

## 3

*Chengjiang:  
Early Record of the Cambrian Explosion*

James W. Hagadorn

*When I found the first fossil . . . I knew right away that it was an arthropod with paired appendages, extending forward, as if it was swimming on the moistened surface of a mudstone. But I realized that you could see the impression of the soft body parts. That night I put the fossils under my bed. But because I was so excited, I couldn't sleep very well. I got up often and pulled out the fossils just to look at them.*

This is how Chinese paleontologist Hou Xianguang (personal communication, 2000) describes his initial reaction to the discovery of the Chengjiang Lagerstätte. In 1984, Hou was working on bradoriid-rich deposits at Maotian Hill, near the town of Chengjiang in the Yunnan Province of China (Figure 3.1). He split open a rock on the west face of the mountain to reveal an unusual arthropod: the soft-bodied trilobite *Naraoia* (Gore 1993; Monastersky 1993). Although a few obscure soft-bodied fossils from the Chengjiang deposit had been published (Mansuy 1912; Pan 1957), Hou was the first to recognize both Chengjiang's status as a Lagerstätte and its link to other soft-bodied deposits like the Burgess Shale. Considering the impact this deposit has had on the paleontological community, his enthusiastic reaction was more than justified.

The Chengjiang deposit is a conservation Lagerstätte that contains a variety of soft-bodied and biomineralized metazoans representing one of the earliest records of the Cambrian explosion in metazoan diversity. The Chengjiang biota is quite diverse, including algae, acritarchs, sponges, chancellorids, anemones, ctenophores, hyoliths, inarticulate

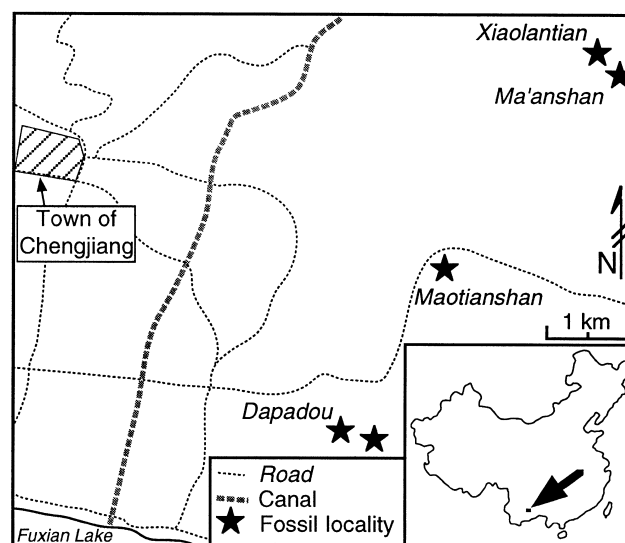


FIGURE 3.1 Chengjiang fossil localities. (Modified from Chen and Erdtmann 1991)

and linguloid brachiopods, paleoscolecs, priapulids, echinoderms, trilobites, primitive chordates including fish, trace fossils, several types of armored lobopods, a varied assemblage of arthropods, and a variety of taxonomically enigmatic forms. The abundance of specimens and prolific advance of recent fossil discoveries in this deposit stems partly from the spectacular soft-tissue preservation in the deposit, and partly from the pervasive labor-intensive collecting efforts that have been focused on outcrops in the Chengjiang area. Before the recent burst of activity on the Chengjiang Lagerstätte, the earliest known metazoan fauna with such great diversity and strong resemblance to extant phyla was the Burgess Shale fauna of the Canadian Rockies, which came to prominence 75 years earlier (Chapter 4).

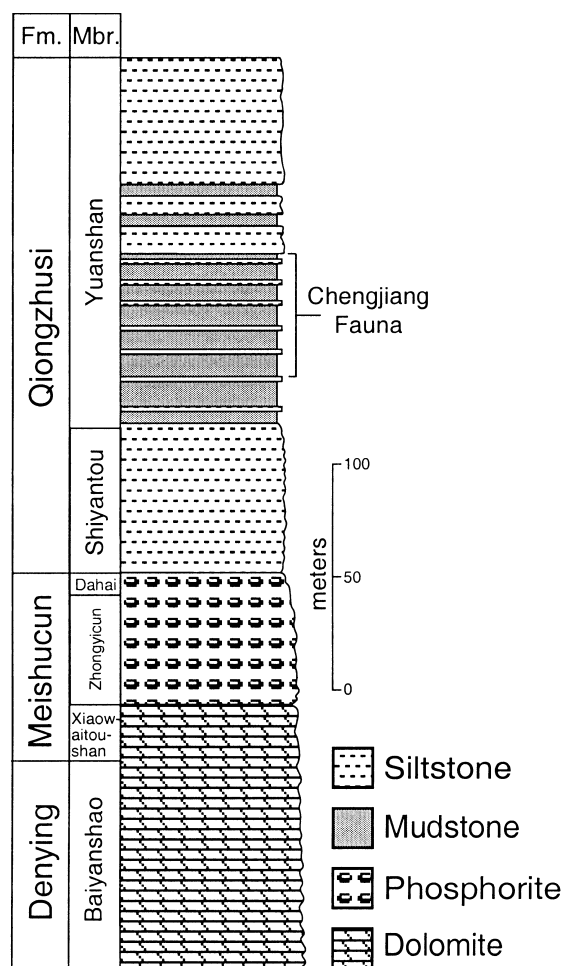
In addition to expanding the temporal and geographic distribution of Burgess Shale-type faunas, the Chengjiang deposit is notable because it contains a variety of taxa that have radically affected our understanding of the deep history of many fossil groups (e.g., the agnathan-like *Haikouichthys*), as well as articulated forms, which elsewhere were previously known from only fragmentary remains (e.g., the net-like plates of *Microdictyon*). The presence of possible stem-group fossils in the deposit has also provided the opportunity for further speculation about early metazoan phylogenies and the origin of body plans, by providing a morphological groundtruthing for molecular-based phylogenies. In addition to its importance for individual clades, the entire Chengjiang community is significant, simply because it has greatly reduced estimates of the time during which metazoans diversified and colonized marine habitats

shortly after the onset of the Cambrian. Before its discovery and the recalibration of the Cambrian timescale (Bowring et al. 1993; Landing et al. 1998), paleontologists' main view of Cambrian diversity was dominated by the Burgess Shale, which reflects a snapshot of Cambrian life nearly 10 Ma later.

