

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

HOU XIAN-GUANG, RICHARD J. ALDRIDGE, JAN BERGSTRÖM,
DAVID J. SIVETER, DEREK J. SIVETER AND FENG XIANG-HONG

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Cricocosmia jinningensis, complete specimen (RCCBYU 10218), $\times 8.0$; Mafang.

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CONTENTS

Foreword	ix
Preface	xi
Part One Geological and Evolutionary Setting of the Biota	1
1 Geological time and the evolution of early life on Earth	3
2 The evolutionary significance of the Chengjiang biota	8
3 The discovery and initial study of the Chengjiang Lagerstätte	10
4 The distribution and geological setting of the Chengjiang Lagerstätte	16
5 The taphonomy and preservation of the Chengjiang fossils	23
6 The paleoecology of the Chengjiang biota	25
Part Two Chengjiang Fossils	29
7 Algae	30
<i>Fuxianospira gyrata</i> Chen & Zhou, 1997	30
<i>Sinocylindra yunnanensis</i> Chen & Erdtmann, 1991	32
8 Phylum Porifera	34
<i>Triticispongia diagonata</i> Mehl & Reitner, 1993	34
<i>Saetaspongia densa</i> Mehl & Reitner, 1993	36
<i>Choiella radiata</i> Rigby & Hou, 1995	38
<i>Choiella xiaolantianensis</i> Hou <i>et al.</i> , 1999	40
<i>Allantospongia mica</i> Rigby & Hou, 1995	42
<i>Leptomitus teretiusculus</i> Chen <i>et al.</i> , 1989	44
<i>Leptomitella conica</i> Chen <i>et al.</i> , 1989	46
<i>Paraleptomitella dictyodroma</i> Chen <i>et al.</i> , 1989	48
<i>Paraleptomitella globula</i> Chen <i>et al.</i> , 1989	50
<i>Quadrolaminiella diagonalis</i> Chen <i>et al.</i> , 1990	52
9 Phylum Cnidaria	54
<i>Xianguangia sinica</i> Chen & Erdtmann, 1991	54
10 Phylum Ctenophora	56
<i>Maotianoascus octonarius</i> Chen & Zhou, 1997	56
11 Phylum Nematomorpha	58
<i>Cricocosmia jinningensis</i> Hou & Sun, 1988	58
<i>Palaeoscolex sinensis</i> Hou & Sun, 1988	60
<i>Maotianshania cylindrica</i> Sun & Hou, 1987	62

CONTENTS

12 Phylum Priapulida	64
<i>Palaeopriapulites parvus</i> Hou <i>et al.</i> , 1999	64
<i>Protopriapulites haikouensis</i> Hou <i>et al.</i> , 1999	66
<i>Acosmia maotiania</i> Chen & Zhou, 1997	68
<i>Paraselkirkia jinningensis</i> Hou <i>et al.</i> , 1999	70
<i>Archotuba conoidalis</i> Hou <i>et al.</i> , 1999	72
13 Phylum Hyolitha	74
<i>Lineivitus opimus</i> Yu, 1974	74
<i>Burithes yunnanensis</i> Hou <i>et al.</i> , 1999	76
<i>Ambrolinevitus maximus</i> Jiang, 1982	78
<i>Ambrolinevitus ventricosus</i> Qian, 1978	80
14 Phylum Lobopodia	82
<i>Luolishania longicruris</i> Hou & Chen, 1989	82
<i>Paucipodia inermis</i> Chen <i>et al.</i> , 1995	84
<i>Cardiodictyon catenulum</i> Hou <i>et al.</i> , 1991	86
<i>Hallucigenia fortis</i> Hou & Bergström, 1995	88
<i>Microdictyon sinicum</i> Chen <i>et al.</i> , 1989	90
<i>Onychodictyon ferox</i> Hou <i>et al.</i> , 1991	92
15 Anomalocarididae (phylum uncertain)	94
<i>Anomalocaris saron</i> Hou <i>et al.</i> , 1995	95
<i>Amplectobelua symbrachiata</i> Hou <i>et al.</i> , 1995	96
<i>Cucumericrus decoratus</i> Hou <i>et al.</i> , 1995	98
<i>Parapeytoia yunnanensis</i> Hou <i>et al.</i> , 1995	100
16 Phylum Arthropoda	102
<i>Urokodia aequalis</i> Hou <i>et al.</i> , 1989	103
<i>Fuxianhuia protensa</i> Hou, 1987	104
<i>Chengjiangocaris longiformis</i> Hou & Bergström, 1991	106
<i>Pisinnocaris subconigera</i> Hou & Bergström, 1998	108
<i>Dongshanocaris foliiformis</i> (Hou & Bergström, 1998)	110
<i>Canadaspis laevigata</i> (Hou & Bergström, 1991)	112
<i>Kunmingella douvillei</i> (Mansuy, 1912)	114
<i>Isoxys auritus</i> (Jiang, 1982)	116
<i>Isoxys paradoxus</i> Hou, 1987	118
<i>Yunnanocaris megista</i> Hou, 1999	120
<i>Leanchoilia illecebrosa</i> (Hou, 1987)	122
<i>Jianfengia multisegmentalis</i> Hou, 1987	124
<i>Tanglangia caudata</i> Luo & Hu, 1999	126
<i>Fortiforceps foliosa</i> Hou & Bergström, 1997	128
<i>Occacaris oviformis</i> Hou, 1999	130
<i>Forfexicaris valida</i> Hou, 1999	132
<i>Pseudoiulia cambriensis</i> Hou & Bergström, 1998	134

