interpret the anterior complex of filamentous arches, the sac-like structures, and rods as a feeding organ, consistent with interpretations of the filamentous arches as a food-filtering system.

Yunnanozoon is unknown outside the Chengjiang biota. It occurs at several localities in the Chengjiang (Maotianshan, Ma'anshan, Xiaolantian) and Haikou areas (Mafang, Ercaicun).

Key references

Hou *et al.* 1991; Chen Jun-yuan *et al.* 1995a; Dzik 1995; Shu *et al.* 2003b, 2010; Conway Morris & Caron 2012; Cong *et al.* 2015.

Figure 25.5 ***Yunnanozoon lividum***. **(a)** RCCBYU 10310a, ×4.0; Ercaicun, Haikou, Kunming. **(b)** YKLP 13005a, ×1.8; Ercaicun, Haikou, Kunming. **(c)** YKLP 13008, ×3.9; Mafang, Haikou, Kunming. **(d)** RCCBYU 10323a, ×5.1; Ercaicun, Haikou, Kunming


(a)
(b)
(c)
(d)

26 Vetulicolians

This group comprises bilaterian animals with an unusual body plan that appears to combine arthropod and deuterostome features. The body is divided into a carapace-like anterior part, which shows subtle segmentation, and a more clearly segmented tail. The genus *Vetulicola* was initially regarded as arthropodan, but the absence of preserved appendages in any specimens and the presence on each side of the carapace of a lateral groove housing five apparent slits creates problems with that assignment. With the idea that *Vetulicola*, *Banffia*, *Didazoon*, and *Xidazoon* (= *Pomatrum*) form a natural group came the proposal that it be regarded as a distinct phylum, the Vetulicolia (Shu *et al.* 2001b), placed among the primitive deuterostomes. Later studies supported the monophyly of the group (e.g., Aldridge *et al.* 2007), but also proposed a number of different possible phylogenetic placements, including arthropods (Chen Jun-yuan 2008), ecdysozoans (Bergström 2010), stem or crown-group chordates (Gee 2001; García-Bellido *et al.* 2014), or tunicates (Lacalli 2002). A.B. Smith (2012) reasoned that, if the vetulicolians did indeed possess pharyngeal gill slits, then they could best be considered as enigmatic total group deuterostomes. The systematic position of the group is still a matter of debate. However, as long as vetulicolians are considered to form a monophyletic group, it is not possible to sustain the proposal by Shu *et al.* (2010) that they record the sequential development of deuterostome characters, as the genus with the most of these characters, *Vetulicola*, is also a derived vetulicolian.

Genus *Heteromorphus* Luo & Hu *in* Luo, Hu, Chen, Zhang & Tao, 1999

Heteromorphus confusus (Chen & Zhou, 1997)

This is a fairly common species, with specimens usually preserved as a thin, reddened film. Complete specimens are uncommon, but reach 5.5 cm in length. The anterior body varies from torpedo-shaped, tapering to a rounded anterior edge, to subrectangular with a straight, vertical anterior end. The posterior end of the anterior body is marked by short angular projections both dorsally and ventrally. Lateral grooves are apparent, though poorly defined, on some specimens. The tail is long, flat, and broad, tapering posteriorly; there is a slight constriction where it attaches to the anterior body. It shows clear segmentation or annulation, often accompanied by wrinkling; the number of segments is difficult to ascertain, but may be about 30. A dark axial line in the tail of some specimens appears to represent the gut, which extends posteriorly to a terminal anus.

The streamlined shape suggests that *Heteromorphus* was nektonic or nektobenthic, propelled by the tail. There is no direct evidence from gut contents to demonstrate how it fed, but it may have been a filter feeder or a nektobenthic consumer, feeding selectively from the sediment surface (Aldridge *et al.* 2007).

Heteromorphus is restricted to the Chengjiang biota, but the related genus *Banffia* (to which *H. confusus* was initially assigned) is known from the middle Cambrian Burgess Shale of British Columbia (Walcott 1911b; Caron 2005).

Key references

Chen Jun-yuan & Zhou 1997; Hou *et al.* 1999; Aldridge *et al.* 2007.

The Cambrian Fossils of Chengjiang, China: The Flowering of Early Animal Life, Second Edition. Hou Xian-guang, David J. Siveter, Derek J. Siveter, Richard J. Aldridge, Cong Pei-yun, Sarah E. Gabbott, Ma Xiao-ya, Mark A. Purnell, Mark Williams.

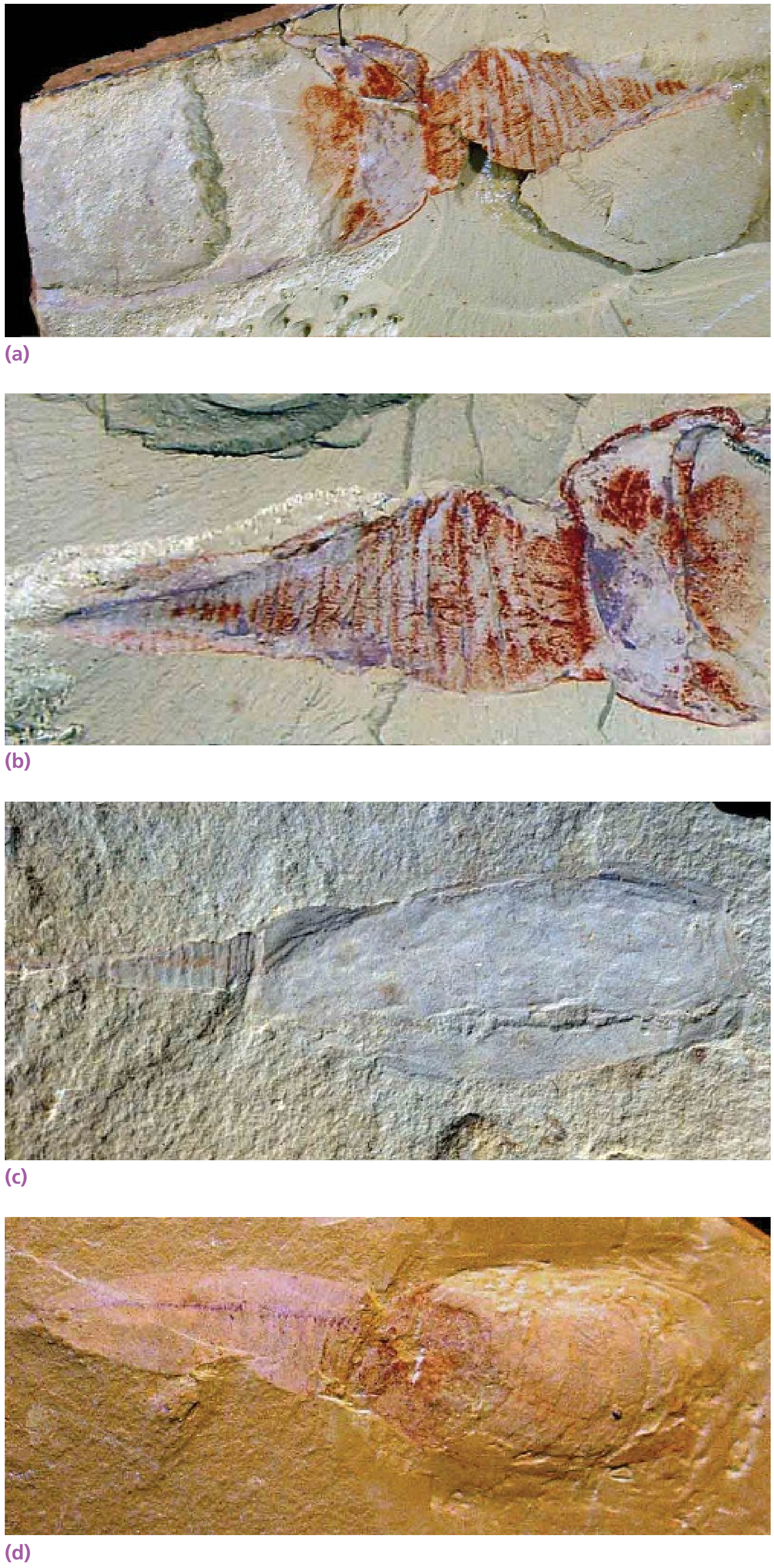


Figure 26.1 ***Heteromorphus confusus***. **(a)** YKLP 10916a, ×2.1; Mafang, Haikou, Kunming. **(b)** YKLP 10916b, ×3.6; Mafang, Haikou, Kunming. **(c)** YKLP 10917, ×3.5; Mafang, Haikou, Kunming. **(d)** YIGS Hz-f-6-364, ×2.0; Ercaicun, Haikou, Kunming.

