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The Chengjiang fauna – the oldest preserved animal community

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Abstract. The Chengjiang fauna, an exceptionally well-preserved fossil lagerstatte, from the lower part of the Lower Cambrian *Eoredlichia-Wutingaspis* Biozone in the Kunming area, Yunnan Province, China is generally introduced, including the research history of the area, stratigraphy in the interval with soft-bodied fossils, geological setting, depositional environment, discovery, distribution, significance and faunal association. The Chengjiang lagerstatte yields various mineralized and nonmineralized skeletons and internal soft parts of organisms, as well as complete soft-bodied animals. The fauna includes virtually all animal phyla that were previously known from the Middle Cambrian and vividly reproduces the appearance of the oldest Phanerozoic animals.

Key words: Chengjiang fauna, China, Lagerstätten, Lower Cambrian, soft-bodied fossils, Yunnan Province

Introduction

In the fossil record there seem to be virtually no meta-zoan animals found in the Precambrian. Ediacara-type fossils in the Upper Precambrian are readily accepted as organisms, but there are strong arguments against accepting them as being related to younger metazoans. The Ediacaran fossils are interpreted as members of a distinct lineage of vendobionts, representing an extinct category of organisms in the pre-Cambrian (Bergström, 1993; Seilacher, 1993).

There is a strongly expanding appearance of varied fossils at the base of the Cambrian. More complex and diversified trace fossils start to appear in the Cambrian (Bergström, 1990). The first diverse shelly fossils, known as small shelly fossils, come on scene somewhat higher in the sequence. Afterwards, the small shelly fossils begin to give way for the first trilobites and other arthropods, inarticulate brachiopods, sponges, echinoderms and archeocyathids, marking the development of typical Cambrian assemblages (Briggs *et al.*, 1994). Our understanding of the “Cambrian explosion” was based mainly on those trace fossils and shelly assemblages just mentioned. The exceptionally well-preserved soft-bodied Chengjiang fauna was discovered in the lower part of the *Eoredlichia-Wutingaspis* Biozone of the Lower Cambrian Heilinpu (formerly

Qiongzhusi) Formation in Kunming area, Yunnan Province, China in 1984 (Zhang and Hou, 1985). Most animals found in the Chengjiang fauna lacked a mineralized skeleton and are therefore only preserved under the unusual conditions represented in this lagerstatte (Hou *et al.*, 1991).

The Chengjiang fauna was named after Chengjiang, a small county of Yunnan Province, because soft-bodied fossils of the fauna were first found at Maotianshan, a small hill in Chengjiang county (Figure 1). In 2001, the Maotianshan fossil sites in Chengjiang county came under effective protection as part of the National Geological Park of China.

Chengjiang county is about 52 km southwest of Kunming, the capital city of Yunnan Province (Figure 1). It is easy to reach by expressway and two-lane highway from Kunming. After 18 years of extensive study, the Chengjiang fauna is known to occur widely in Kunming and its surroundings. The fossil sites extend some 100 kilometers from east to west and north to south (Figure 1). Particularly, the main localities of the Chengjiang soft-bodied fossils are situated near Lake Dianchi and Lake Fuxian, the largest lakes in Yunnan. It is convenient to reach the main localities from Kunming city. It should be noted that the weather in this area is pleasant and the scenery is attractive all year round.