<i>Waptia ovata</i> (Lee, 1975)	136
<i>Clypecaris pteroidea</i> Hou, 1999	138
<i>Combinivalvula chengjiangensis</i> Hou, 1987	140
<i>Odaraia? eurypetala</i> Hou & Sun, 1988	142
<i>Pectocaris spatiosa</i> Hou, 1999	144
<i>Branchiocaris? yunnanensis</i> Hou, 1987	146
<i>Parapaleomerus sinensis</i> Hou <i>et al.</i> , 1999	148
<i>Naraoia longicaudata</i> Zhang & Hou, 1985	150
<i>Naraoia spinosa</i> Zhang & Hou, 1985	152
<i>Eoredlichia intermedia</i> (Lu, 1940)	154
<i>Kuanyangia pustulosa</i> (Lu, 1941)	156
<i>Yunnanoccephalus yunnanensis</i> (Mansuy, 1912)	158
<i>Retifacies abnormalis</i> Hou <i>et al.</i> , 1989	160
<i>Squamacula clypeata</i> Hou & Bergström, 1997	162
<i>Kuamaia lata</i> Hou, 1987	164
<i>Skioldia aldna</i> Hou & Bergström, 1997	166
<i>Saperion glumaceum</i> Hou <i>et al.</i> , 1991	168
<i>Cindarella eucalla</i> Chen <i>et al.</i> , 1996	170
<i>Xandarella spectaculum</i> Hou <i>et al.</i> , 1991	172
<i>Sinoburius lunaris</i> Hou <i>et al.</i> , 1991	174
<i>Acanthomeridion serratum</i> Hou <i>et al.</i> , 1989	176
17 Phylum Brachiopoda	178
<i>Diandongia pista</i> Rong, 1974	178
<i>Longtancunella chengjiangensis</i> Hou <i>et al.</i> , 1999	180
<i>Lingulelloreteta malongensis</i> (Rong, 1974)	182
<i>Lingulella chengjiangensis</i> Jin <i>et al.</i> , 1993	184
<i>Heliomedusa orientata</i> Sun & Hou, 1987	186
18 Phylum? Vetulicolia	188
<i>Vetulicola cuneata</i> Hou, 1987	188
<i>Banffia confusa</i> Chen & Zhou, 1997	190
19 Phylum Chordata	192
<i>Myllokunmingia fengjiao</i> Shu <i>et al.</i> , 1999	192
20 Enigmatic animals	194
<i>Allonnia phrixothrix</i> Bengtson & Hou, 2001	194
<i>Batofasciculus ramificans</i> Hou <i>et al.</i> , 1999	196
<i>Dinomischus venustus</i> Chen <i>et al.</i> , 1989	198
<i>Eldonia eumorpha</i> (Sun & Hou, 1987)	200
<i>Facivermis yunnanicus</i> Hou & Chen, 1989	202
<i>Jiucunia petalina</i> Hou <i>et al.</i> , 1999	204
<i>Maanshania crusticeps</i> Hou <i>et al.</i> , 1999	206
<i>Parvulonoda dubia</i> Rigby & Hou, 1995	208