Genus *Pomatrum* Luo & Hu *in* Luo, Hu, Chen, Zhang & Tao, 1999

Pomatrum ventralis Luo & Hu *in* Luo, Hu, Chen, Zhang & Tao, 1999

Pomatrum ventralis is known from more than a hundred specimens, most of which are incomplete. Complete specimens reach 10 cm in length. Preservation is as a flat, commonly gray film, with relief evident in the lateral pouches and gut of some specimens.

The anterior and posterior bodies are of similar length. The anterior body is deeper, ovoid, and smooth, divided into six segments that are most prominent anteriorly. There is a round oral opening, surrounded by a prominent oral disk, which is divided into inner and outer regions. The inner region displays fine radiating lines, some of which extend into the less well-defined outer region. Laterally on the anterior body there are five cowl-shaped, pouch-like structures that appear to underlie a lateral groove. The tail is relatively narrow, tapering anteriorly and posteriorly, with numerous segments marked by transverse wrinkle zones; there is a slight constriction at the junction with the anterior body. At least two specimens show well-preserved guts in the tail, filled with sediment; one appears to be straight and tubular, the other is clearly spiralled.

Two described specimens, identified as *Pomatrum* cf. *ovalis*, display small subrectangular projections, one on each side of the oral cavity just above the line of the lateral groove; the nature of these structures is unknown.

Like other vetulicolians, *Pomatrum* was probably an active swimmer, and possibly a nektobenthic consumer, although its shape is less streamlined than that of some other genera.

Pomatrum is extremely similar to *Xidazoon* Shu *et al*., 1999, and several authors have considered the two to be synonymous. *Didazoon* Shu & Han *in* Shu *et al.* 2001b, is also very similar, but is discriminated on the basis of a less well-developed oral disk and a more quadrate anterior body. All three genera are known only from the Chengjiang biota.

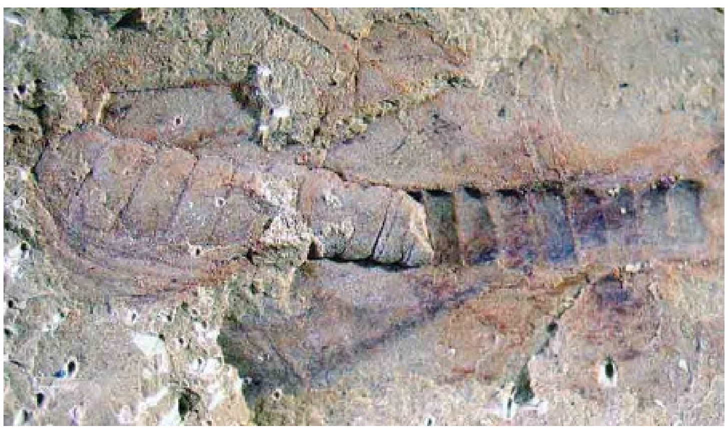
Key references

Shu *et al.* 1999a; Aldridge *et al.* 2007.

Figure 26.2 ***Pomatrum ventralis***. **(a)** YKLP 10909, ×1.0; Haikou, Kunming. **(b), (c)** YKLP 10912, ×1.4, ×8.3; Haikou, Kunming. **(d)** *Pomatrum* cf. *ventralis*, YKLP 10914a, ×1.3; Mafang, Haikou, Kunming.

(a)

(b)



(c)

(d)

Genus *Yuyuanozoon* Chen, Feng & Zhu *in* Chen, Feng, Zhu, Ma & Li, 2003

Yuyuanozoon magnificissimi Chen, Feng & Zhu *in* Chen, Feng, Zhu, Ma & Li, 2003

This species is known from a single specimen, from the Chengjiang biota. It is 2 cm in total length, with the anterior body 12 cm long and the tail 8.2 cm long. The anterior body is ovoid, 5.3 cm high at its highest point, with a smooth surface; there is no evidence of an oral disk. Six segments are subtly identifiable, with five cowl-shaped, pouch-like structures present laterally at the segment boundaries; these pouches are connected by tubular structures to form a continuous feature that narrows posteriorly. Radiating structures associated with each of the pouches were initially interpreted to be gill filaments (Chen Ai-lin *et al.* 2003), but have subsequently been considered to be narrow grooves located on the interior of the body wall that functioned as part of the vascular system (Ou *et al.* 2012a).

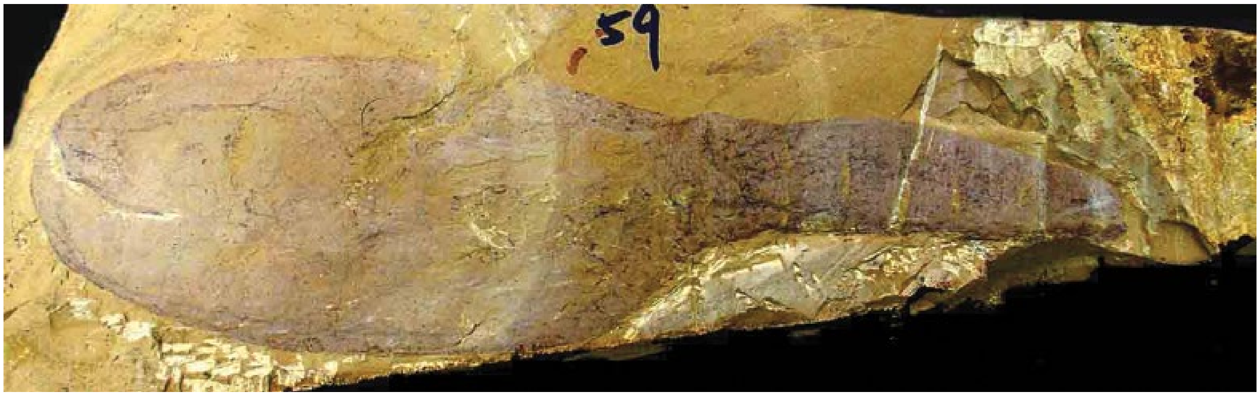
The tail is 2 cm in maximum height, with subparallel dorsal and ventral edges that converge posteriorly to a rounded termination. The dorsal edge is contiguous with the dorsal edge of the anterior body. Seven segments are clearly identifiable in the tail; the first six are of subequal size and the posterior-most is about twice the length of the others. An indentation at the posterior tip may represent the anus, and subparallel axial lines in the tail may delimit the alimentary canal.

Yuyuanozoon magnificissimi is considered to have been a swimmer, with a reasonably streamlined anterior body. The relatively small size and apparently cylindrical cross-section of the tail suggest that it was less agile than other vetulicolians (Chen Ai-lin *et al.* 2003).

Key references

Chen Ai-lin *et al.* 2003; Aldridge *et al.* 2007; Ou *et al.* 2012a.

Figure 26.3 ***Yuyuanozoon magnificissimi*. (a), (b)** CFM 00059, ×0.8, ×1.3; Chengjiang County.



(a)

(b)

Genus *Beidazoon* Shu, 2005

Beidazoon venustum Shu, 2005

Beidazoon venustum is an uncommon species, known from fewer than 20 specimens.

This is the smallest of known vetulicolians, ranging from 0.8 to 2 cm in length, with a strongly sclerotized bipartite body. The anterior body is subrectangular in shape, with a vertical or near vertical anterior edge and a more rounded posterior edge; the dorsal edge is straight or gently convex, the ventral edge more convex, curving upward posteriorly. A distinct narrow margin is present anteriorly, dorsally, and ventrally. The surface of the anterior body is characterized by numerous small, closely spaced nodes, and there is a prominent, narrow lateral groove, with some specimens showing five rhomboidal structures similar to those of *Vetulicola*.

The tail arises from the dorsal portion of the anterior body and comprises seven segments; the proximal three are slender and the distal four show gradual expansion to form a paddle-like structure. The terminal segment is subquadrate and larger than the others. In different specimens the tail is preserved directed horizontally, dorsally, or ventrally, suggesting considerable flexibility in life. There is a straight axial gut leading to a terminal anus.

The mobility of the tail suggests that *Beidazoon* was an active swimmer. Like other vetulicolians, it was probably a filter feeder and/or a selective feeder from the sediment surface.