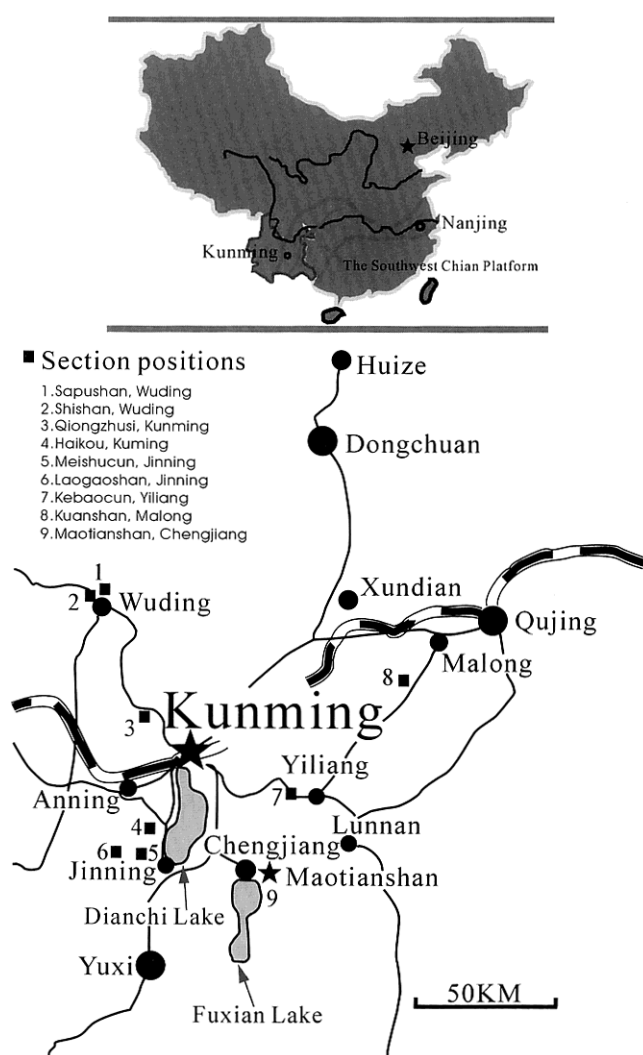


Figure 1. Position map of Yunnan Province (above) and index map of the Kunming area (below), eastern Yunnan, showing distribution of the Chengjiang Lagerstätte locations (block diagrams with numbers 1-9). The Lagerstätte was discovered at the locality labeled as Maotianshan (star with number 9).

History of Research in Kunming area, eastern Yunnan

The study of the Lower Cambrian in the Kunming area has a long history. The earliest study was made from September 1903 to January 1904 by French scientists (e.g., Lantenois, 1907). Later, the French scientists J. Deprat and H. Mansuy studied the geology and paleontology of this area in 1909 and 1910 (e.g., Mansuy, 1912). Subsequently, the Lower Cambrian of the area was extensively investigated and studied and much geological literature published during the 1930s and 1940s (e.g., Chen, 1939;

Wang, 1941) including information on the occurrence of phosphorite deposits and the Lower Cambrian stratigraphic succession in the area (e.g., Chiang *et al.*, 1964; Qian and Bengtson, 1989). Lu (1941) systematically studied the Lower Cambrian stratigraphy and trilobites at Qiongzhusi (Qiongzhu Temple, a famous tourist attraction) in Kunming city. He established the stratotype section of the Lower Cambrian and divided the Lower Cambrian into the Qiongzhusi (old spelling Chiungchussu), Canglangpu (Tsanglangpu) and Longwangmiao (Lungwangmiao) Formations. The sequence in the section at Qiongzhusi has long been taken as a standard for stratigraphical subdivision and correlation not only within the Southwest China Platform, but also throughout China and even in the redlichiid realm as a whole (e.g., Zhou and Yuan, 1982).

Ho (1942) first measured the section at Maotianshan in Chengjiang county during his investigation of the Lower Cambrian phosphorite reserves. The section measured by Ho in 1940 extended from Dalongtan village, where the Department of Geology of Zhongshan University was located, to Maotianshan. Zhongshan University was moved to Chengjiang county from Guangzhou (Canton) in 1939 and 1940 in order to escape from the war. Ho (1942) introduced the term "Maotianshan shale system" for the Lower Cambrian mudstone from which he recovered bradoriid fossils throughout the sequence (p. 101). The Chengjiang fauna was discovered in the sequence in 1984 (Zhang and Hou, 1985). Huo (1956) described the Lower Cambrian bradoriids from Shaanxi and Yunnan. The geographic origin is not known for three specimens of *Kunmingella* (Huo, 1956, pl. 2, figs. 10-12). Based on their preservational characteristics, they appear to have been collected from Maotianshan in Chengjiang county (compare with pls. 1 and 2 in Hou *et al.*, 2002).