CONTENTS

<i>Rotadiscus grandis</i> Sun & Hou, 1987	210
<i>Yunnanozoon lividum</i> Hou <i>et al.</i> , 1991	212
21 Species recorded from the Chengjiang biota	214
References	218
Index	229

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 which 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" which have stimulated much debate: were they missing links on the stem-groups of known animals, or completely new designs which 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 seafloor 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 lobopods; 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.

This book brings together marvellous color photographs to provide us with an album of Cambrian life. It is the first comprehensive “field guide” to the Chengjiang fauna. Think of it as the equivalent of one of those manuals people take to the Great Barrier Reef to identify the marine life—but here the seafloor is 525 million years old. It is a world full of surprises. The velvet worms—today represented by tropical terrestrial animals—were then much more diverse, some of them plated, spiky, odd-looking creatures. Marvel at the preservation of the comb jelly, the most delicate of marine organisms, destroyed today by the glance of an oar, but here preserved for hundreds of millions of years in almost incredible detail. Worms seem almost to be laid out upon the dissecting slab ready for inspection.

This book is much more than a mere picture gallery. The Chengjiang animals are tangible evidence of the evolutionary forcing house at the base of the Paleozoic that generated the “roots” of all the biodiversity of our living world. They bear upon fundamental questions about the generation of novelty of design. Is it feasible that so many radically different patterns of organismic construction could be derived from a common ancestor after the alleged “snowball Earth” some 600 million years ago? If so, what are the implications for genetic development? Could permutations in the expression of homeobox genes be responsible for the apparently rapid diversification of these animals? The beautiful fossil remains laid out upon their slabs of mudstone are recalcitrant facts that have to be incorporated into any scenario of molecular evolution, an invitation to further discovery, a challenge to biologists and paleontologists of the future. One thing is certain: the evidence from China will be forever built into the scientific edifice.

Or you can, if you prefer, take a delight in the aesthetic qualities of the images. You can allow your imagination to travel back to a world in which the sea swarmed with not-quite-shrimps, and the giant predator *Anomalocaris* preyed upon almost-amphioxus. Several of these animals had eyes: they looked over the living seafloor just as we contemplate the carcasses of the organisms they once observed. Paleontology is not a “dead” science. Its principal concern is to bring to life worlds that would otherwise lie forgotten and undiscovered within the rocks. It is to be hoped that this book will stimulate another generation in the quest for animals still undreamed of, vanished ecosystems still waiting to be unearthed.

Richard Fortey

PREFACE

The finding in 1984 of the Chengjiang biota, in rocks of Early Cambrian age in Yunnan Province, China, was one of the most significant paleontological discoveries of the twentieth century. The abundant and exquisite fossils, preserving fine details of the hard parts and soft tissues of animals and primitive plants approximately 525 million years old, are simply wondrous objects in their own right. More significantly, they are vital keys in helping to unravel the evolution of multicellular organisms during a period of time when such life forms first become common in the fossil record.

The Chengjiang biota is well known to practitioners and students of geology and biology through many papers published in specialist journals and in volumes resulting from scientific meetings. Much of the primary documentation is in Chinese. This is the first book in English to present an overview of the fauna, and has resulted from long established links between Professor Hou Xian-guang, the discoverer of the Chengjiang biota, and colleagues at the universities of Leicester and Oxford and the Swedish Museum of Natural History in Stockholm. The number of species known from the Chengjiang biota easily exceeds 100. Details on the authorship of each species 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 should be treated herein. We have simply provided a selection, with phyla ordered in accordance with the phylogeny of Nielsen (2001), to illustrate the range and nature of the biota. The systematic position of many Chengjiang species within their phyla is controversial and has in some cases attracted widely different opinions. Within each phylum, therefore, the order of treatment of the species does not follow any one "favored" scheme; rather, they are arranged with generally "allied" taxa together. 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 more widely known and appreciated by scientists and the public at large.