Bullivetula variola Aldridge *et al.,* 2007 is a junior synonym of *B. venustum*.

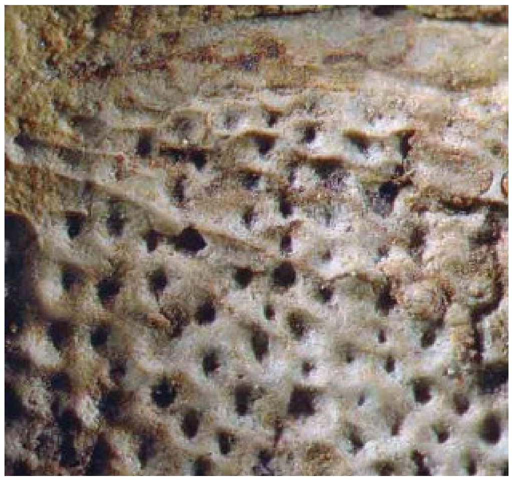
The genus is only known from the Chengjiang biota.

Key references

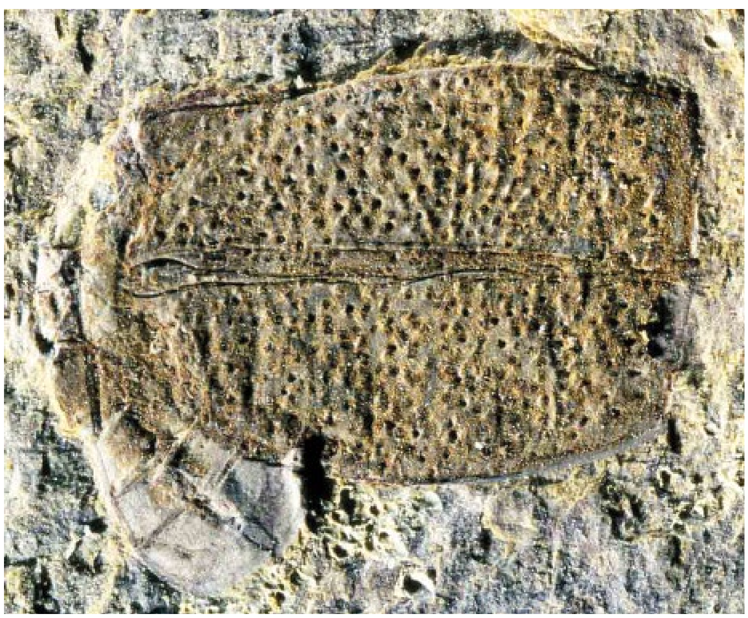
Shu 2005; Aldridge *et al.* 2007.

Figure 26.4 ***Beidazoon venustum***. **(a), (b)** YKLP 10907, ×4.6, ×19.0; Ercaicun, Haikou, Kunming. **(c)** YKLP 10908a, ×10.0; Ercaicun, Haikou, Kunming.

(a)



(b)



(c)

Genus *Vetulicola* Hou, 1987

Vetulicola cuneata Hou, 1987

This is a fairly common animal known from numerous specimens, mostly from the Chengjiang area. It is usually found laterally compressed.

The holotype is 9.2 cm long and 3.2 cm high. The anterior body is elongate but relatively robust, comprising two lateral valves that are conjoined, perhaps fused, along a pinched marginal zone. The anterior termination is tapered, with dorsal and ventral lips surrounding an opening that is V-shaped in lateral view. The surface is smooth, with faint annulation evident in some specimens; five primary annulations occur, with second- and third-order annulations more rarely distinguishable. Evidence of longitudinal body musculature is preserved on a few specimens. There is a triangular, fin-like extension of the dorsal margin at the posterior end of the anterior body, and a shorter projection at the ventral margin at the posterior end. A lateral groove is present on each side, terminating short of the posterior edge of the anterior body. Five rhomboidal swellings on the groove overlie internal pouches with filamentous structures and there are oval openings, interpreted as pharyngeal openings (e.g., Ou *et al.* 2012a), connecting the pouches to the exterior.

The tail extends from the dorsal margin of the anterior body and is one-third to one-quarter of the height. It comprises seven segments, with articulating facets evident in the proximal three. The posterior four segments are extended on both sides into flaps, producing an ovoid structure; there are differences of interpretation in the literature as to whether these flaps are symmetrical or asymmetrical and as to whether they are disposed vertically or horizontally. An axial structure in the tail appears to represent a straight gut, terminating at the tip of the last segment.

The streamlined body shape and mobility of the tail suggest that *Vetulicola cuneata* was an active swimmer. There is controversy concerning the mode of propulsion of the tail; some authors have considered it to have moved vertically (e.g., Aldridge *et al.* 2007), whereas others interpret the motion to be lateral (e.g., Shu *et al.* 2010). It may be that the motion was more complex than envisaged to date. Ou *et al.* (2012a) considered that *Vetulicola* was a filter feeder, with feeding enhanced by active pumping of water through the pharyngeal slits.

Vetulicola cuneata has also been reported from the lower Cambrian of Canada (Butterfield 2005). Additional species of *Vetulicola* are also present in the Chengjiang biota: *Vetulicola rectangulata* Luo & Hun *in* Luo *et al.*, 1999 is distinguished by a subrectangular anterior body with a nearly vertical anterior edge; *Vetulicola monile* Aldridge *et al.*, 2007, is characterized by two distinct lateral rows of nodes on the anterior body, one below and one above the lateral groove.

Key references

Hou 1987c; Shu *et al.* 2001b, 2010; Chen Jun-yuan 2004; Aldridge *et al.* 2007; Ou *et al.* 2012a.

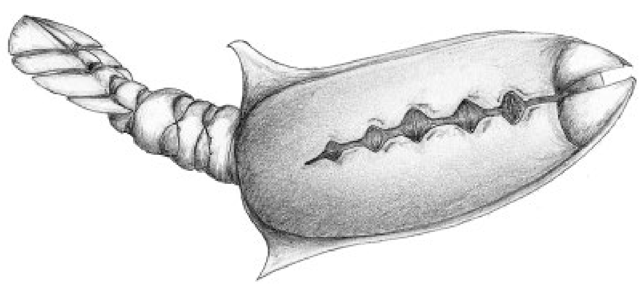
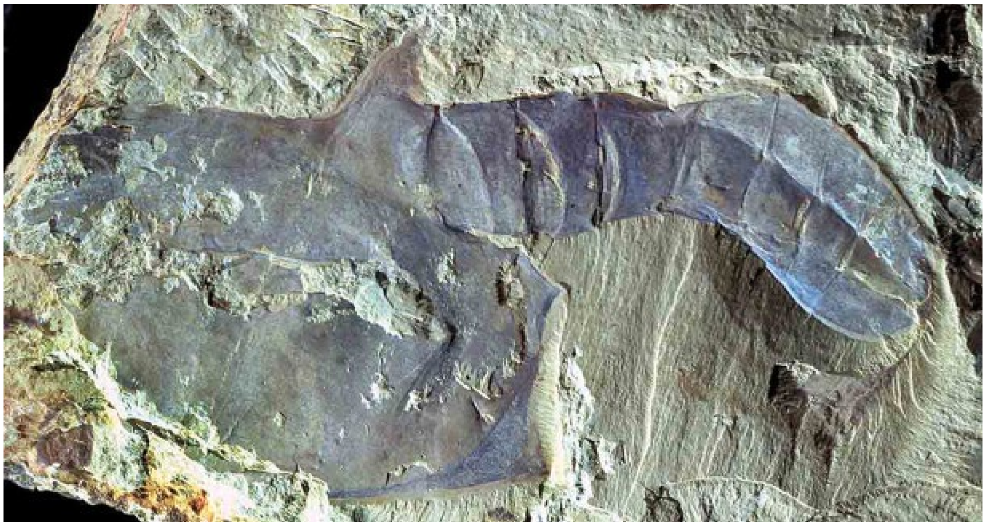


