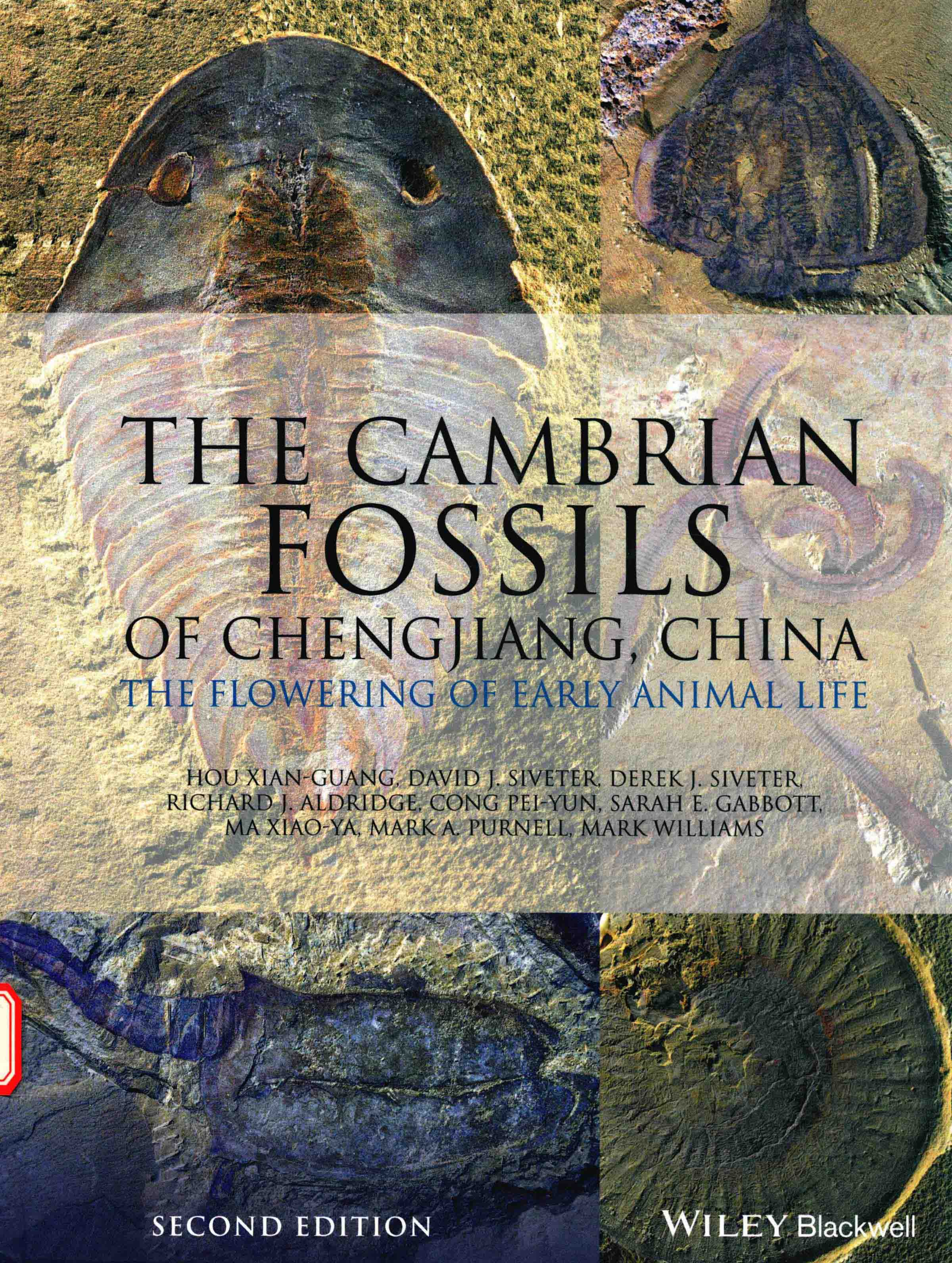


THE CAMBRIAN FOSSILS OF CHENGJIANG, CHINA

THE FLOWERING OF EARLY ANIMAL LIFE

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

SECOND EDITION

WILEY Blackwell

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

WILEY Blackwell

This edition first published 2017 © 2017 by John Wiley & Sons Ltd.
First edition published 2004 © 2004 by Blackwell Science Ltd.