Research support underpinning this book is gratefully acknowledged from the Ministry of Science and Technology of China (G2000077702; Pandeng-95-Zhuan-01; 2002CB714007); the National Natural Science Foundation of China (No. 40272017); the Department of Science and Technology of Yunnan Province (No. 2001D0002R); the Natural Science Foundation of Yunnan Province (No. 2002D0006m); Yunnan University; the Royal Swedish Academy of Sciences; the Swedish Museum of Natural History; the Swedish Institute; the Swedish Natural Science Foundation; the Royal Society (Joint Project Q812); and the universities of Leicester and Oxford.

We thank in particular Lucy Siveter and also Chris Parks (Image Quest 3-D, Oxon, England), for invaluable assistance with computer-based photographic illustrations. Zhang Xi-guang, Ma Xiao-ya and Zhao Jie (Research Center for Chengjiang Biota, Yunnan University) kindly supplied unpublished information, and Rennison Hall (University Museum of Natural History, Oxford) and Michael Lear (Filey, North Yorkshire, England) provided technical help. We are grateful to Pollyanna von Knorring and Javier Herbozo (Swedish Museum of Natural History) for their skill in drawing many of the

reconstructions of the fossils featured in this book. We are indebted to Professor Derek Briggs (Yale University) for his constructive review of the manuscript. Thanks also to the staff at, or those associated with, Blackwell Publishing (Oxford) who were involved in bringing this book to fruition: Ian Francis for accepting the outline proposal, Delia Sandford the managing editor, and Jane Andrew, Cee Brandson, Jo Egré, and Rosie Hayden for their various editorial inputs.

All of the Chengjiang specimens figured in this book are from the Lower Cambrian Yu'an-shan Member, Heilinpu (formerly Qiongzhusi) Formation, of Yunnan Province. Certain specimens have been illustrated previously in the scientific literature, but one of us (Derek J. S.) re-photographed some of these for this book, together with very many other specimens that are figured herein for the first time. The figured Chengjiang material is housed at the Research Center for the Chengjiang Biota, Yunnan University (RC-CBYU), and the Nanjing Institute of Geology and Palaeontology (NIGPAS), Academia Sinica, the People's Republic of China.

PART
ONE

GEOLOGICAL AND
EVOLUTIONARY
SETTING OF
THE BIOTA

1 GEOLOGICAL TIME AND THE EVOLUTION OF EARLY LIFE ON EARTH

Our planet is some 4,600 million years old. We have no direct record of Earth history for the first 700 million years or so, but rocks have been found that date at least as far back as 3,800 million years, and perhaps even more than 4,000 million years. Earth history has been divided up into three eons: the Archean, the Proterozoic, and the Phanerozoic (Fig. 1.1); the Archean and Proterozoic are jointly termed the Precambrian. The boundary between the extremely ancient Archean and the very ancient Proterozoic is drawn at 2,500 million years, while the beginning of the Phanerozoic (literally meaning “manifest life”) is recognized by evolutionary changes shown by fossil animals about 545 million years ago. The Proterozoic is divided into three periods, the Paleoproterozoic (2,500–1,600 million years), the Mesoproterozoic (1,600–1,000 million years), and the Neoproterozoic (1,000–545 million years). The earliest period of the Phanerozoic eon is called the Cambrian, after the old Latin name for Wales, and it was during this time that almost all the animal groups we now know on Earth made their initial appearances. Some of the most important fossil evidence for these originations has come from the Chengjiang biota of southwest China—the subject of this book.

The record of life on Earth, however, goes much further back in time, perhaps nearly as far as the record of the rocks. Possible microfossils that resemble cyanobacteria have been reported from rocks as old as 3,500 million years in Australia (Schopf 1993) and there is circumstantial evidence from geochemical studies that carbon isotopes were being fractionated by organic processes as long ago as 3,860 million years (Mojzsis *et al.* 1996). However, there is a need to treat these 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, for example, Brasier *et al.* 2002, Fedo & Whitehouse 2002, van Zuilen *et al.* 2002).