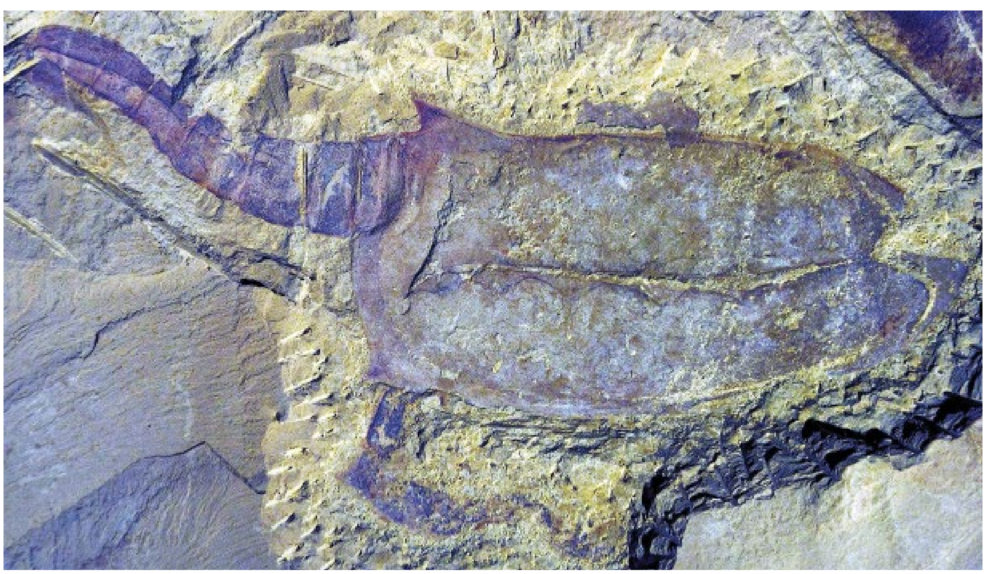
Figure 26.5 Reconstruction of ***Vetulicola cuneata*** (modified from Aldridge *et al.* 2007).

Figure 26.6 ***Vetulicola cuneata.*** **(a)** YKLP 10903, ×1.8; Ma'anshan, Chengjiang. **(b)** RCCBYU 10298, ×1.3; Dapotou, Chengjiang. **(c)** YKLP 13896, ×1.7; Ma'anshan, Chengjiang.



(a)

(b)



(c)

27 Animals of Uncertain Affinity

The vast majority of organisms in the Chengjiang biota are assigned to a handful of metazoan clades, mostly within the Bilateria. However, a few continue to defy placement even with the epithet of "uncertain affinity" at a taxonomic level equivalent to phylum or superphylum. Of these 20 or so taxa, we deal here only with three genera: *Stromatoveris;* the chancelloriid *Allonnia;* and the chancelloriid-like *Nidelric*. Chancelloriids are a truly enigmatic group of animals that might be part of a paraphyletic assemblage of stem and crown Bilateria (Bengtson 2005).

Genus *Nidelric* Hou, Williams, Siveter, Siveter, Gabbott, Holwell & Harvey, 2014

Nidelric pugio Hou, Williams, Siveter, Siveter, Gabbott, Holwell & Harvey, 2014

Only a single specimen of the possible chancelloriid *Nidelric pugio* is known. It is compressed, but retains some relief, and like the Chengjiang chancelloriid *Allonnia* it is commonly highlighted in the rock by a reddish color imparted by iron oxide.

The ovoid body of *N. pugio* is just over 9 cm long (Hou *et al.* 2014). Single element spines are present at low-density over the whole surface of the animal, with the greatest concentration along the margins of the body and at the broader end. The spines are elongate-triangular in profile and gradually tapering; they have variable preservation but are typically 2.0 to 4.6 mm long, and about 2 mm broad at their base, sharply pointed distally, and are preserved overlapping each other at the body margins, suggesting that they might have been concentrated into rows. At the broader end of the body small and larger spines occur adjacent to each other, but generally the spines become smaller toward the narrower end of the body; many of the spines also point outward in the direction of the narrow end of the body. The margins and distal portions of the spines are covered with a sculpture of small triangular scales.

Exceptionally preserved articulated skeletons (scleritomes) are known for the chancelloriids *Chancelloria* Walcott, 1920, *Allonnia* Doré & Reid, 1965, and *Archiasterella* Sdzuy, 1969, each genus being distinguished by the arrangement of the complex multi-element spines within the spine-rosettes. Although the external spines of *Nidelric* are single elements that are not fused into rosettes, the overall anatomy of its body suggests a radial symmetry and a possible biological affinity with chancelloriids. The single-element spines of *Nidelric* are also very similar to the blade-like spines of the unnamed, small (about 2 cm long) metazoan referred to as a chancelloriid from the slightly younger Cambrian Guanshan biota of China (Hu *et al.* 2013), signaling that animals with this morphology may have been more widespread in early Cambrian Chinese faunas.

The ovoid body shape suggests that *N. pugio* possessed a sac-like morphology in life, and was likely sessile. *N. pugio* was likely a component of the benthos, possibly being anchored to the seabed, though no anchoring structures are preserved. The mode of feeding in *N. pugio* is unknown. It displays no evidence of structures that could be used for predation or locomotion. It may, like sponges and putatively for chancelloriids, have been a filter feeder, though again there are no preserved structures to confirm or refute this. The outward-pointing spines of *N. pugio* were likely designed to deter predation in a sessile organism without the functional means of escape, and this is consistent with the surface arrangement of its spines.

Key reference

Hou *et al.* 2014.

The Cambrian Fossils of Chengjiang, China: The Flowering of Early Animal Life, Second Edition. Hou Xian-guang, David J. Siveter, Derek J. Siveter, Richard J. Aldridge, Cong Pei-yun, Sarah E. Gabbott, Ma Xiao-ya, Mark A. Purnell, Mark Williams.

Figure 27.1 ***Nidelric pugio***. YKLP11081a, ×1.2; Mafang, Haikou, Kunming.

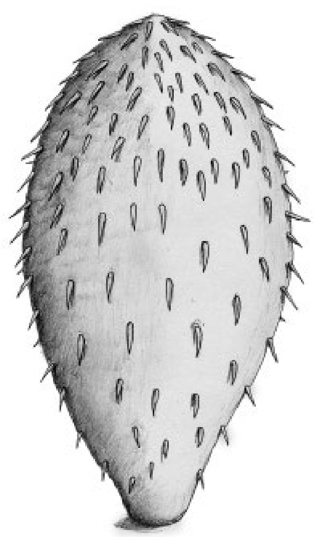


Figure 27.2 Reconstruction of ***Nidelric pugio***.

Genus *Allonnia* Doré & Reid, 1965

Allonnia phrixothrix Bengtson & Hou, 2001

Allonnia phrixothrix is a chancelloriid. Chancelloriids are enigmatic fossils well known from scattered sclerites found in many Cambrian sites. Complete specimens of the animals are rare, but several are known from the Chengjiang biota, especially from Haikou; they are uncommon at Chengjiang. The specimens are 4 cm or more in length and comprise a sac-like body with a flexible skin (integument) covered with spiny sclerites. The fossils are compressed, but retain some relief and are highlighted in the rock by a reddish coloring imparted by iron oxide.

The wall of each of the triradiate sclerites is thin and was probably originally formed of aragonite; this wall encloses an internal cavity, now preserved as a clay infilling. Each ray is about 8 mm long and attached to the integument at its base; two of the rays are positioned close to the body surface with the third directed outward. Between the sclerites the integument is folded, showing that it was flexible in life, and displays a conspicuous rhombic pattern that appears to be caused by small imbricating platelets, each about 30 × 60 µm in size. In places the platelets become elongated, perhaps forming small spinules that protruded from the surface.

Chancelloriids were initially interpreted as sponges (Walcott 1920), an opinion that has been followed and endorsed by many subsequent authors. Contrasting views have been put forward by other workers (*inter alia*, Mehl 1996; Bengtson & Hou 2001; Janussen *et al*. 2002; Bengtson 2005; Porter 2008). Mehl (1996), for example, considered that the sclerites were covered by an outer layer of tissue in life and that their mode of formation indicated an affinity with tunicates. Bengtson and Hou (2001) disputed this assignment and pointed out possible homologies between the sclerites of chancelloriids and those of coeloscleritophorans, including the halkeriids. Further evidence of the microstructural similarity in these sclerites was provided by Porter (2008). The debate is currently open (see Bengtson 2005 for an overview).

Chancelloriid ecology is also unresolved. Bengtson and Hou (2001) regarded the sclerites of *A. phrixothrix* to be too scattered to have served a supportive function and suggested that their prime purpose was as protection against predators. The organisms may have been attached to the seabed at the narrower, basal end. They may have been suspension feeders, but there is no evidence in the fossils as to where nutrient-bearing water may have entered and exited the body cavity. There may have been an apical opening or openings that cannot be observed on the laterally compressed fossils, or there may have been tiny openings in the integument that were involved in water circulation. There is no evidence of any prey-capture organs such as tentacles, but another possibility is that nutrition was obtained through a symbiotic relationship with algae or bacteria.