Registered Office
John Wiley & Sons Ltd., The Atrium, Southern Gate, Chichester, West Sussex, PO19 8SQ, UK

Editorial Offices
9600 Garsington Road, Oxford, OX4 2DQ, UK
The Atrium, Southern Gate, Chichester, West Sussex, PO19 8SQ, UK
111 River Street, Hoboken, NJ 07030-5774, USA

For details of our global editorial offices, for customer services and for information about how to apply for permission to reuse the copyright material in this book, please see our website at www.wiley.com/wiley-blackwell.

Library of Congress Cataloging-in-Publication Data are available

ISBN: 9781118896389

A catalogue record for this book is available from the British Library.

Wiley also publishes its books in a variety of electronic formats. Some content that appears in print may not be available in electronic books.

Cover images: © All images courtesy of Derek J. Siveter.
Cover design by Wiley

Set in 10/11.5pt Minion by SPi Global, Pondicherry, India
Printed and bound in Singapore by Markono Print Media Pte Ltd

10 9 8 7 6 5 4 3 2 1

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.

Research support underpinning this book was principally provided by the National Natural Science Foundation of China (U1302232, 41372031, 41572015, and c6153002); the Department of Science and Technology of Yunnan Province (2015HC029 and W8110305); Yunnan Province; Yunnan University; the Royal Society (International Joint Project IE131457); the Leverhulme Trust (EM 2014-068); and the universities of Leicester and Oxford. Support is also acknowledged from the Natural Environment Research Council (NE/K004557/1; and Independent Research Fellowship NE/L011751/1). We are grateful to Dr David Baines for his skill in drawing the reconstructions of the fossils featured in this book. Lisa Barber drafted the diagrams. We are indebted to Professor Paul Selden for his constructive review of the manuscript. Kathy Syplywczak skilfully guided the manuscript through to publication.

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 Micro-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.

Contents

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

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.