It is quite probable, however, that fossils are present in rocks of Archean age, albeit extremely rarely. All of these sparse organic remains are microscopic, sometimes filamentous, and may be associated with laminated sedimentary structures known as stromatolites (Fig. 1.2a). Modern stromatolitic structures are built up through microbial growth, with successive layers of sediment being trapped by the microbial mats. The resulting forms are commonly dome-like or columnar, and these characteristic shapes can also be recognized in Archean sediments up to 3,500 million years in age. Once again, the very oldest stromatolites are somewhat controversial, and it is possible that they could have been constructed by abiotic processes rather than by living organisms (Grotzinger & Rothman 1996).

The micro-organisms 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). It is normally considered that most Precambrian examples were simpler, primarily constructed by the “blue-green” cyanobacteria, although the very earliest may have been built by anaerobic photosynthetic bacteria (Walter 1994). If we accept the combined evidence from putative microfossils, stromatolites and carbon isotopes, then it appears that life may have begun on Earth as much as 3,500 million years ago and that these life forms may have included micro-organisms that could generate their own energy by photosynthesis. But it is certain that the debate surrounding the nature of the earliest traces of life is far from over.

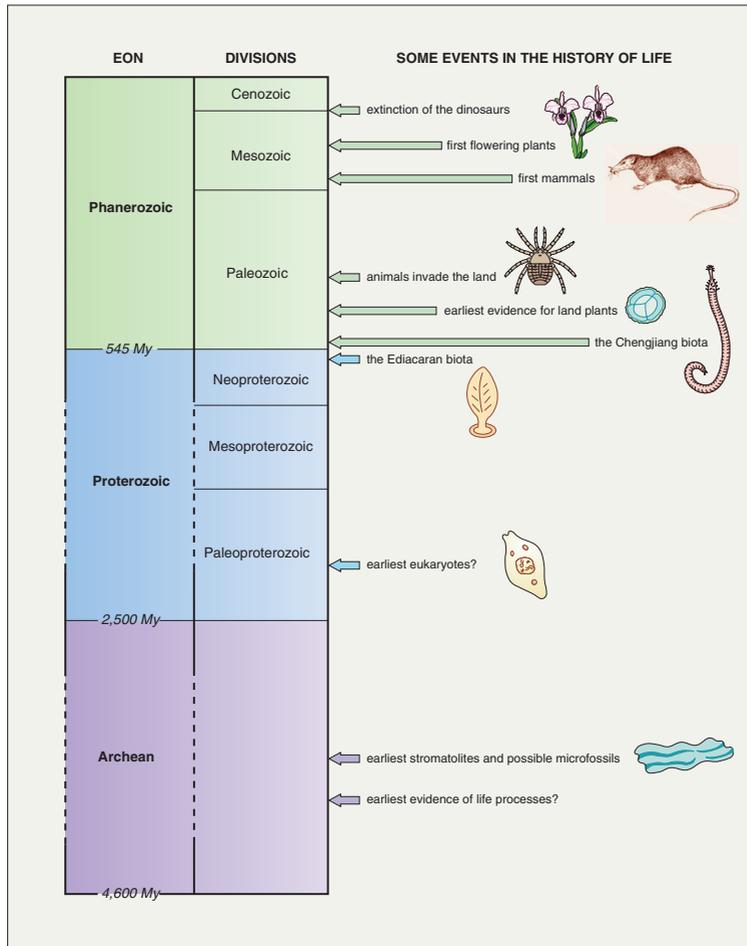


Figure 1.1 The geological time scale, showing some major events in the history of life.