## GEOLOGICAL CONTEXT

At the time of this writing, the Lower Cambrian stratigraphic nomenclature for this region is in a state of flux. For the purposes of this chapter, the framework established by Luo et al. (1984) and modified by Chen et al. (1996) and Chen and Zhou (1997) is used.

The Chengjiang soft-bodied fossils occur primarily within the Maotianshan Shale, which is one of four proposed units within the Yuanshan Member of the Qiongzhusi Formation (Lu 1941; Ho 1942; Luo et al. 1984; Chen et al. 1996; Chen and Zhou 1997) (Figure 3.2). The Qiongzhusi Formation is underlain by the lowest Lower Cambrian Meishucun Formation, which is dominated by a 15 to 20 m thick condensed sequence of phosphatic hardgrounds, dolomitic and stromatolitic phosphorites, and metabentonites (Zhang et al. 1997; Zhu 1997). The Meishucun is capped by a glauconite-bearing phosphatic conglomerate, the Dahai Member, and is thought to record a shallowing-upward sequence cut by a hiatus of unknown duration. Unconformably overlying the Meishucun Formation is the 100 to 150 m thick Shiyantou Member of the Qiongzhusi Formation, which consists of four units: a thin phosphatic conglomerate overlain by a thicker clay member, a black silty shale member, and a siltstone member (Chen et al. 1996; Chen and Zhou 1997; Zhu 1997). The base of the Shiyantou records a rapid deepening event, followed by a shoaling sequence from dysaerobic black shale facies into more aerobic dark gray siltstones intercalated with gray sharp-based dolomitic silty tempestites, including well-developed slump and loading structures (Zhu 1997). Like the Shiyantou Member, the Yuanshan Member is 100 to 150 m thick and composed of four units representing a shoaling-upward sequence. Basal units are dominated by black siltstones and concretion-laden black shales, overlain by thinbedded clays and shales of the fossiliferous Maotianshan Shale unit, and interbedded mudstones and dolomitic siltstones of the upper unit. The 50 m thick Maotianshan Shale unit has numerous storm-dominated features, such as graded bedding, wave ripples, tool marks, and flute casts, suggesting formation through deposition of distal mud-tempestites. The Yuanshan Member grades upward into sandstones, siltstones, and mudstones of the Guansan Member of the Canglangpu Formation, which represents the shallower wave-dominated subtidal-intertidal component of the upward-shoaling sequence recorded in the Yuanshan.



**FIGURE 3.2** Stratigraphic section of Lower Cambrian units of the central Yunnan region. (Modified from Chen and Erdtmann 1991)

Although soft-bodied fossils extend as far upward as the Canglangpu Formation, the lowest and most abundant occurrences are found in the Maotianshan Shale, which corresponds to the *Eoredlichia* trilobite biozone and is underlain by the earliest trilobites (*Abadiella* zone) and bradoriids. These are, in turn, underlain by three small shelly fossil zones, the uppermost of which is indicative of a late Atdabanian age (Qian 1977; Zhou and Yuan 1982; Zhang and Hou 1985; Hou 1987a, 1987d; Chen, Hou, and Lu 1989c; Conway Morris 1989; Qian and Bengtson 1989). Although reliable chronostratigraphic age estimates are not available for the Chengjiang section, carbon isotope stratigraphy and acritarch biostratigraphy corroborate trilobite biostratigraphic data that suggest a post-Tommotian age for the deposit (Zang 1992; Zhang et al. 1997).

The Chengjiang fauna has been documented from a number of localities in southern China, most notably at localities near the town of Chengjiang, located about 50 km southeast of Kunming, in Yunnan Province (Figure 3.1). In addition to the original and most well documented locality at Maotianshan, a number of fossiliferous localities have been documented from exposures of the Yuanshan Member in east-central Yunnan (e.g., Dapotou, Fengkoushao, Haikou, Meishucun, and Xiaolantian) (Hou and Sun 1988; Hou and Bergström 1997; Luo et al. 1997). Fossils occur in at least 10 horizons within this unit, and because the mudstones are very gently dipping, outcrops spanning the fossiliferous interval are exposed laterally for as much as 100 km (Chen and Erdtmann 1991; Hou and Bergström 1991).

## PALEOENVIRONMENTAL SETTING

Fossiliferous units are thought to have been deposited in a detrital belt located along the margin of the Yangtze Platform (Hou and Sun 1988; Chen and Erdtmann 1991). Before the terminal Neoproterozoic, the Yangtze Platform was part of a landmass that was likely separated from the two other landmasses (North China–Tarim and South Tibet) that later formed China (Jiang 1992). During the Cambrian, widespread evidence suggests, the Yangtze Platform was a shallow tropical sea bordered by relatively high-relief landmasses on three sides that was open (and deepened) to the east. Chengjiang was likely located in a bay that was in this seaway (Hou 1987a). During terminal Neoproterozoic–Early Cambrian time, this basin experienced several shallowing events, likely resulting from larger-scale eustatic shifts as well as local tectonism within the basin (Luo et al. 1984; Liang, Fang, and van de Voo 1990; Zhang et al. 1997; Zhu 1997).

Soft-bodied fossils of the Maotianshan unit are preserved in finely laminated 1 to 3 mm thick graded mudstones that have sharp-bottomed laminated silty bases overlain by nonlaminated clays. These beds are intercalated with 1 to 50 cm thick fine-grained nonfossiliferous sandstones. The presence of flute marks, storm wave ripples, and rare hummocky cross-stratification indicates rapid deposition of beds below or near storm wave base (Shu, Geyer, et al. 1995; Zhu 1997). Grading within mudstone and siltstone layers suggests that fossils were likely entrained in and/or buried by a series of microturbidites deposited in a relatively quiescent setting; fine-grained sandstones likely reflect the influence of sporadic strong storm events.