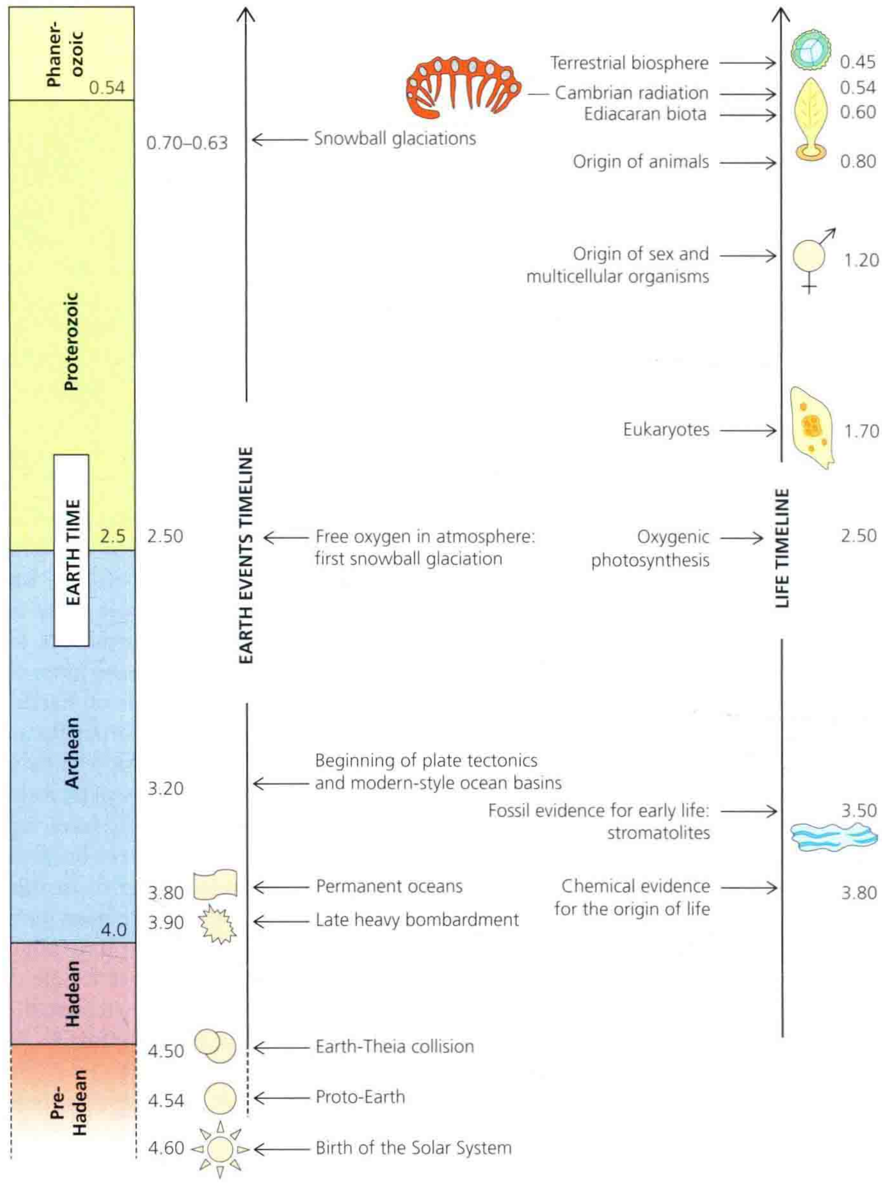
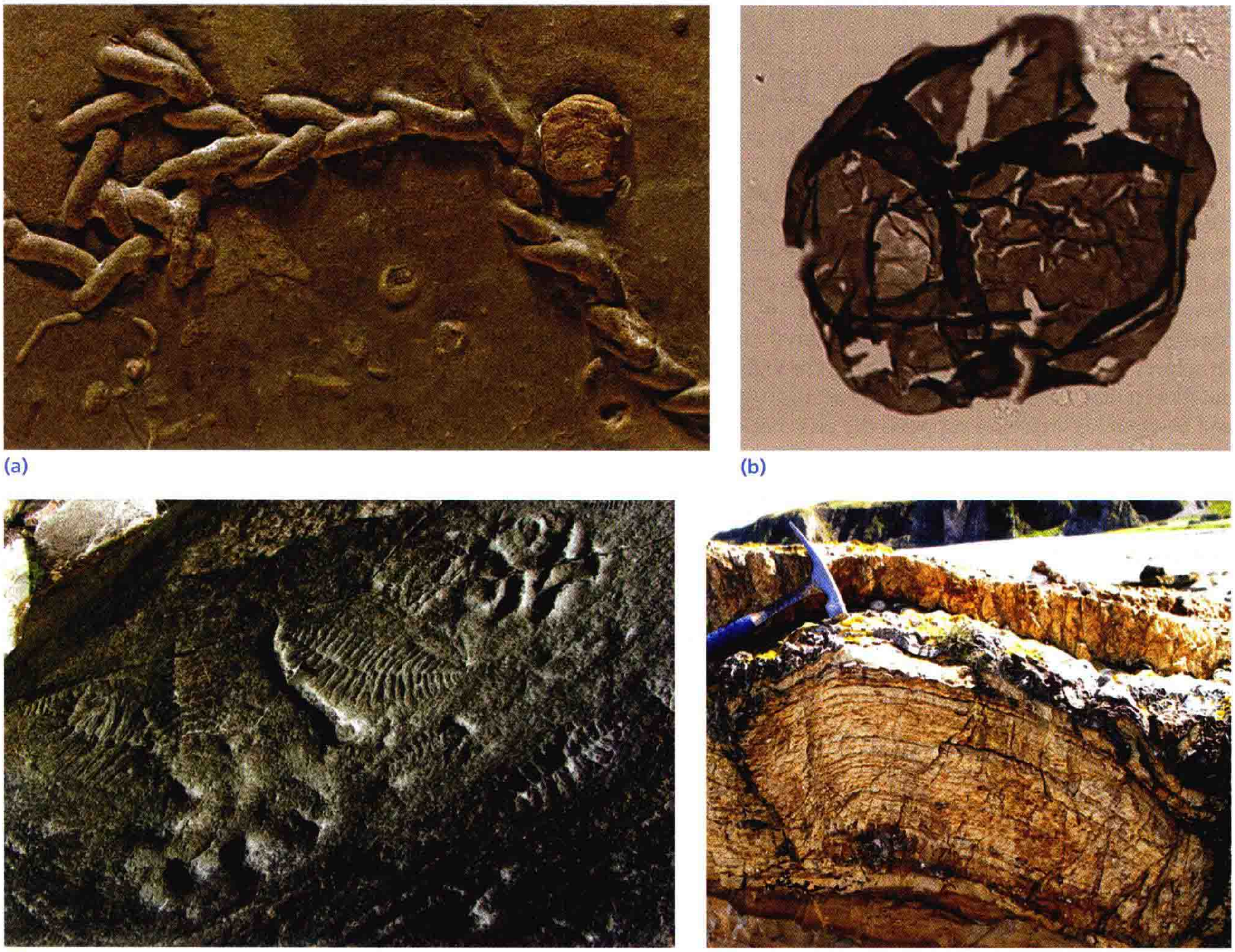


Figure 1.1 Some major events in the history of the Earth and early life.

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.