There is a much richer and less controversial preserved record of life in 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). Geochemical evidence also indicates that oxygen levels in the atmosphere had begun to build up, reaching about 1% of the current level. There are also biomolecular data showing that one of the most significant steps in evolutionary history had taken place by this time—the appearance of eukaryotic cells (Brocks *et al.* 1999). Eukaryotes are distinguished

from the more primitive prokaryotes by their larger size, and by their much more complicated organization with a discrete nucleus, containing DNA organized on chromosomes, and a variety of organelles within the cytoplasm. Simple algal cysts with a cell size larger than any known in modern prokaryotic organisms date back to about 2,100 million years (Han & Runnegar 1992). Somewhat more complex spherical and spinose forms (“acritarchs”, Fig. 1.2b), presaging a diversification of eukaryotic micro-organisms, have been reported from rocks in northern Australia nearly 1,500 million years old (Javaux *et al.* 2001). Records also indicate that, by the late Mesoproterozoic, a



Figure 1.2 (a) A late Archean (about 2,700-million-year old) stromatolite, from the Fortescue Group of Meentheena, Western Australia; lens cap for scale (courtesy of Clive A. Boulter). (b) A Proterozoic acritarch (about 1,400 million years old), from the Roper Group, Northern Territory, Australia; width of specimen about $50\ \mu\text{m}$ (courtesy of Christopher A. Peat). (c) A fossil embryo from the Precambrian Doushantuo phosphorite of south China; width of specimen $505\ \mu\text{m}$ (courtesy of Xiao Shu-hai). (d) *Charniodiscus arboreus* (Glaessner, 1959), from the Ediacaran biota of South Australia (South Australian Museum specimen SAMP19690a); length of specimen 40 cm (courtesy of A. Bronikov and Dimitri Grazhdankin).

variety of groups of red and green algae had appeared.

This diversification of eukaryotes continued through the Neoproterozoic. Exceptionally

well-preserved specimens in the Doushantuo Formation of South China show that by about 590 million years ago multicellular algae were highly diverse and that the communities probably in-

cluded brown algae (Xiao *et al.* 1998, 2002). Particularly remarkably, phosphorites from the same formation have yielded embryos, probably of animals, three-dimensionally preserved in the early stages of cleavage (Xiao *et al.* 1998, Xiao 2002). The embryos are consistently about half a millimeter in diameter, compartmentalized into two, four, eight, or more internal bodies (Fig. 1.2c). Associated with them are tiny sponges, with monaxonal (single-axis) spicules and preserved soft tissues (Li *et al.* 1998). This incredible assemblage of fossils may record some of the earliest stages of the evolution of metazoan animals.

Metazoa are characterized by the grouping together of numerous cells, with different sets of cells fulfilling different specialized functions. The first metazoans must have arisen during the Proterozoic from a single-celled eukaryotic ancestor, but there is considerable debate about the timing of this event. Molecular clock calculations, which assume a regular substitution rate within selected genes, suggest that divergence of the metazoans occurred more than 1,000 million years ago (Wray *et al.* 1996), but there is no widely accepted fossil record of multicellular animals older than about 600 million years. In fact, the earliest undoubted metazoan body fossils are of about the same age as the Doushantuo embryos. These are part of the Ediacaran biota, named after sites in the Ediacara Hills of South Australia, where diverse macrofossils have been extensively studied.

Ediacaran fossils are now known from more than 30 localities worldwide. Among the earliest fossils that have been allocated to this assemblage are unornamented discs and rings that have been found in the Mackenzie Mountains of Canada (Narbonne *et al.* 1994), although these cannot be grouped unequivocally with the more diverse forms of the true Ediacaran biota (Fig. 1.2d). The specimens from the Mackenzie Mountains are dated as slightly older than 600 million years, and a somewhat greater variety of forms, including discs, triangles and fronds, has been reported from strata in Newfoundland that are 570–580 million years in age (Narbonne & Gehling 2002). The main Ediacaran organisms, however, are