Based on regional paleogeography, the Maotianshan Shale was likely deposited around 60 to 70 km east of the paleoshoreline of the Yangtze seaway and about 600 to 700 km west of the continental slope (Zhang 1987). Flute and groove casts support an easterly current direction for

microturbidite layers in the Maotianshan, and lithofacies stacking patterns suggest that the entire depositional sequence bounding the Chengjiang fauna reflects eastward progradation of a delta, with the fossiliferous Maotianshan Shale reflecting episodic turbid transport of distal marine muds at the foot of the delta front (Chen and Lindström 1991; Lindström 1995; Chen and Zhou 1997). Detailed paleoenvironmental analyses of the Chengjiang are still under way, with a recent study (Babcock, Zhang, and Leslie 2001) suggesting the operation of tidal processes in this environment.

## TAPHONOMY

Fossils are typically preserved in beds consisting of sharp-based, 1 to 2 mm thick graded mud layers overlain by a thin nonlaminated claystone. The lower mudstone appears black to grayish black, and the middle to upper portions of these beds are typically weathered grayish yellow to green. Soft-bodied fossils are preserved as aluminosilicate films (Zhu 1997). Biomineralized skeletons are similarly preserved, but in a decalcified state. In organic-walled fossils, proteins have been replaced by hematite and iron-rich clay minerals through early diagenetic alteration (Jin, Wang, and Wang 1991). However, in a study of bradoriid mineralogy, Leslie et al. (1996) noted that nonmineralized arthropod cuticle contained higher concentrations of phosphorus than the surrounding rock matrix, suggesting that preservation of soft parts may have been mediated by early precipitation of phosphatic minerals. Many of the fossils at Chengjiang localities are severely weathered, appearing as reddish, ferric oxide-stained films on a yellow-weathered matrix. This reddish color is thought to result from oxidation of finely dispersed framboidal pyrite on bedding and fossil surfaces. This pyrite may have been produced by bacterial activities during early fossil diagenesis (Chen and Erdtmann 1991).

Fossils are moderately compressed, as indicated by wrinkling of convex and cylindrical shapes (Hou 1987b), and the appendages of arthropods are commonly visible through the body or carapace. Such appendages are expressed as shallow furrows and reflect decay and collapse of the underlying appendage and compression of the overlying exoskeleton into the vacant space (Chen, Zhou, and Ramsköld 1995a; Hou and Bergström 1997). Organisms characterized by exoskeleton-like carcasses are typically preserved roughly parallel to the bedding, with their appendages and related features penetrating several laminae in both upward and downward directions (Hou, Ramsköld, and Bergström 1991). Thus, rocks tend to cleave along the exoskeletal dorsal surface or along the upper margin of the valve (e.g., bradoriids, trilobites), and although some of the appendages are visible on split slabs, more commonly they are buried beneath sediment laminae.

In general, fossils appear to be exquisitely preserved because they have undergone minimal transport and sustained minimal postburial taphonomic overprinting (Hou, Chen, and Lu 1989). For example, even in transported specimens, delicate features such as exopod setae are preserved in three dimensions (Hou and Bergström 1997). Some forms may have been buried *in situ*, including lingulid brachiopods preserved with their pedicle traces extending obliquely downward into underlying layers (Jin, Hou, and Wang 1993) or infaunal priapulid worms, such as *Mao-tianshanina*, buried in their burrows (Sun and Hou 1987b).

Although the majority of the fossils were likely transported, many were probably buried while still alive or perhaps very shortly after death. Examples of live transport followed by burial include epibiotic forms preserved in attached position, such as the onychophoran-like *Microdictyon*, which was apparently buried while still attached to its shelled host *Eldonia* (Chen, Zhou, and Ramsköld 1995a, 1995b). Although the mere occurrence of soft-tissue preservation is often used as evidence to support minimal transport, Chengjiang includes several examples that are particularly convincing, including the probable cnidarian *Cambrorhytium* preserved still attached to a lingulid shell in life position (Chen et al. 1996). Evidence for catastrophic burial also includes the presence of sediment in the pharynx of mobile vertebrates found in the deposit (Shu, Luo, et al. 1999), as well as indirect evidence such as the overall rarity of mobile swimmers in these deposits (but see Vannier and Chen 2001), suggesting that mobile animals may have been able to avoid benthic sediment flows. Other forms, such as the predator *Anomalocaris*, seem to have undergone significant decay before burial (Hou and Bergström 1997).

Death of preserved organisms is interpreted to have occurred as a result of asphyxia, although it is unclear whether asphyxia is related to suffocation by repeated benthic sediment flows or by incursion of oxygen-depleted waters. Evidence for entrainment of faunas by abundant microturbidite flows has been mentioned. Hou and Bergström (1991) suggest that shelfward movement of the oceanic oxygen minimum zone or periodic upwelling of oxygen-deficient waters (mediated by transgressive conditions) over the outer portions of the central Yunnan continental shelf caused frequent anoxic poisoning of the fauna. Absence of escape burrows in the deposit lends support to this anoxia-poisoning hypothesis. In either case, evidence for asphyxia includes everted worm proboscises, coiling in soft-bodied worms, and extended mantle setae in inarticulate brachiopods (Sun and Hou 1987b; Hou and Sun 1988; Jin and Wang 1992). Other specimens exhibit features indicative of metabolic stasis, such as an extruded esophagus (Chen and Erdtmann 1991).

Relevant to the oxygenation debate is a detailed taphonomic study by Babcock and Chang (1997), in which they examined disarticulation pat-

terns of the relatively common soft-bodied arthropod *Naraoia* and compared them with decay of a modern limulid. Like most arthropods in the deposit, naraoiid skeletons became pliable several hours after death, as evidenced by wrinkling patterns within dorsal and posterior shields. More important, however, is evidence suggesting that in oxygenated water, post-mortem naraoiid appendages could remain articulated for weeks, and their two exoskeletal shields could remain articulated for months. In anoxic water, such features might even remain articulated for years. Together, this evidence suggests that *Naraoia*, and perhaps many of the other components of this arthropod-dominated Lagerstätte, could reflect dead skeletons swept into amalgamated storm deposits.