Chancelloriid sclerites are common fossils in lower upper Cambrian strata, with complete specimens known from the Burgess Shale and the Chengjiang Lagerstätten.

Key references

Bengtson & Hou 2001; Janussen *et al.* 2002; Bengtson 2005.

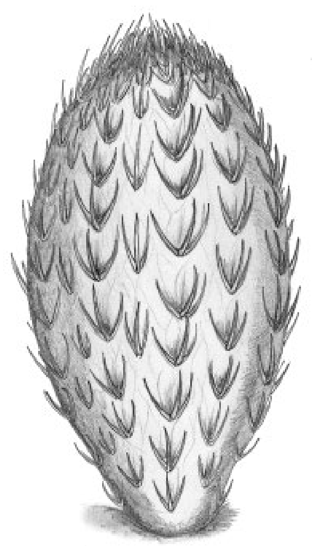
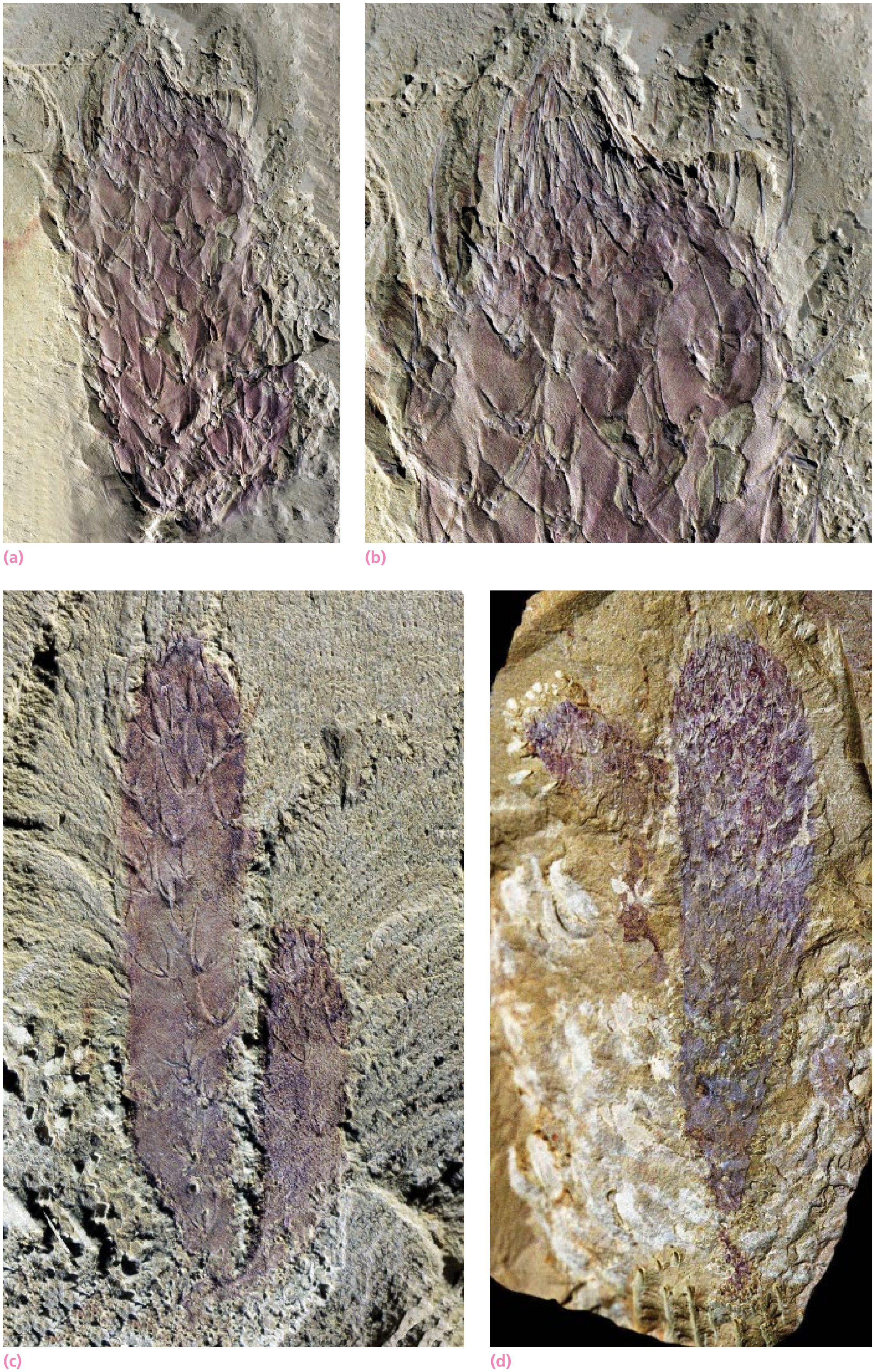


Figure 27.3 Reconstruction of ***Allonnia phrixothrix*** (modified from Hou *et al.* 2004a).

Figure 27.4 ***Allonnia phrixothrix***. **(a), (b)** RCCBYU 10160a, ×2.1, ×3.5; Xiaolantian, Chengjiang. **(c)** YKLP 13897, ×7.7; Fengkoushao, Chengjiang. **(d)** RCCBYU 10301, ×2.0; Mafang, Haikou, Kunming.



Genus *Stromatoveris* Shu *et al.*, 2006

Stromatoveris psygmoglena Shu *et al.*, 2006

Stromatoveris psygmoglena is a rare species, known only from a few dozen specimens. Most specimens are preserved strongly oblique to the bedding plane of the rock. The body of the animal splits irregularly, to form part and counterpart, with relatively high relief to the rock matrix.

The animal appears to be leaf-like in overall shape – a frond – with a short stalk. The so-termed upper surface of the frond has clear branches with pronounced relief, each separated by a channel-like depression; the other, so-called lower surface, has an ovoid smooth area. The upper surface contains about 15 elongate branches that arise from a midline structure (rachis). Each branch bears transverse, closely spaced striations. The distal-most part of the upper surface is mostly smooth; only the rachis can be recognized. The lower surface of the frond is divided into two parts: a distal, ovoid-shaped, and normally concave smooth region, and a proximal region that bears subdued ridges that splay in the opposite direction to the branches of the upper surface. Tiny, ovoid ornamental structures are present between the ridges. The stalk is almost smooth, short, and slightly narrower than the frond.

The affinity of *S. psygmoglena* remains enigmatic. The original authors interpreted this fossil as a Cambrian residual species of Ediacaran fronds (so-called vendobionts) and argued for a close relationship with ctenophores (Shu *et al.* 2006). The presumed occurrence of cilia on the branches was suggested to appear to represent precursors of the diagnostic comb rows of ctenophores. However, the links between *S. psygmoglena* and vendobionts has been questioned based on both morphological and ecological criteria (Antcliffe & Brasier 2007; Laflamme *et al.* 2013).