found in rocks spanning an interval from about 565 to 543 million years ago, immediately above tillites that record the most extensive glacial episode in Earth history. Many workers have related the variety of soft-bodied forms found in these strata to well-known animal phyla, principally the Cnidaria, Annelida, Mollusca, Arthropoda, and Echinodermata. Although sponges, cnidarians and molluscs are almost undoubtedly represented, Seilacher (1992) proposed that most of these fossils 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 commentator has even suggested that they are not animals at all, but represent a range of lichens (Retallack 1994). More recently, Seilacher *et al.* (2003) have argued that the vendobionts were gigantic unicellular organisms living within biotopes as part of an ecological system consisting almost entirely of primary producers and decomposers. Whatever their relationships, the Ediacaran taxa almost all disappeared by the beginning of the Cambrian, with just a few specimens in Cambrian strata suggesting that these forms persisted for a while alongside their more familiar successors. If Seilacher and his co-workers are correct, the extinction of the Vendobionta was followed by an immediate radiation of metazoan animals that, until that time, had been a minor component of the biota. The concomitant development of hard parts instigated more complex trophic webs, with carnivores, scavengers, and consumers diversifying in the Early Cambrian seas.

One open question at the moment is whether the Doushantuo embryos are the early life stages of Ediacaran organisms, or whether they represent other taxa. Most commentators have compared them to the embryos of nematode worms, flatworms, arthropods, or cnidarians, but this in itself does not provide an answer.

Other evidence of animal life in the Neoproterozoic comes from trace fossils. Several of these, particularly the earlier ones, are controversial, but trace fossil assemblages are clearly recognizable in strata coeval with the Ediacaran biotas, and in

strata that are perhaps slightly older than the diverse Ediacaran assemblages. 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 the sediment. The animals 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 bilateral “worms” with hydrostatic skeletons.

There are recent claims of much older trace-like

fossils from Western Australia, where parallel pairs of ridges, straight or curved, occur in rocks dated as more than 1,200 million years old (Rasmussen *et al.* 2002). Intriguingly, these traces are associated with discoidal imprints that are possibly of biogenic origin and might represent the earliest Ediacara-type fossils discovered to date. This discovery serves to illustrate the fact that new finds of Proterozoic fossils are being reported at an ever-increasing rate, and it is clear that scenarios for the evolution of Precambrian life are facing continuing modification as these new data appear.

2 THE EVOLUTIONARY SIGNIFICANCE OF THE CHENGJIANG BIOTA

The Cambrian bears witness to a remarkable increase in the abundance, types and groups of fossils in the rock record, a feature considered by many to represent a major radiation in the evolution of life, the so-called “Cambrian Explosion”. In essence all of the major groups of life that are known from the present day can be traced back to the Cambrian. This is captured not only in the earliest fossil evidence of the hard skeletal parts of animals but also by the occurrence of several exceptionally preserved fossil biotas (Konservat-Lagerstätten), in which the soft parts of animals and entirely soft-bodied life forms are represented. The Upper Cambrian microarthropod-dominated “Orsten” fauna of Sweden (Müller 1979; see references in Walossek & Müller 1998), the celebrated Middle Cambrian Burgess Shale assemblage of British Columbia (e.g. Briggs *et al.* 1994, Conway Morris 1998) and the Lower Cambrian biotas from Sirius Passet in Greenland (e.g. Conway Morris & Peel 1995, Budd 1998) and from Chengjiang, are the key Cambrian Konservat-Lagerstätten. The Chengjiang biota (Fig. 2.1) is exceptional in providing a comprehensive and very early window on the nature of Phanerozoic life.

Although the first appearance of many forms of multicellular life in the Cambrian has traditionally been taken to indicate a major diversification of life (see Gould 1989), the evolutionary events that gave rise to the metazoans possibly occurred deep in Proterozoic time (Fortey *et al.* 1996, 1997,