Regardless of tenuous evidence for possible reduction of benthic oxygen levels, the mere presence of a diverse biota (described later) certainly suggests that the water column in this setting was sufficiently oxygenated to allow colonization by a rich pelagic and benthic marine community. Sediments in this environment may have been characterized by low oxygen levels or fluctuating salinity (Babcock, Zhang, and Leslie 2001), thus inhibiting the scavenging that would have ordinarily damaged the many nonmineralized carcasses buried in the sediment (Babcock and Chang 1997).

Decay of organisms may also have been inhibited through post-mortem sealing by microbial mats. Evidence for postmortem coating of sediment-covered carcasses by bacterial sheaths is suggested by a bluish surface stain that occurs on many of the segmented worms, brachiopods, and sea anemones (Chen and Erdtmann 1991). In addition, low pyrite levels and the presence of sulphide mineral coatings on carcasses suggest that sulfate reduction was minimal during sediment deposition (Chen and Erdtmann 1991).

Although some of the aforementioned information is incomplete, it is worth noting that taphonomic study of this deposit is still in a nascent state, largely because the majority of the focus thus far has been on the paleobiology of Chengjiang organisms. Taphonomic work has mostly focused on isolated fossils. Lithologic, geochemical, and petrographic data, as well as related taphonomic information, have rarely been collected in direct association with the fossils (but see Zhu 1992; Leslie, Babcock, and Chang 1996; Leslie et al. 1996; Babcock and Chang 1997).

## PALEOBIOLOGY

Given the recent discovery of Chengjiang, it is not surprising that the vast majority of work on the deposit has focused on the systematics of the faunas and their evolutionary significance. Because intense collecting efforts at multiple Chengjiang quarries seem to yield new taxa almost monthly, the following is (at best) only a cursory overview of the



more notable organisms described from this Lagerstätte. Readers are directed to Chen, Cheng, and Iten (1997) and Hou et al. (1999) for richly illustrated perspectives on this deposit, and, for a systematic review of the arthropods, to Hou and Bergström (1997).

Megascopic algae are common members of the Chengjiang biota, and many forms consist of only algal thalli, like *Yuknesia* sp. More elaborate forms also occur and include delicate, long, slender looping forms such as *Sinocylindra yunnanensis* or the beautiful helically coiled *Megaspirellus houi* (Chen and Erdtmann 1991). The most common alga is *Fuxianospira gyrata*—a tightly coiled form commonly found splayed in large looping strings on bedding planes (Chen and Zhou 1997).

Chengjiang contains one of the oldest and most spectacularly preserved articulated sponge communities (but see Steiner et al. 1993; Mehl and Erdtmann 1994; Gehling and Rigby 1996; Brasier, Green, and Shields 1997). Sponges are typically preserved articulated or aligned on bedding planes, along with coarse algal debris. Sponges have the second-highest diversity of the Chengjiang metazoan groups (Chen, Hou, and Lu 1989c; Chen, Hou, and Li 1990; Rigby and Hou 1995), with more than 15 genera and 30 species represented among over 1,000 specimens. Sponges are dominated by the tubular Demospongea, including thin-walled balloon- or fan-shaped forms like *Leptomitrus teretiusculus*, *Leptomitella conica*, and *Paraleptomitella dictyodroma* (Chen, Hou, and Lu 1989c), and spinose funnel-shaped forms like *Choiella radiata* (Rigby and Hou 1995). Although rare, hexactinellids also occur, and are represented by the large globose reticulate *Quadrolaminiella diagonalis* (Chen, Hou, and Li 1990; Reitner and Mehl 1995), the sac-shaped *Crumillospongia* sp., and the elongate fan-shaped *Halichondrites* sp. (Chen and Zhou 1997). Taxonomically enigmatic sponge-like forms are also known, including several undescribed species of the sac-like spiculate *Chancelloria* sp. (Chapter 4; Chen and Zhou 1997).

Rare anemone-like forms suggest the presence of cnidarians on the Chengjiang seafloor, and include forms with sac-shaped bodies capped by distal tentacles, such as *Xianguangia sinica* (Chen and Erdtmann 1991). These specimens have as many as 16 long flexible tentacles, each of which is lined with exquisitely preserved feathery setae along the medial ridge. A funnel-shaped solitary form described as *Cambrorhytium* is also known and, although rare, occurs attached to *Lingulepis* valves or to other *Cambrorhytium* (Chen and Zhou 1997).

Ctenophores have recently been reported from the deposit, and include the smooth lobed form *Sinoascus papillatus* and the spectacular globose form *Maotianoascus octonatus*. *Maotianoascus* has eight petaloid lobes, and each comb-row preserves impressions of delicate cilia and ciliary support structures (Chen and Zhou 1997).

As in the Burgess Shale, there is a diverse assemblage of priapulid worms in the Chengjiang Lagerstätte, including elongate forms such as

*Maotianshania*, ornamented forms such as *Palaeoscolex*, segmented forms such as *Cricocosmia*, and possible U-shaped forms such as *Acosmia maotiania* (Sun and Hou 1987b; Hou and Sun 1988; Hou and Bergström 1994; Chen and Zhou 1997). Worms are typically preserved flattened either parallel or nearly parallel to bedding in the shales and mudstones (Jiang 1992). The most common priapulid is *Maotianshania cylindrica*, which may constitute as much as 5 percent of the fauna (Figure 3.3). Like many of the worms, *Maotianshania* exhibits nearly perfect preservation—not only are its proboscis, trunk annulations, setae, and intestinal canal preserved, but even the spiny papillae on its everted proboscis are visible.