Stratigraphy across Precambrian-Cambrian boundary

Eastern Yunnan (including the Kunming area) has good exposures in the well developed sequence around the Precambrian-Cambrian boundary, with thick Lower Cambrian deposits and abundant fossils. Therefore eastern Yunnan, and especially the Kunming area, has served as a typical area for the Precambrian-Cambrian boundary and Lower Cambrian stratigraphy since the early part of the twentieth century. The Meishucun section in Jinning county has been selected as a candidate for a global stratotype section and a point for the Precambrian-Cambrian boundary (Luo *et al.*, 1984).

In the Kunming area, the uppermost part of what is thought to be Precambrian is known as the Xiaowaitoushan and Baiyanshao Members of the Yuhucun Formation. They are largely composed of dolomite with only simple

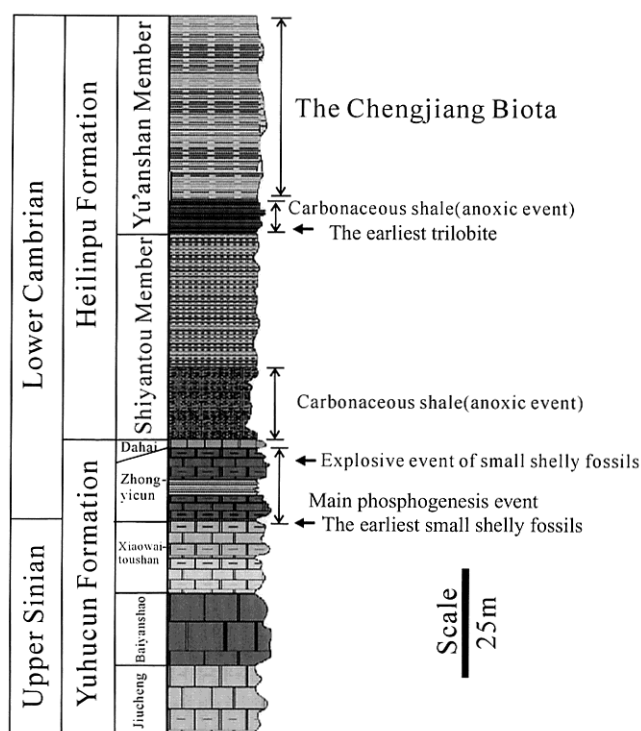


Figure 2. The succession near the Precambrian-Cambrian boundary in the Kunming area, showing the stratigraphical position of the Chengjiang Lagerstätte (modified from Hou and Bergström, 1997).

surface traces and shallow burrows in the Baiyanshao Member (Zhu *et al.*, 2001). Beginning in the lowermost Cambrian, shelly elements, known as “small shelly fossils”, first appear and suddenly become abundant in the Zhongyicun Member of the Yuhucun Formation, being composed of phosphorites with shale intercalations. The Shiyantou Member of the Heilipu Formation consists of black siltstone, yielding trace and small shelly fossils, deposited in relatively shallow water, as indicated by the presence of hummocky cross-bedding, a feature typical of deposits developed above the storm wave base. The Yu'an Shan Member of the Heilipu Formation, about 150 m thick, yields the Chengjiang soft-bodied fossils in its lower part (Figure 2; Hou, 1987). Its base consists of black mudstone that includes the oldest trilobite *Parabadiella*. This unit is followed by grey and yellow-grey mudstone with siltstone interbeds and with the trilobites *Wutingaspis* and *Eoredlichia*. The fossils (including soft-bodied fossils) occur in the mudstone, not in the siltstone interbeds. The Chengjiang deposits may have been supplied by turbidite flows or storms (Hou *et al.*, 1991).

The Lower Cambrian biostratigraphy has been established on the basis of shelly fossils at its base and trilobite