Conway Morris 1997b, Walossek 1999; see also Bergström 1991, 1994). Thus, the nature and validity of the “Cambrian Explosion” attracts intense debate (see Wills & Fortey 2000). Some authors conclude that the explosion is real (Conway Morris 2000a). Some consider that it is a false explosion, perhaps a preservational window when, *inter alia*, animals became larger and acquired the hard parts that offered greater fossilization potential (Fortey *et al.* 1996, 1997). In support of the latter opinion it has been argued that the presence in the Early Cambrian of relatively advanced forms of, for example, arthropods (e.g. Siveter *et al.* 2001a), implies that less derived members of the phylum and other less derived metazoan groups must have differentiated still earlier in time (Fortey *et al.* 1996, 1997, Fortey 2001; see Siveter *et al.* 2001b). Other researchers have stressed that the appearance of body plans familiar from modern animals (“crown groups” of their terminology) mostly appeared after the Early Cambrian (Budd & Jensen 2000, Budd *et al.* 2001; see also Conway Morris 2000b) and favor a model of progressive metazoan diversification through the end of the Proterozoic to beyond the Cambrian. Whatever the truth of what happened to life across the Precambrian–Cambrian boundary and why, it is undisputed that the body fossils and trace fossils of the Chengjiang biota offer unparalleled insight into biodiversity, paleobiology, autecology and community structure for a crucial period in the history of life.



Figure 2.1 A cache of Chengjiang fossils from near Haikou: the arthropods *Fuxianhuia* (lower right) and *Eoredlichia* (a trilobite, lower left) and various worms (top left), $\times 1.1$.

3 THE DISCOVERY AND INITIAL STUDY OF THE CHENGJIANG LAGERSTÄTTE

The Chengjiang Lagerstätte was discovered by Hou Xian-guang in 1984 and is now known from many localities of the Yu'an-shan Member, Heilinpu Formation, over a wide area of eastern Yunnan Province. The first soft-bodied fossils to be found were from Maotianshan (Maotian Hill; Fig. 3.1), about 6km east of the county town of Chengjiang. The Kunming-Chengjiang area of Yunnan Province is one of the best-known geological areas of China. From the pioneer days of geological exploration in China it had been appreciated that the Lower Cambrian of eastern Yunnan Province is richly fossiliferous. As early as the first decade of the twentieth century the Frenchmen Honoré Lantenois (1907), Jaques Deprat (1912), and Henri Mansuy (1907, 1912) studied the geology and paleontology of the region (Figs 3.2–3.4), resulting in publications that featured new fossils including trilobites and other arthropods. As part of mapping and other general geological survey work, the Lower Cambrian in this area was also extensively studied in the 1930s and 1940s (see Babcock & Zhang 2001, Hou *et al.* 2002b). Indeed, the sequence has long been taken as a standard for the stratigraphic subdivision and correlation of the Cambrian, not only within the Southwest China (Yangtze) Platform but also throughout China and beyond.

In June 1984 Hou Xian-guang, then a member of the Nanjing Institute of Geology and Paleontology of the Chinese Academy of Sciences, arrived in Kunming City to begin his second stint of fieldwork for his research on bradoriid arthropods (Hou *et al.* 2002b). Already in 1980 he had systematically collected bradoriids at the Qiongzhusi section in Kunming City and from Sichuan

Province. That the Kunming-Chengjiang area is especially rich in bradoriids was elucidated much earlier, by Professor Yang Zui-yi, during the 1930s (see Ho 1942). As a consequence of hostilities within China, Yang's Department of Geology at Zhongshan University had moved from Guangzhou City in Guangdong Province to the village of Donglongtan, situated about 55km southeast of Kunming and a mere 1.5km west of Maotianshan. Following fieldwork in Jinning County southwest of Kunming, Hou Xian-guang had travelled to Chengjiang town and then on by cart to the nearby small village of Dapotou, where a team from the Geological Bureau of Yunnan Province was living, prospecting for phosphorite deposits in the Lower Cambrian. After reviewing the Heilinpu Formation at several nearby localities, systematic collection of bradoriids near Hongjiachong village was undertaken with the help of a hired farm worker, but the sequence was demonstrably incomplete and a section on the west slope of Maotianshan was finally selected for detailed study (Fig. 3.5).

The mudstone blocks that the farm worker dug out at Maotianshan were scoured for bradoriids. Work was notably easier than at Dapotou and Hongjiachong, because the rock was strongly weathered. At about three o'clock in the afternoon of Sunday July 1, a semicircular white film was discovered in a split slab, and was mistakenly thought to represent the valve of an unknown crustacean. With the realization that this and a second, subelliptical exoskeleton represented a previously unreported species, breaking of the rock in a search for additional fossils continued apace. With the find of another specimen, a 4–5 cm