Tentaculates are also present, represented by the two spectacularly preserved forms *Eldonia eumorpha* and *Rotadiscus grandis*. Each of these disk-shaped lophophorates contains a U-shaped intestine, concentrically arranged growth lines on the convex surfaces of their disks, and a tentacle-shaped lophophore (Sun and Hou 1987a; Dzik 1991; Chen, Zhu, and Zhou 1995; Dzik, Zhao, and Zhu 1997). These presumably benthic epifaunal forms are typically compressed into thin disks or flat films between shale and mudstone bedding planes (Sun and Hou 1987a) and are often covered with epibionts, such as the linguloid brachiopods *Lingulella* and *Lingulepis*, the lobopod *Microdictyon*, as well as a number of other taxonomically enigmatic epizoans (Chen, Zhou, and Ramsköld 1995a, 1995b; Dzik, Zhao, and Zhu 1997).

Among the more typical Cambrian skeletonized invertebrates, Chengjiang's lingulate brachiopods are of particular interest because they are among a handful of brachiopods that contain fossilized pedicles (Liu 1979; Jin, Hou, and Wang 1993). Some of the more elaborate forms are *Lingulepis malongensis* (Figure 3.4) and *Lingulella chengjianensis*, each



**FIGURE 3.3** *Maotianshania cylindrica*. Lower specimen length is approximately 1.7 cm. (Photo courtesy of Hou Xianguang, Nanjing Institute of Geology and Palaeontology, China)





**FIGURE 3.4** *Lingulepis malongensis*. Length of specimen is approximately 4 cm. (Photo courtesy of Hou Xiangang, Nanjing Institute of Geology and Palaeontology, China)

of which has looping vermiform pedicles with well-preserved cuticular fibers. Less elaborate nonpediculate brachiopods are also present, such as the very common nonmineralized form *Heliomedusa orientalis*. It is characterized by a biconvex shape and delicate features, including setae and apparent nerves (Jin and Wang 1992), but because its closely spaced setae are distributed along its entire shell margin, it was inadvertently identified as a hydrozoan in its initial description (Sun and Hou 1987a). Subsequent interpretations of its distinctive setal arrangement suggest that in life position, *H. orientalis* lay on the seafloor with its shell open (Jin and Wang 1992).

Other typical Cambrian organisms include trilobites (discussed later) and hyoliths. Hyolithids are quite common at some Chengjiang localities, where they typically occur as concentrations aligned in apparent alimentary canals and in coprolites (Chen et al. 1996). Many of the hyoliths, such as *Ambrolinevitus* sp., exhibit growth lines and are preserved with opercula and helens intact.

Arthropods are the most common group at Chengjiang, in both number of specimens and number of species (Hou and Bergström 1991, 1997). Although the most common arthropods (constituting approximately 80 percent of the total number of individuals) are the tiny bivalved bradoriids, arthropods exhibit a wide size range in the deposit (from less than 1 mm up to 0.5 m) and, overall, are the largest organisms among the Chengjiang fauna. More than half of the over 80 described taxa from Chengjiang are arthropods, including a number of forms also known from the Burgess Shale, such as *Anomalocaris*, *Canadaspis*, *Leanchoilia*, *Naraoia*, *Waptia*-like forms, and members of the family Helmetidae (Zhang and Hou 1985; Hou 1987b, 1987d; Hou and Bergström 1991; Chen, Ramsköld, and Zhou 1994; Luo et al. 1997; Shu, Luo, et al. 1999). Like the nonarthropod taxa, nonmineralized arthropods exhibit spectacular preservation, including well-preserved eyes, digestive organs, appendages, and fine surface textures.

Despite their status as the most common fossil in Chengjiang, only a few (of the many thousands) of the ostracod-like bradoriids are preserved associated with soft-tissue preservation. Among the more spectacular of these forms is *Kunmingella douvillei*, which often exhibits well-preserved stalked eyes, uniramous antennae, appendages of thoracic segments, and a long telson with furcal rami (Hou and Bergström 1997; Hou 1999). *Isoxys auritus* and *I. paradoxus* are another common component of the arthropod fauna, and are characterized by a body enclosed in a large bivalved carapace (Hou 1987c; Shu, Zhang, and Geyer 1995). Although the abdomen of *Isoxys* is poorly defined due to enclosure by the bivalved carapace, a number of specimens exhibit soft-part preservation of stalked eyes and trunk limbs bearing pairs of foliaceous exopods fringed with setae.

Among the soft-bodied arthropods, *Naraoia* predominates—comprising nearly 7 percent of the total number of Chengjiang specimens and 10 percent of the arthropods—and is preserved in all manner of orientations within beds (Zhang and Hou 1985; Leslie, Babcock, and Chang 1996). Like *Naraoia* from the Burgess Shale (Chapter 4), two species are present (*Naraoia spinosa* and *N. longicaudata*) and are characterized by relatively large anterior and dorsal shields and elongate antennae directed antero-laterally. These shields were joined together so that the animal could enroll—as indicated by the many enrolled and partially enrolled specimens at Chengjiang. Where preserved fully extended on bedding surfaces, hundreds of specimens exhibit near-perfect preservation of segmented uniramous antennae, biramous limbs, mouth, esophagus, appendages, delicate appendage setae, and other organs (Zhang and Hou 1985; Chen, Edgecombe, and Ramsköld 1997).

A number of the other bivalved arthropods, such as *Canadaspis laevigata* and *Chuandianella ovata*, are preserved with extruded abdomens, antennae, biramous appendages bearing spine-tipped podomeres, alimentary tract, and stalked eyes (Hou and Bergström 1991, 1997). Among these, *Vetulicola cuneatus* is notable because of its large partially fused carapace, which bears a pair of lateral slits; its paddle-shaped abdomen; and its lack of locomotive appendages (Hou 1987c; Hou and Bergström 1991).