assemblages in the sequence above. As many as three small skeletal fossil biozones and 11 trilobite biozones are used to divide the Lower Cambrian in this area and elsewhere on the Southwest China Platform. Higher up are Middle and Upper Cambrian rocks. The *Parabadiella* (probably *Abadiella*) Biozone forms the oldest trilobite zone in the Cambrian in the whole of China. The *Parabadiella* Zone is of variable thickness. For example, it is 0.9 m thick in the Maotianshan section in Chengjiang county (Hou, 1987), 2.4 m (overlapped by *Wutingaspis* beds) in the Meishucun section in Jinning county (Luo *et al.*, 1984), and less than 4 m in the Shapushan section in Widing county. The *Parabadiella* interval is thin-bedded and less than 4 m thick in the area and probably represents a very short time interval. It is succeeded by the *Eoredlichia*-*Wutingaspis* Biozone, the lower part of which contains the soft-bodied Chengjiang fauna. The soft-bodied Chengjiang fossils thus occur in the lowermost trilobite biozone, zone 4, counting from the oldest of the Cambrian zones. This obviously indicates that the Chengjiang lagerstätte is fairly low down in the Lower Cambrian, although certainly not at the base. Therefore, the Chengjiang fauna appears to be a good representative of the first post-small shelly fossil faunas and may provide an unprecedented insight into the morphology of very early representatives of a number of still living phyla, as well as some extinct ones. This means an insight into perhaps the end of the “Cambrian explosion” time.

Taking the Meishucun section in Jinning county as an example, the stratigraphic sequence around the Precambrian-Cambrian boundary can be summarized in Figure 3.

Geological setting and depositional environment of Chengjiang lagerstätte

The Kunming area is located near the southwestern margin of the Southwest China Platform (Figure 1). This area is often considered as a shallow sea open toward the east and is on the east side of the Central Yunnan Old Land, from where the sea became progressively deeper towards the east. Paleogeographically, the Kunming area had the Central Yunnan Old Land to the east, the Niutoushan Old Land to the north and west, and the western littoral part of the shallow sea of the Southwest China Platform to the north. Based on the reconstruction of the early Cambrian continental position (Briggs *et al.*, 1994, p. 36, figure 2.8), the Chengjiang lagerstätte was on a latitude of about 14° North. The Chengjiang fauna probably lived in a tropical sublittoral sea.

The Chengjiang lagerstätte is in the lower part of the Yu'an Shan Member of the Lower Cambrian Heilipu Formation (Figure 2). The lithology of the Yu'an Shan

Middle Devonian	Haikou Formation		Fine-grained sandstone	
Lower Cambrian	Heilipu Formation	Yu'anshan Member	8. Yellow-green mudstone, intercalated with thin- to thick-bedded sandstone, yielding the soft-bodied Chengjiang fossils, 44.7m thick. 7. Black carbonaceous mudstone, yielding trilobites <i>Wutingaspis</i> in the upper and middle parts and <i>Parabadiella</i> at the bottom, 27.7m thick.	
		Shiyantou Member	6. Black siltstone, yielding trace fossils and small shelly fossils, 54m thick.	
		Dahai Member	5. Arenaceous dolomite, intercalated with striped cherts, yielding small shelly fossils, 1.1m thick.	
	Upper Sinian	Yuhucun Formation	Zhongyicun Member	4. Phosphorite with a 1.6m thick intercalation of dolomitic clay, yielding small shelly and trace fossils, 11.6m thick. —Precambrian-Cambrian boundary—
			Xiaowaitou-shan Member	3. Arenaceous dolomite with intercalation of chert strip, 8.2m thick.
		Baiyanshao Member	2. Thick-bedded dolomite, intercalated with algal dolomite and siliceous rock, 165.2m thick.	
		Jiucheng Member	1. Thin-bedded, argillaceous dolomite and black carbonaceous siltstone, 20m thick	
		Donglong-tan Formation		Thick-bedded or massive dolomite

Figure 3. Stratigraphic sequence around the Precambrian-Cambrian boundary at the Meishucun section in Jinning county, Yunnan Province (modified from Luo *et al.*, 1984).