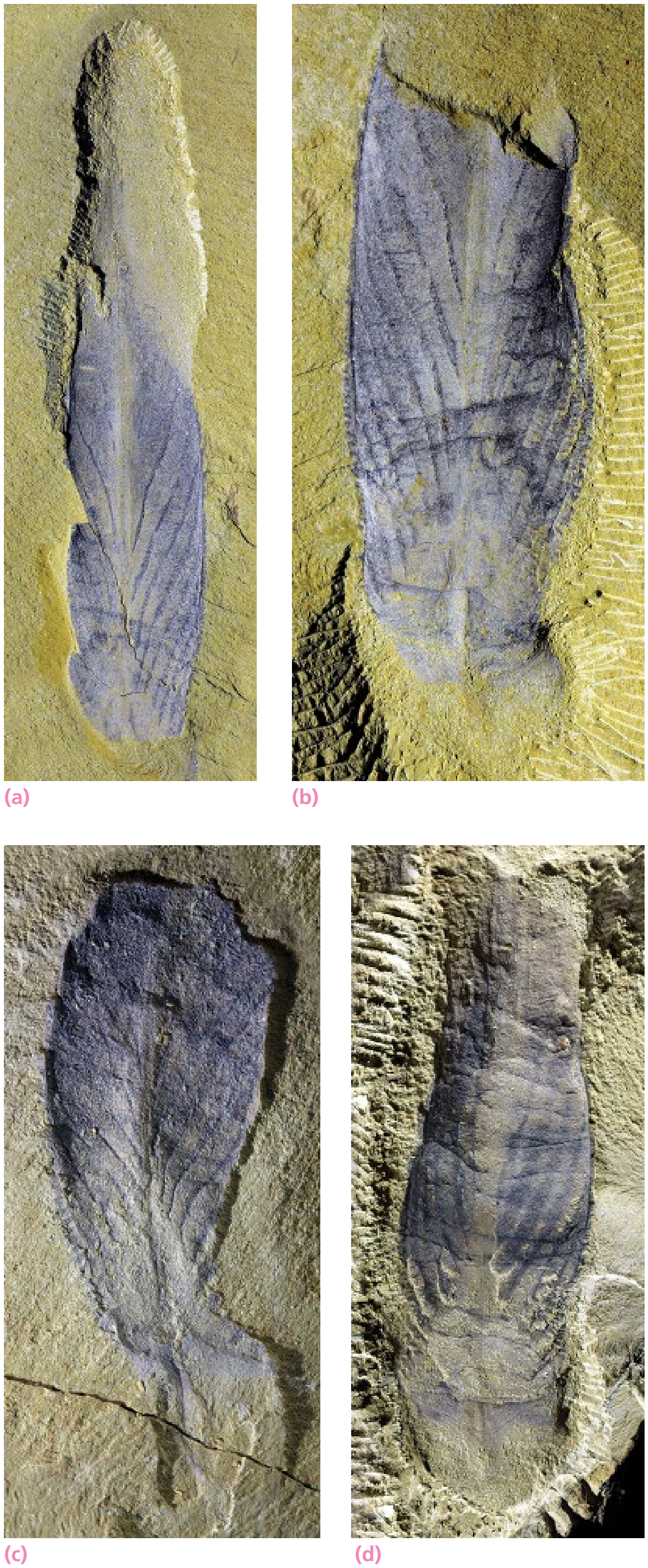
Mud-infill is present between the upper and lower surfaces of *S. psygmoglena*, and is normally more pronounced in the stalk area. This has been taken to indicate that the interior of the animal was probably hollow during life. A benthic life has been suggested, with the stalk embedding the frond in the sea floor, but it is unknown whether or not the frond stood upright during life (Shu *et al.* 2006).

S. psygmoglena is currently only known from two localities of the Chenjiang Lagerstätte, in the Haikou and Jinning areas.

Key references

Shu *et al.* 2006; Antcliffe & Brasier 2007; Laflamme *et al.* 2013.

Figure 27.5 ***Stromatoveris psygmoglena***. **(a)** YKLP 13898a, ×2.5; Xiaolantian, Chengjiang. **(b)** YKLP 13899b, ×3.0; Xiaolantian, Chengjiang. **(c)** YKLP 13900b, ×4.1; Xiaolantian, Chengjiang. **(d)** YKLP 113901, 2.1; Xiaolantian, Chengjiang.


(a)
(b)
(c)
(d)

28 Species Recorded from the Chengjiang Biota

Up to the end of 2015 more than 250 species, covering a wide range of major animal groups, have been established based on fossils from the Chengjiang Lagerstätte.

Algae

Enteromorphites intestalis Xu, 2001
Fuxianospira gyrata Chen & Zhou, 1997+
Longfenshania cordata Xu, 2002
Megaspirellus houi Chen & Erdtmann, 1991+
Plantulaformis sinensis Xu, 2002
Punctariopsis latifolia Xu, 2001
Punctariopsis simplex Xu, 2001
Sinocylindra yunnanensis Chen & Erdtmann, 1991
Yuknessia sp. of Chen & Erdtmann, 1991+
+ Regarded as coprolites by Steiner *et al.* (2005)

Ctenophora

Batofasciculus ramificans Hou *et al.*, 1999
Galeactena hemispherica Ou *et al.*, 2015
Gemmactena actinala Ou *et al.*, 2015
Maotianoascus octonarius Chen & Zhou, 1997
Sinoascus papillatus Chen & Zhou, 1997
Thaumactena ensis Ou *et al.*, 2015
Trigoides aclis Luo & Hu *in* Luo *et al.*, 1999
Yunnanoascus haikouensis Hu *et al.*, 2007

Porifera

Allantospongia mica Rigby & Hou, 1995
Choia carteri Walcott, 1920
Choia xiaolantianensis Hou *et al.*, 1999
Choiaella radiata Rigby & Hou, 1995
Crumillospongia biporosa Rigby, 1986
Cystospongia globose Wu, Zhu & Steiner, 2014
Halichondrites ellisa Walcott, 1920
Hamptonia chengjiangensis Wu, Zhu & Steiner, 2014
Hazelia palmata Walcott, 1920
Ischnspongia dendritica Wu, Zhu & Steiner, 2014
Leptomitella confusa Chen, Hou & Lu, 1989
Leptomitella conica Chen, Hou & Lu, 1989
Leptomitus teretiusculus Chen, Hou & Lu, 1989
Paradiagoniella magna Chen *et al.*, 2014
Paradiagoniella xiaolantianensis Chen *et al.*, 2014
Paraleptomitella dictyodroma Chen, Hou & Lu, 1989
Paraleptomitella globula Chen, Hou & Lu, 1989
Ptilispongia maotianshanensis Wu, Zhu & Steiner, 2014
Quadrolaminiella crassa Chen, Hou & Li, 1990
Quadrolaminiella diagonalis Chen, Hou & Li, 1990
Saetaspongia densa Mehl & Reitner *in* Steiner *et al.*, 1993
Takakkawia lineata Walcott, 1920
Triticispongia diagonata Mehl & Reitner *in* Steiner *et al.*, 1993
Valospongia cf. *gigantis* Rigby, 1983

Cnidaria

Archisaccophyllia kunmingensis Hou *et al.*, 2005
Cambrohydra ercaia Hu, 2005
Priscapennamarina angusta Zhang & Babcock, 2001
Xianguangia sinica Chen & Erdtmann, 1991

Entoprocta

Cotyledion tylodes Luo & Hu *in* Luo *et al.*, 1999 (? = *Cambrotentacus sanwuia* Zhang & Shu *in* Zhang *et al.*, 2001)

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Phoronida

Iotuba chengjiangensis Chen & Zhou, 1997 (=*Eophoronis chengjiangensis* Chen, 2004)

Brachiopoda

Alisina sp. of Zhang *et al*., 2011
Diandongia pista Rong, 1974
Heliomedusa orienta Sun & Hou, 1987
Kuangshanotreta malungensis Zhang, Holmer & Hu *in* Wang *et al*., 2012
Kutorgina chengjiangensis Zhang *et al*., 2007
Lingulella chengjiangensis Jin, Hou & Wang, 1993
Lingulellotreta malongensis (Rong, 1974)
Longtancunella chengjiangensis Hou *et al*., 1999
Xianshanella haikouensis Zhang & Han, 2004
Yuganotheca elegans Zhang, Li & Holmer *in* Zhang *et al*., 2014

Mollusca

Helcionella yunnanensis Zhang & Babcock, 2002

Annelida

Archaeogolfingia caudata Huang *et al*., 2004
Cambrosipunculus tentaculatus Huang *et al*., 2004
Maotianchaeta fuxianella Chen, 2004

Trochozoa of uncertain affinity

Ambrolinevitus maximus Jiang, 1982
Ambrolinevitus meishucunensis Jiang, 1994
Ambrolinevitus platypluteus Qian, 1978
Ambrolinevitus ventricosus Qian, 1978
Burithes yunnanensis Hou *et al*., 1999 (? = *Glossolites magnus* Luo & Hu *in* Luo *et al*., 1999)
Linevitus flabellaris Qian, 1978
Linevitus opimus Yu, 1974
Nectocaris pteryx Conway Morris, 1976 (=*Petalilium latus* Luo & Hu *in* Luo *et al*., 1999; ? = *Vetustovermis planus* Glaessner, 1979)
Wiwaxia papilio Zhang, Smith & Shu, 2015