*Fuxianhuia protensa* is one of the more spectacularly preserved of the megathoracic arthropods (Figure 3.5), and is characterized by a short head shield bearing bulbous eyes and raptorial uniramous appendages, a wide segmented trunk bearing biramous limbs, an elongated legless abdomen, and posterior fins bearing telson-like spines (Hou 1987b; Hou and Bergström 1991; Chen, Edgecombe, et al. 1995). This unusual suite of characteristics has led to debate about its taxonomic affinity, with arguments for a chelicerate (Wills 1996) or a primitive euarthropod affinity suggested (Chen, Edgecombe, et al. 1995; Hou and Bergström 1997).

The small, but delicately preserved jawless arthropod *Jianfengia multisegmentalis* (Figure 3.6) is also of note, largely because of the exquisite preservation of nearly all its appendages, including features of its head, segmented trunk, and paddle-like telson. These include a pair of giant pre-oral appendages capped by four distal spines, possible stalked eyes, a streamlined body, and 22 post-cephalic segments bearing biramous endopods, each of which is characterized by spinose podomeres and broad teardrop-shaped exopods (Hou 1987a; Hou and Bergström 1991).

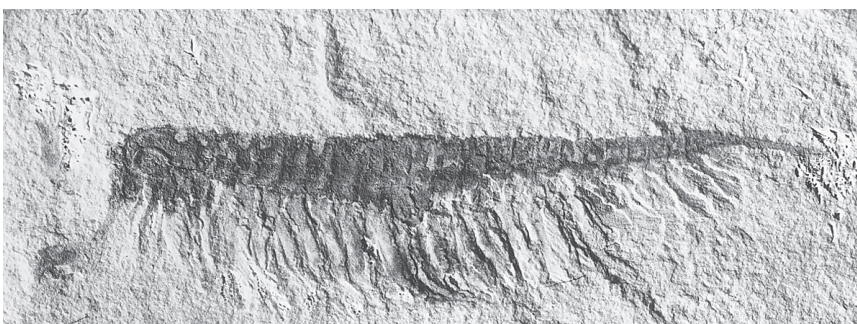
Trilobites are a relatively minor component of the fauna, in terms of both diversity and abundance. Although most of the trilobites are preserved as complete carapaces (rather than disarticulated exuviae), soft-part preservation is extremely rare among the calcified forms (Zhang and Hou 1985; Zhang 1987; Shu, Geyer, et al. 1995). Careful removal of





**FIGURE 3.5** *Fuxianhuia protensa*. Length of specimen is approximately 10 cm. (Photo courtesy of Hou Xianguang, Nanjing Institute of Geology and Palaeontology, China)

exoskeletal elements from rock surfaces allowed Shu, Geyer, et al. (1995) and Hou and Bergström (1997) to document spectacularly preserved antennae, biramous appendages, and digestive tracts in the many Redlichiacean trilobites of the deposit, such as *Eoredlichia intermedia* and *Kuanyangia* sp. A variety of soft-bodied trilobite-like arthropods is also known, including forms like *Kuamaia lata* and *Retifacies abnormis*. These taxa are similar to forms from the Burgess Shale (Chapter 4) in that they are characterized by a wide, flat, thin carapace composed of a head shield, thorax, and long tail shield (Hou 1987b; Hou, Chen, and Lu



**FIGURE 3.6** *Jianfengia multisegmentalis*. Length of specimen is 1.7 cm. (Photo courtesy of Hou Xianguang, Nanjing Institute of Geology and Palaeontology, China)

1989), but differ in that some specimens preserve stalked eyes, biramous appendages, and jointed antennae covered with setae.

Perhaps the most exciting recent discoveries at Chengjiang are of putative early chordates, including a tunicate (Shu et al. 2001), an agnathan-like fish (Shu, Luo, et al. 1999), and pipiscid-like forms (Shu, Conway Morris, et al. 1999). For example, the extremely rare eel-like *Cathaymyrus diadexus* is thought to be preserved with its pharyngeal gill slits, myotomes, and notochord-like structures intact (Shu, Conway Morris, and Zhang 1996). The lamprey-like *Haikouichthys ercaicuensis* possesses a probable branchial basket and dorsal fin with prominent fin-radials, and the hagfish-like *Mylokunmingia fengjiao* has well-developed gill pouches and probable hemibranchs (Shu, Luo, et al. 1999). Both forms are notable because they contain distinctive chordate features, including complex myomeres, a pericardial cavity, paired ventral fin-folds, and probable imprints of a cartilagenous skull. Not only do these agnathans extend the range of fish by 45 Ma, but they suggest the presence of a Neoproterozoic ancestry for chordates (Shu, Luo, et al. 1999). A possible precursor to the agnathans is also preserved, in the probable pipiscid *Xidazoon stephanus* (Shu, Conway Morris, et al. 1999). This taxon, known from only two specimens on a single bedding plane, has a segmented sac-like body with an exquisitely preserved feeding apparatus characterized by a circlet of plates. *Xidazoon* is notable because it extends the stratigraphic range of this group from the upper Carboniferous to the Cambrian, and because it may reflect a primitive stem-group deuterostome (Shu, Conway Morris, et al. 1999). Perhaps related to *Xidazoon* is *Yunnanozoon lividum* (Figure 3.7), a blade-shaped or-



**FIGURE 3.7** *Yunnanozoon lividum*. Length of specimen is approximately 3.5 cm. (Photo courtesy of Hou Xiangang, Nanjing Institute of Geology and Palaeontology, China)



ganism with segmented musculature (Hou, Ramsköld, and Bergström 1991) and perhaps a circum-oral set of plates (Dzik 1995). However, there is some debate as to the affinity of this form, with early work suggesting that it constituted the earliest chordate (Chen, Dzik, et al. 1995; Dzik 1995; Chen and Li 1997), and subsequent work suggesting a hemichordate affinity (Shu, Zhang, and Chen 1996), or possibly neither (Shu, Conway Morris, et al. 1996; Bergström et al. 1998; Conway Morris 1998). Discovery of *Haikouella*, similar in many ways to *Yunnanozoon*, has furthered the debate with the suggestion that they both be considered as early craniates (Chen, Huang, and Li 1999).