Member was often described as shale but in fact is composed of mudstone with thin to thick intercalations of siltstone in the lower part and silty mudstone with thin intercalations of siltstone in the upper part. The soft-bodied fossils occur only in finely laminated mudstone wherever fine-grained sediments were deposited quickly under dysaerobic or anaerobic conditions. The rapid burial may have prevented the destruction of the carcasses by bioturbation, scavengers, carnivores and current activity and protected them also against the slower bacterial decay. The Chengjiang fauna so buried may be allochthonous, with turbidity mudflows carrying the carcasses down a slope to a still deeper anoxic zone (Seilacher, 1991). However, the postures and the excellent preservation of the Chengjiang fauna show little evidence of transport. Linguloid brachiopods are occasionally preserved with their pedicles still obliquely buried in the sediments, extending down from the bedding plane. Five individuals of *Archotuba conoidalis* adhered to a hyolith shell (Figure

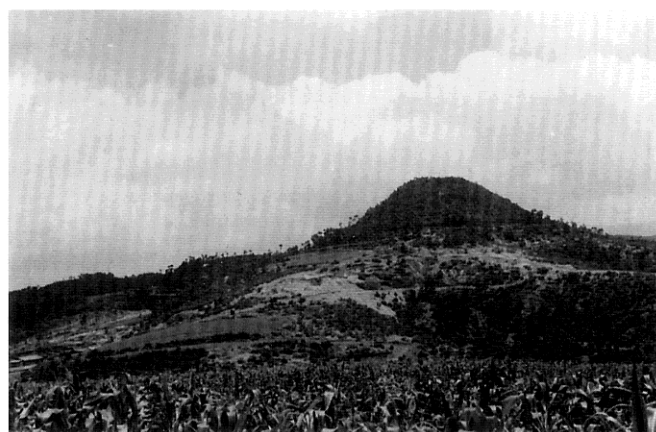


Figure 4. Maotianshan (Maotian hill) in Chengjiang county, where the Chengjiang fauna was discovered on 1 July 1984.

8.3). In particular, the preservation of the linguloids can only be interpreted as resulting from embedding on the site where they lived. There are strong indications for *in-situ* preservation of at least the infaunal components (Hou *et al.*, 1991; Bergström, 1991). According to M. Lindström, the Chengjiang sediments may be wind-blown and derived from an adjacent land area (the Central-Yunnan Old Land or the Niutoushan Old Land), as is indicated by the presence of several well-sorted, fine fraction sandstone tongues intercalating in the sequence. This does not in itself explain the death of the infaunal animals (Bergström, 1991).

Discovery and distribution of Chengjiang fauna

Although the Lower Cambrian Chengjiang fauna is distributed in an area of the Province of Yunnan with working transport facilities, its discovery is quite recent. It was only in 1984 that the fauna was found by the senior author after some 20 days of fieldwork. The initial reason for the fieldwork was his research program involving the study of bradoriid arthropods (Figure 17), which were well known to occur abundantly in the Lower Cambrian on the Southwest China Platform (Lu *et al.*, 1981). According to his diary, he arrived in the town of Chengjiang County in the morning on 19 June 1984 after finishing collections at the Meishucun Section in Jinning county. He moved to Dapotou village from the town by cart in the morning on 20 June and was boarded and lodged with a geological team that was then stationed at Dapotou village. It would take about one hour to walk from Dapotou village to Maotianshan. On July 1st, around 3 o'clock in the afternoon, while collecting bradoriid fossils at the west slope of Maotianshan as usual (Figure 4), he suddenly saw a surpris-

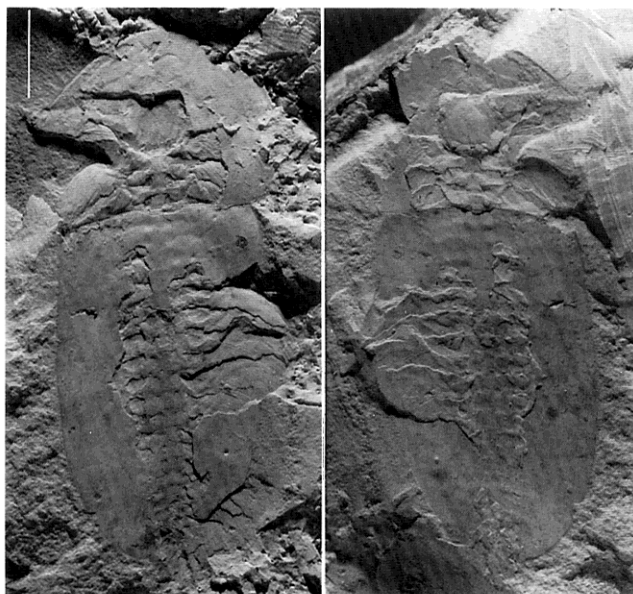


Figure 5. The holotype of *Naraoia longicaudata*, part and counterpart, the first soft-bodied specimen discovered at Maotianshan, Chengjiang on 1 July 1984. Scale bar: 5 mm.