Priapulida and relatives

Acosmia maotiania Chen & Zhou, 1997
Anningvermis multispinosus Huang, Vannier & Chen, 2004
Archotuba elongata (Luo & Hu *in* Luo *et al*., 1999) (=*Cambrorhytium* sp. nov. of Chen & Zhou, 1997; =*Archotuba conoidalis* Hou *et al*., 1999)
Corynetis brevis Luo & Hu *in* Luo *et al*., 1999
Cricocosmia jinningensis Hou & Sun, 1988
Eximipriapulus globocaudatus Ma *et al*., 2014
Gangtoucunia aspera Luo & Hu *in* Luo *et al*., 1999
Lagenula striolata Luo & Hu *in* Luo *et al*., 1999
Laojieella thecata Han *et al*., 2006
Mafangscolex sinensis (Hou & Sun, 1988)
Maotianshania cylindrica Sun & Hou, 1987
Oligonodus specialis Luo & Hu *in* Luo *et al*., 1999
Omnidens amplus Hou, Bergström & Yang, 2006
Palaeopriapulites parvus Hou *et al*., 1999
Paraselkirkia sinica (Luo & Hu *in* Luo *et al*., 1999) (=*Paraselkirkia jinningensis* Hou *et al*., 1999)
Paratubiluchus bicaudatus Han *et al*., 2004
Sabellidites yunnanensis Luo & Zhang, 1986
Sandaokania latinodosa Luo & Hu *in* Luo *et al*., 1999
Sicyophorus rarus Luo & Hu *in* Luo *et al*., 1999 (=*Protopriapulites haikouensis* Hou *et al*., 1999)
Tabelliscolex chengjiangensis Han *et al*. 2007
Tabelliscolex hexagonus Han, Zhang & Shu, 2003
Tylotites petiolaris Luo & Hu *in* Luo *et al*., 1999
Xiaoheiqingella peculiaris Hu *in* Chen *et al*., 2002 (=*Yunnanpriapulus halteroformis* Huang, Vannier & Chen, 2004)

Lobopodians

Antennacanthopodia gracilis Ou & Shu *in* Ou *et al*., 2011
Cardiodictyon catenulum Hou, Ramsköld & Bergström, 1991
Diania cactiformis Liu *et al*., 2011
Hallucigenia fortis Hou & Bergström, 1995
Jianshanopodia decora Liu *et al*., 2006
Luolishania longicruris Hou & Chen, 1989 (=*Miraluolishania haikouensis* Liu & Shu *in* Liu *et al*., 2004)
Megadictyon haikouensis Luo & Hu *in* Luo *et al*., 1999
Microdictyon sinicum Chen, Hou & Lu, 1989
Onychodictyon ferox Hou, Ramsköld & Bergström, 1991
Onychodictyon gracilis Liu *et al*., 2008
Paucipodia inermis Chen, Zhou & Ramsköld, 1995 (=*Paucipodia haikouensis* Luo & Hu *in* Chen *et al*., 2002)

Anomalocaridids

Amplectobelua symbrachiata Hou, Bergström & Ahlberg, 1995
Anomalocaris saron Hou, Bergström & Ahlberg, 1995
Anomalocaris sp. of Hou, Bergström & Ahlberg, 1995
Cucumericrus decoratus Hou, Bergström & Ahlberg, 1995
Lyrarapax unguispinus Cong *et al*., 2014

Euarthropoda

Acanthomeridion serratum Hou, Chen & Lu, 1989
Alalcomenaeus sp. of Tanaka *et al*., 2013
Almenia spinosa Hou & Bergström, 1997
Branchiocaris? *yunnanensis* Hou, 1987
'*Canadaspis*' *laevigata* (Hou & Bergström, 1991) (=*Canadaspis eucallus* Chen & Zhou, 1997; =*Perspicaris*?

sp. of Hou 1987; ? = *Yiliangocaris ellipticus* Luo & Hu *in* Luo *et al.*, 1999)
Chengjiangocaris longiformis Hou & Bergström, 1991 (? = *Cambrofengia yunnanensis* Hou *et al.*, 1999)
Chuandianella ovata (Lee, 1975)
Cindarella eucalla Chen, Ramsköld, Edgecombe & Zhou *in* Chen *et al.*, 1996
Clypecaris pteroidea Hou, 1999 (? = *Ercaicunia multinodosa* Luo & Hu *in* Luo *et al.*, 1999)
Combinivalvula chengjiangensis Hou, 1987
Comptaluta inflata (Zhang, 1974)
Comptaluta leshanensis (Lee, 1975)
Diplopyge forcipatus Luo & Hu *in* Luo *et al.*, 1999
Diplopyge minutus Luo & Hu *in* Luo *et al.*, 1999
Dongshanocaris foliiformis (Hou & Bergström, 1998)
Eoredlichia intermedia (Lu, 1940)
Ercaia minuscula Chen, Vannier & Huang, 2001
Erjiecaris minuscula Fu, Zhang & Budd, 2014
Forfexicaris valida Hou, 1999
Fortiforceps foliosa Hou & Bergström, 1997
Fuxianhuia protensa Hou, 1987
Glossocaris oculatus Luo & Hu *in* Luo *et al.*, 1999
Haifengella corona Zhao, Hu, Zheng & Zhu, 2014
Haikoucaris ercaiensis Chen, Waloszek & Maas, 2004
Isoxys auritus (Jiang, 1982)
Isoxys curvirostratus Vannier & Chen, 2000
Isoxys paradoxus Hou, 1987 (? = *Isoxys elongatus* Luo & Hu *in* Luo *et al.*, 1999)
Jianfengia multisegmentalis Hou, 1987
Jiucunella paulula Hou & Bergström, 1991
Kangacaris shui Zhang, Fu & Dai, 2012
Kuamaia lata Hou, 1987
Kuamaia muricata Hou & Bergström, 1997
Kuanyangia sp. of Hou & Bergström, 1997
Kunmingella douvillei (Mansuy, 1912)
Kunmingella typica Huo & Shu, 1985
Kunmingocaris bispinosus Luo & Hu *in* Luo *et al.*, 1999
Kunyangella cheni Huo, 1965
Kwanyinaspis maotianshanensis Zhang & Shu, 2005
Leanchoilia illecebrosa (Hou, 1987) (=*Dianchia mirabilis* Luo & Hu *in* Luo *et al.*, 1997; =*Leanchoilia asiatica* Luo & Hu *in* Luo *et al.*, 1997; =*Yohoia sinensis* Luo & Hu *in* Luo *et al.*, 1997; =*Zhongxinia speciosa* Luo & Hu *in* Luo *et al.*, 1997; ? = *Apiocephalus elegans* Luo & Hu *in* Luo *et al.*, 1999)
Liangshanella liangshanensis Huo, 1956
Mafangia subscalaria Luo & Hu *in* Chen *et al.*, 2002
Mafangocaris multinodus Luo & Hu *in* Chen *et al.*, 2002
Malongella bituberculata Luo & Hu *in* Chen *et al.*, 2002
Misszhouia longicaudata (Zhang & Hou, 1985)
Naraoia halia Simonetta & Delle Cave, 1975
Naraoia spinosa Zhang & Hou, 1985
Occacaris oviformis Hou, 1999
Ovalicephalus mirabilis Luo & Hu *in* Chen *et al.*, 2002
Parapaleomerus sinensis Hou *et al.*, 1999
Parapeytoia yunnanensis Hou, Bergström & Ahlberg, 1995
Pectocaris eurypetala (Hou & Sun, 1988) (? = *Jugatacaris agilis* Fu & Zhang, 2011)
Pectocaris spatiosa Hou, 1999
Pisinnocaris subconigera Hou & Bergström, 1998 (? = *Jianshania furcatus* Luo & Hu *in* Luo *et al.*, 1999)
Primicaris larvaformis Zhang *et al.*, 2003
Pseudoiulia cambriensis Hou & Bergström, 1998
Pterotrum triacanthus Luo & Hu *in* Chen *et al.*, 2002
Pygmaclypeatus daziensis Zhang, Han & Shu, 2000
Retifacies abnormalis Hou, Chen & Lu, 1989 (=*Retifacies longispinus* Luo & Hu *in* Luo *et al.*, 1997; =*Tuzoia* sp. of Shu 1990)
Rhombicalvaria acantha Hou, 1987
Saperion glumaceum Hou, Ramsköld & Bergström, 1991
Shankouia zhenghei Chen *et al. in* Chen, 2004 (? = *Liangwangshania biloba* Chen, 2005)
Sidneyia sinica Zhang & Shu *in* Zhang, Han & Shu, 2002
Sinoburius lunaris Hou, Ramsköld & Bergström, 1991
Skioldia aldna Hou & Bergström, 1997
Squamacula clypeata Hou & Bergström, 1997
Sunella cf. *shenensis* (Huo, 1965)
Synophalos xynos Hou *et al.*, 2009
Syrrhaptis intestinalis Luo & Hu *in* Luo *et al.*, 1999
Tanglangia longicaudata Luo & Hu *in* Luo *et al.*, 1999
Tsunyiella diandongensis Tong *in* Huo & Shu, 1985
Urokodia aequalis Hou, Chen & Lu, 1989
Wutingaspis tingi Kobayashi, 1944
Wutingella binodosa Zhang, 1974
Xandarella spectaculum Hou, Ramsköld & Bergström, 1991
Yunnanocaris megista Hou, 1999
Yunnanocephalus yunnanensis (Mansuy, 1912)
Zhenghecaris shankouensis Vannier *et al.*, 2006