Among the more enigmatic fossils at Chengjiang is *Anomalocaris*, which is also known from Burgess Shale-type localities (Chapters 4 and 5), a large predatory animal that exhibits an unusual combination of arthropod- and aschelminth-like features, including a disk-like mouth, anterior crustacean-shaped frontal appendages, lateral flaps along its torso, stalked eyes, and segmented walking legs (Chen, Ramsköld, and Zhou 1994; Hou, Bergström, and Ahlberg 1995) (Figure 3.8). Although the number of anomalocariid taxa present in this deposit is debated (Minicucci 1999), key forms include *A. saron*, *Cucumericrus decoratus*, and *Parapeytoia yunnanensis*. These taxa are characterized by transverse rows of scales, walking legs on each appendage, a fan-shaped tail, and a backward-facing inverted mouth (Hou, Bergström, and Ahlberg 1995). In addition to the articulated anomalocariid specimens, a number of isolated, very large putative anomalocariid mouths have been found, each characterized by several circlets bearing numerous sharp, inwardly pointing teeth (Chen, Erdtmann, and Steiner 1992); presumably such teeth were employed in macrophagous predation (Nedin 1999).

Perhaps some of the most famous forms from Chengjiang are the so-called lobopodians, a group of onychophoran-like, small segmented animals bearing a dorsal or dorso-lateral series of plates, spines, or sclerites.



**FIGURE 3.8** *Anomalocaris saron*. Length of specimen is 8 cm. (Photo courtesy of Junyuan Chen, Nanjing Institute of Geology and Palaeontology, China)





**FIGURE 3.9** *Microdictyon sinicum*. Width of specimen is approximately 2 cm. (Photo courtesy of Hou Xiangang, Nanjing Institute of Geology and Palaeontology, China)

At least six lobopod taxa are known, including *Cardiodictyon catenulum*, *Hallucigenia fortis*, *Luolishania longicruris*, *Microdictyon sinicum*, *Onychodictyon ferox*, and *Paucipodia inermis* (Chen, Hou, and Lu 1989a; Hou and Chen 1989b; Hou, Ramsköld, and Bergström 1991; Ramsköld and Hou 1991; Chen, Zhou, and Ramsköld 1995a; Hou and Bergström 1995). In some forms, the mouth is visible at the anterior end of the head region, and an apparent anal extension is present in other forms. Of these taxa, *Luolishania* and *Microdictyon* are mentioned shortly. *Hallucigenia*, perhaps the most famous lobopod from Chengjiang, is discussed in Chapter 4 (Ramsköld and Hou 1991; Ramsköld 1992; Hou and Bergström 1995).

*Microdictyon* is one of the more heavily armored lobopods, bearing 10 pairs of netted phosphatic plates on its lateral margins, just above its 10 pairs of elongate soft legs (Chen, Hou, and Lu 1989b) (Figure 3.9). The plates on *Microdictyon* are unusual in that they may not have grown by accretion of mineralized tissue, but by molting (Chen, Hou, and Lu 1989c). Thus, despite the similarity of *Microdictyon* to other lobopodians, the taxonomic assignment of *Microdictyon*, and hence the placement of its enigmatic mode of biomineralization into an evolutionary context, is unclear. However, *Microdictyon*'s fame among the Chengjiang lobopods does not stem merely from the evolutionary significance of its biomineralization mechanism. Before the discovery of articulated specimens at Chengjiang, *Microdictyon*'s rounded, oval, and polygonal phosphatic plates were well-known microfossil components of Lower Cambrian deposits all over the world (Bengtson, Matthews, and Missarzhevsky 1986; Chen, Zhou, and

Ramsköld 1995b). Until the discovery of articulated specimens of *Microdictyon* at Chengjiang, the origin of these plates was unknown. In fact, the function of the plates is still not well understood, with some authors suggesting a defensive function, and others noting a resemblance to schizochroal trilobite eyes (Dzik 1993). Regardless, the mere occurrence of this taxon in the Early Cambrian suggests the possible early development of protective armor and may give clues to the sources of many of the other enigmatic small shelly fossils found in other Cambrian deposits (Bengtson, Matthews, and Missarzhevsky 1986).

*Luolishania* is another peculiar Chengjiang lobopod, which, together with *Microdictyon*, is characterized by a pair of terminal legs and a small anal extension (although the anterior–posterior interpretation of this taxon is controversial) (Chen, Hou, and Lu 1989b; Hou and Chen 1989b; Chen, Zhou, and Ramsköld 1995b; Hou and Bergström 1995). This taxon is of interest because it has very small plates (Hou and Bergström 1995) and has segmentation similar to that of the lobopod *Xenusion auerswaldae* from the Lower Cambrian of the Baltic (Chapter 5; Dzik and Krumbiegel 1989). In particular, some authors (Chen and Erdtmann 1991) have suggested that it may be intermediate between annelids and arthropods, perhaps providing an ancestral link among the onychophorans, hexapods, and myriapods.

Another problematic taxon perhaps related to extant entoprocts or echinoderms is *Dinomischus venustus*, known from only 13 specimens. These stalked organisms may have been attached to the seafloor and had a cup-shaped body circled by petal-like rays, each of which bears radial canals and corrugated banding (Chen, Hou, and Lu 1989a; Chen and Erdtmann 1991). Based on these features, a solitary sessile passive suspension-feeding mode of life is inferred (Conway Morris 1977).

Another enigmatic taxon is the worm-like *Facivermis yunnanicus*, which is characterized by an elongated cylindrical body capped by a tapered papillated head bearing five pairs of finely annulated tentacles. This form, known from only five specimens, has been variously allied with the annelids (Hou and Chen 1989b), the lobopodians (Hou, Ramsköld, and Bergström 1991), and the lophophorates (Chen, Zhu, et al. 1995). Obviously, more specimens must be collected before its taxonomic affinity can be fully resolved.