ingly well-preserved fossil of a kind that had previously only been seen in the much younger Burgess Shale in British Columbia, Canada. It was later determined as the holotype of a species of the genus *Naraoia* (Figure 5; Zhang and Hou, 1985). The find is noted both in his field diary and in his daily diary. He was more than excited at the discovery of the soft-bodied specimen. The find turned all his attention towards collecting soft-bodied fossils (see Hou and Bergström, 1997).

The collecting of soft-bodied fossils at Maotianshan ranged from 1984 till 1988. The collecting was redirected to new localities in 1989 and 1990, such as Xiaolantian, Ma'an Shan and Fengkoushao. Work was also carried out at Dapotou and Hongjiachong because of living close to them during 1984 to 1987. All these localities are in Chengjiang county and extend some 12 km from north to south (Hou and Bergström, 1997, p. 4, figure 1b). Soft-bodied fossils were also found in the well-known Meishucun section in Jinning County in August 1984 and collected there for one day again in August 1986 (Hou and Sun, 1988). New-built houses were welcoming above the quarry at the Meishucun section at the return there in 1988. At Haikou, Kunming, the Chengjiang fauna has been collected since 1993 (Luo *et al.*, 1997). Elements of the Chengjiang fauna have also been collected from the Kebaocun section in Yiliang county, the Sapushan and Sishan sections in Wuding county and the Guanshan section in Malong county (Figure 1; Hou and Bergström,

1997, p. 6; Hou *et al.*, 1999, p. 25–27). Well-preserved fossil localities are fairly few because of limiting factors: beds should be well exposed, the rock weathered, and there should be transport facilities.

Significance of Chengjiang fauna

The oldest soft-bodied fauna that was previously well known is from the Middle Cambrian Burgess Shale in Canada. This is too long after the beginning of the Cambrian to give any direct insight into the “Cambrian Explosion”, or to the earliest Phanerozoic fauna. The Chengjiang fauna offers a more direct glimpse of the true taxonomic diversity, morphological complexity and ecological prosperity of life on Earth perhaps at the end of the “Cambrian Explosion” interval. It provides critical evidence of the first results of the “Cambrian Explosion” and has dramatically expanded our knowledge of this formative interval. The fauna also indicates that a number of animal phyla came into being during this interval, almost at the same time. Despite this, there is no reason to think of large numbers of big leaps in the evolution. There must have been a large number of empty prospective niches, and some factor in the environment, perhaps a rise in oxygen pressure, suddenly made it possible for animals to adapt to all these niches, developing different body designs and lifestyles. Starting from simple animals, evolution could have gone very fast, even with dominantly gradual change. Most animal phyla in the fauna are the same as they are today, with the basic characteristics already present. The limits of their morphological evolution were established during the “Cambrian Explosion” and have persisted to the present day.

The excellent preservation of the Chengjiang fauna can be used for a reinterpretation of some fossils. *Microdictyon* was first described from net-like plates recovered from rocks by acid extraction (Bengtson *et al.* 1986). This kind of plate is widely distributed in the Lower and Middle Cambrian around the world. We did not know what animal was represented by the plates, in fact we did not even know if it represented a complete animal or part of an animal. Complete individuals of *Microdictyon* (Figure 14.1) in the Chengjiang fauna gave us a satisfactory answer. *Hallucigenia* is a well-known animal from the Middle Cambrian Burgess Shale, Canada. It was named after the seemingly bizarre and dreamlike appearance of the animal. The Chengjiang *Hallucigenia* (Figure 14.3) proved the reconstruction based on material from the Burgess Shale to be upside-down (Ramsköld and Hou, 1991; Hou and Bergström, 1995). *Anomalocaris* and similar forms are widely distributed in Canada, Poland, China and Australia. They were among the largest and perhaps most fierce animals in the Cambrian sea. *Anomalocaridids* also were considered

to be bizarre, odd animals, as again expressed in the name. Again the Chengjiang material provides a good control. To general surprise, but as concluded by one of us already from Burgess Shale material (Bergström, 1986), these animals from the Chengjiang fauna were preserved with sturdy paired, more or less segmented legs on the underside (Figures 11, 12). The new insight into, and general acceptance of, anomalocaridid morphology seems to be a key step to the understanding of this group of animals (Hou *et al.*, 1995).