Chaetognatha

Protosagitta spinosa Hu *in* Chen *et al.*, 2002 (? = *Eognathacantha ercainella* Chen & Huang, 2002)

Hemichordata

Galeaplumosus abilus Hou *et al.*, 2011

Ambulacraria of uncertain affinity

Eldonia eumorpha (Sun & Hou, 1987) (=*Yunnanomedusa eleganta* Sun & Hou, 1987)
Phlogites longus Luo & Hu *in* Luo *et al.*, 1999 (=*Phlogites brevis* Luo & Hu *in* Luo *et al.*, 1999; =*Cheungkongella ancestralis* Shu *et al.*, 2001; ? = *Calathites spinalis* Luo & Hu *in* Luo *et al.*, 1999)
Rotadiscus grandis Sun & Hou, 1987

Chordata

Cathaymyrus diadexus Shu, Conway Morris & Zhang, 1996
Cathaymyrus haikouensis Luo & Hu *in* Luo *et al.*, 2001
Myllokunmingia fengjiaoa Shu, Zhang & Han *in* Shu et al., 1999 (? = *Haikouichthys ercaicunensis* Luo, Hu & Shu *in* Shu *et al.*, 1999; ? = *Zhongjianichthys rostratus* Shu, 2003)

Shankouclava anningense Chen *et al*., 2003 (=*Shankouclava shankouense* Chen *et al*., 2003)
Zhongxiniscus intermedius Luo & Hu *in* Luo *et al*., 2001

Bilateria of uncertain affinity

Dianchicystis jianshanensis Shu *et al*., 2004
Dinomischus venustus Chen, Hou & Lu, 1989
Facivermis yunnanicus Hou & Chen, 1989 (? = *Xishania longiusula* Hu *in* Chen *et al*., 2002)
Vetulocystis catenata Shu *et al*., 2004
Yunnanozoon lividum Hou, Ramsköld & Bergström, 1991 (=*Haikouella lanceolata* Chen *et al*., 1999; =*Haikouella jianshanensis* Shu *et al*., 2003)

Vetulicolians

Beidazoon venustum Shu, 2005 (=*Bullivetula variola* Aldridge *et al*., 2007)
Didazoon haoae Shu & Han *in* Shu *et al*., 2001
Heteromorphus confusus (Chen & Zhou, 1997) (? = *Heteromorphus longicaudatus* Luo & Hu *in* Luo *et al*., 1999)
Pomatrum ventralis Luo & Hu *in* Luo *et al*., 1999 (? = *Xidazoon stephanus* Shu, Conway Morris & Zhang *in* Shu *et al*., 1999)
Vetulicola cuneata Hou, 1987
Vetulicola monile Aldridge *et al*., 2007
Vetulicola rectangulata Luo & Hu *in* Luo *et al*., 1999
Yuyuanozoon magnificissimi Chen, Feng & Zhu *in* Chen *et al*. 2003

Animals of uncertain affinity

Allonnia phrixothrix Bengtson & Hou, 2001 (=*Allonnia junyuani* Janussen *et al*., 2002)
Amiskwia sinica Luo & Hu, 2002
Anthotrum robustus Luo & Hu *in* Luo *et al*., 1999
Cambrocomulitus rarus Yang Xian-feng *et al*., 2013
Chancelloria eros Walcott, 1920
Conicula striata Luo & Hu *in* Luo *et al*., 1999
Discoides abnormis Luo & Hu *in* Luo *et al*., 1999
Hippotrum spinatus Luo & Hu in Luo *et al*., 1999
Jiucunia petalina Hou *et al*., 1999
Maanshania crusticeps Hou *et al*., 1999
Macrocephalus elongatus Luo & Hu *in* Luo *et al*., 1999
Malongitubus kuangshanensis Hu, 2005
Nidelric pugio Hou *et al*., 2014
Parvulonoda dubia Rigby & Hou, 1995
Phacatrum tubifer Luo & Hu *in* Luo *et al*., 1999
Phasganula longa Luo & Hu *in* Luo *et al*., 1999
Pristioites bifarius Luo & Hu *in* Luo *et al*., 1999
Rhipitrus clavifer Luo & Hu *in* Luo *et al*., 1999
Stromatoveris psygmoglena Shu *et al*., 2006

29 Phylogenetic Arrangement of Chapters

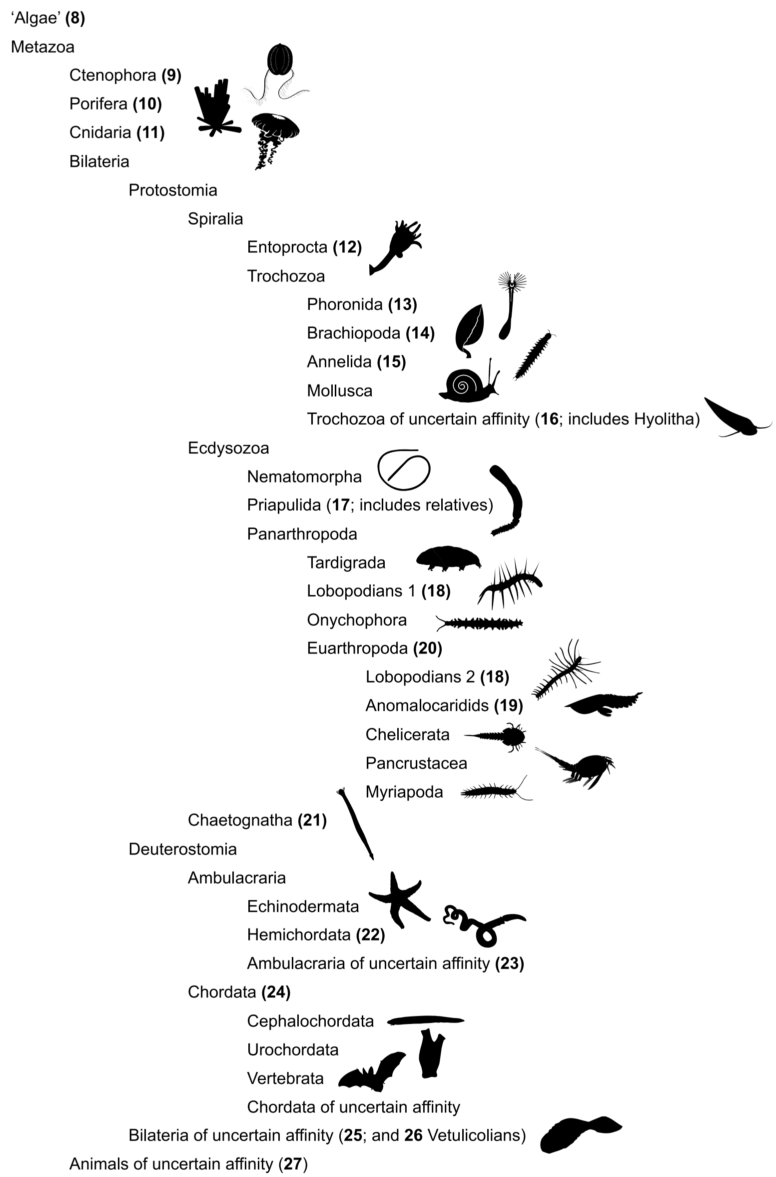

Figure 29.1 Phylogenetic arrangement of chapters. The indentation shows the hierarchy and relative inclusiveness of groups (taxa and clades), but equivalent indentation should not be taken to indicate equivalent taxonomic rank. Numbers given in parentheses are chapter numbers. See Preface for silhouette image credits.

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