In addition to the taxonomically enigmatic taxa mentioned earlier, the Chengjiang assemblage contains numerous other enigmatic faunal elements whose paleobiological importance is certain, but are currently known from only a few specimens. These include the flattened oval-shaped arthropod *Saperion glumaceum*, the eurypterid-like arthropod *Xandarella spectrum* (Hou, Ramsköld, and Bergström 1991), the *Jianfengia*-like arthropod *Alalcomenaeus illecebrosus* (Hou 1987a), possible chelicerates (Babcock and Chang 1996), possible lophophorates (Bab-

cock and Chang 1995), and echinoderm-like forms (Chen and Zhou 1997; Hou et al. 1999).

Finally, the Qiongzhusi Formation contains a well-preserved suite of trace fossils. Although a detailed analysis of traces occurring in individual units (e.g., within the mudstones containing soft-bodied fossils) has not yet been published, Zhu (1997) notes that overall bioturbation within the Maotianshan Shale is weak, and documents trace fossils from only two intervals within a 60 m thick section. Zhu (1997) does note, however, that arthropod-style traces such as *Monomorphichnus* and *Diplichnites* are common through this interval, as well as bed-parallel traces such as *Planolites* and *Palaeophycus*, and trails with a vertical component, including *Arenicolites*, *Chondrites*, and *Treptichnus*. Sun and Hou (1987b) corroborate these observations by noting the presence of tubular burrows and grazing trails on several bedding planes.

## PALEOECOLOGY

Although a systematic paleoecologic analysis of Chengjiang has not yet been published (but see Leslie, Babcock, and Chang 1996), fossiliferous horizons at Chengjiang are much like those at other Burgess Shale-type deposits (Chapters 4 and 5) because they are dominated by arthropods and algae, and over 97 percent of the fauna are nonmineralized forms. Unlike these other deposits, Chengjiang also seems to have a small, but significant number of lobopodians. Dominant members of the arthropod component are bivalved forms such as bradoriids, which comprise nearly 70 percent of available specimens. There are a variety of life habits represented by the Chengjiang biota, including mobile benthic infaunal taxa, mobile and sessile benthic epifaunal taxa, as well as actively and passively mobile pelagic taxa.

In terms of trophic structure, the abundance of algae and acritarchs in the deposit, coupled with the organic-rich nature of the strata in the Qiongzhusi Formation, suggests that the base of the food chain was likely occupied by phytoplankton and zooplankton, as well as detritus from these sources. The infaunal benthic community was dominated by a number of suspension- or deposit-feeding forms, such as lingulate brachiopods, as well as some primary consumers, such as the priapulid worm *Maotianshanian* and the worm-like *Facivermis*. Epifaunal benthic habits were characterized by suspension feeders (such as *Chaoiaella*, *Dinomischus*, *Eldonia*, *Heliomedusa*, *Rotadiscus*, and *Xiangguangia*) and deposit feeders (such as *Clypeacaris* and *Naraoia*). Among these, the poorly preserved bradoriids have the largest number of individuals and the highest biomass and are thought to have been a major food source for most carnivores, as they are commonly found concentrated in ovate flattened coprolites (Leslie, Babcock, and Chang 1996; Chen and Zhou 1997). The presence of such

coprolites, as well as similar hyolithid concentrations, denotes the existence of numerous predators (such as *Luolishania* and *Anomalocaris*) that may have occupied both epifaunal and pelagic habitats. Floating pelagic forms are also well known, such as the ctenophore *Maotianoascus*. Swimming pelagic forms may include a number of the smaller arthropods such as *Isoxys*, as well as chordates such as *Cathaymyrus*, *Haikouichthys*, and *Myllokunmingia*, which represent primary or secondary consumers. Commensal or possibly scavenging modes of life are also suggested by the presence of a variety of epizoans attached to or associated with *Eldonia* and *Rotadiscus*.

Although the amalgamation of transported and *in situ* faunas at Chengjiang complicates interpretation of distinct paleocommunities, when considered together these faunas suggest that Early Cambrian shallow-marine environments were inhabited by a relatively diverse and well-developed marine community. Among the life habits discussed earlier, the epifaunal benthic habit seems to be the best represented—including a variety of suspension- and deposit-feeding organisms reflecting development of several tiering levels rising up to about 30 cm above the seafloor, and perhaps several centimeters beneath it (Chen, Hou, and Lu 1989c).

## CONCLUSIONS

Exquisite soft-body preservation of diverse benthic and pelagic faunas makes Chengjiang one of the most promising of early Paleozoic Lagerstätten. In addition to being well preserved, specimens are abundant, and fossil-bearing units can be traced laterally for approximately 100 km, allowing for intensive collection of fossils from Chengjiang outcrops in the Kunming region.

One of the major contributions of the Chengjiang biota is that it has provided data on the most ancient, diverse group of fossils from which paleontologists can attempt to constrain the evolutionary relationships between and among major animal clades. Although much of the fauna bears most directly on the vagaries of early arthropod evolution (Hou and Bergström 1997; Bergström and Hou 1998; Ramsköld and Chen 1998), the collection of additional nonarthropod taxa promises to extend rigorous phylogenetic analyses to rarer taxa such as the various palaeoscolecoid worms (Hou and Bergström 1994) and the lobopodians (Ramsköld and Chen 1998).

Because of its early occurrence in geologic time, the Chengjiang fauna has been instrumental in advancing our understanding of poorly preserved or enigmatic groups from younger Cambrian Lagerstätten. Furthermore, some Chengjiang taxa (e.g., sponges) have direct analogues in both Ediacaran and Burgess Shale Lagerstätten. Thus, in addition to providing clues about the rates and mechanisms of the Cam-

brian explosion, the Chengjiang fauna may lead to a greater understanding of the connection between organisms that inhabited both the late Proterozoic (Chapter 2) and early Paleozoic (Chapters 4, 5, 6, 7) worlds. Although thousands of specimens have been systematically collected from Chengjiang, the deposit still contains much untapped paleoecologic and taphonomic information—thus, revelation of the impact of this deposit on our understanding of paleobiology and early animal evolution has just begun.

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