Characteristics of Chengjiang faunal community

A group of species living closely enough together for potential interaction is referred to as a community. The some 120 described species of the Chengjiang fauna show very different abundances in terms of number of individuals. There is a single dominant species, the small bivalved bradoriid arthropod *Kunmingella douvillei* (Figure 17), which accounts for 70–80% of the individuals of the entire fauna. The characteristic (subdominant) species are the arthropods *Naraoia longicaudata* (Figure 18.4), *N. spinosa*, *Isoxys auritus*, *Leandroilia illecebrosa* (Figure 18.1), the brachiopod *Heliomedusa orientalis* (Figure 15.2) and the nematomorph worms *Maotianshania cylindrica* (Figure 9.3) and *Cricocosmia jinningensis* (Figure 9.2), each contributing about 2–3% of the individuals in the fauna.

In the Middle Cambrian Burgess Shale fauna, the dominant species is the arthropod *Marrella splendens*, accounting for about 38% of the total individuals of the fauna. The second to fifth most common species, respectively, are the hemichordate “*Ottoia*” *tenuis*, the arthropods *Canadaspis perfecta* and *Burgessia bella* and the priapulid worm *Ottoia prolifica* (Conway Morris, 1986). It is obvious that the two communities are clearly different in their main components, not only of species, but even of genera. The Chengjiang faunal community shares several genera with the Burgess Shale community, such as *Choia*, *Leptomitus*, *Naraoia*, *Leandroilia*, *Canadaspis*, *Hallucigenia*, *Anomalocaris*, *Eldonia*, and *Dinomischus*, but the species are different (see Whittington, 1985; Briggs *et al.*, 1994). The difference between the Chengjiang and Burgess Shale faunal communities is also manifested in the composition of individual groups. For example, in the Chengjiang faunal community there were only five trilobite species, making up less than 10% of the arthropod species of the community and less than 2% of the individuals of the entire community. In the Burgess Shale, however, trilobites comprise over 40% of the arthropod species. This difference in group composition may well indicate that the Chengjiang community represents an early community that existed during the “Cambrian Explosion” interval, whereas

the Burgess Shale community is a more advanced community, as might be expected from its younger age.

The Chengjiang and Burgess faunas are the two best-preserved soft-bodied faunas so far found in Cambrian detrital sediments. They are probably the most completely preserved and described Cambrian communities that we have. Despite the differences pointed out above, there is also a general similarity both on a higher level, with phyla and classes similarly represented, and in the shared possession of several families and genera, such as the families Waptiidae and Helmetiidae and the genera *Leptomitus*, *Isoxys*, *Lingulella* and *Eldonia*. A few of them are also preserved in other Cambrian lagerstätten.

The faunas of the Middle Cambrian Utah Lagerstätten (Robison, 1991) are fairly similar to the Chengjiang and Burgess Shale communities. This may indicate that these represent the general characteristics of one type of community evolving just after new animal phyla had come into existence during the “Cambrian Explosion”. We must not believe that it was the only community type. It is notable that mollusks and echinoderms are poorly represented in both the Chengjiang and Burgess Shale faunas, but we know that they existed. We also notice the apparently much different Sirius Passet fauna from the Lower Cambrian of Greenland, and the completely different Alum Shale fauna from the Upper Cambrian of Sweden (see below). Anyway, it appears that communities or community types of the Chengjiang and Burgess Shale types were widespread, and that there was some evolutionary conservatism of soft-bodied and unmineralized taxa within community groups (also see Robison, 1991).

Communities known from lagerstätten with soft-body preservation are difficult to compare with other communities, since we know almost nothing of what is lost in those with less perfect preservation. The Chengjiang faunal community seems to be the oldest “complete” animal community known to us, although we must always accept that some organisms may not be preserved even in this case. It is composed of soft-bodied, mineralized and unmineralized groups that represent main current phyla. However, we can be convinced that the four small shelly fossil associations underlying the Chengjiang faunal community in the province of Yunnan represent quite different communities, since the same skeletal parts should have been present in the soft-bodied fossil community if they were represented. The Chengjiang fauna and small shelly fossil associations appear to be divided by a distinct evolutionary boundary, marked by the occurrence, for example, of trilobites and bradoriids. The former fauna is characterized by representatives of the present main animal phyla, and the latter three by small shelly and trace fossils that are difficult to place into extant phyla. The Upper Cambrian Alum Shale arthropod fauna (Müller, 1990), also a soft-

bodied Cambrian fauna, is also strikingly different from the Chengjiang fauna. It consists mostly of minute crustaceans and crustacean-like arthropods. The sediments containing the fauna were formed under very low energy conditions and a near absence of oxygen. This community may have lived in a flocculent bottom layer that adapted to a life in a low-oxygen environment (Müller, 1990).

The communities mentioned above represent three types of communities present in the Cambrian. The small shelly community may represent the main phase of the “Cambrian Explosion” while the Chengjiang faunal community was a final outcome of the event, marked by the fact that the main current animal phyla were already present.

Chengjiang fossils

The Chengjiang fauna is considered to have lived in a shallow-water environment (Jin *et al.*, 1991). As preserved, it is an autochthonous taphocoenosis or a taphocoenosis of negligible transport (Hou *et al.*, 1991), as indicated by such features as the wonderful preservation of the pedicle of lingulids and the details in appendages of small bivalved bradoriid arthropods (Hou *et al.*, 1999), which are missing in the lingulids and bradoriid arthropods of the Burgess Shale community. The differences in preservation reflect not only the different taphonomies of the two communities, but also differences in preservation quality between different types of Konservat-Lagerstätten (Seilacher, 1970). The importance of preservation quality in Konservat-Lagerstätten is fully indicated in the history of interpretation of *Hallucigenia* (Hou and Bergström, 1995).

The Chengjiang fossils include individually preserved carapaces and whole individuals with variously preserved soft parts. The remains are flattened, but there is a distinct relief in the detailed structures of the animals. For example, the endopod and exopod with its setae of the arthropod limbs often show little evidence of flattening (Hou and Bergström, 1997). In addition, the Chengjiang fossils are preserved in soft mudstone which makes exposure by preparation fully possible. In this respect, the hard Burgess Shale material has presented a much harder task. The preserved quality of the detailed structures in the Chengjiang fossils is high. For example, hairs or setae on the legs in lobopods (Figure 14.4) and bradoriids (the whole animal being 3–5 mm long) can be well preserved. Some Chengjiang fossils are preserved in their original association, as is shown by, for example, *Longtancunella chengjiangensis* (Figure 15.3) shows some 10 brachiopod individuals of this species growing on the shell of an unknown animal.

The Chengjiang fauna contains abundant and diverse organisms, including algae (Chen and Erdtmann, 1991), sponges (Chen *et al.*, 1989; Rigby and Hou, 1995; Hou



Figure 6. Alga, *Fuxianospira gyrata*, one of the most abundant algae and preserved with twisted mass of threads, from Haikou, Kunming. Scale bar: 5 mm.

et al., 1999), ctenophorans (Chen and Zhou, 1997), cnidarians (Chen and Zhou, 1997), nematomorphs (Hou and Bergström, 1994), priapulids (Hou *et al.*, 1999), anomalocaridids (Hou *et al.*, 1995), brachiopods (Jin and Wang, 1992; Jin *et al.*, 1991, 1993), hyoliths (Hou *et al.*, 1999), lobopods (Hou and Bergström, 1995), bradoriid arthropods (Hou *et al.*, 1996, 2002b) and a broad variety of non-trilobite and non-bradoriid arthropods (Hou and Bergström, 1997), discoidal fossils (echinoderms) (Hou *et al.*, 1999), vertebrates (Shu *et al.*, 1999; Hou *et al.*, 2002a) and some problematical taxa as well (Hou *et al.*, 1999). About 120 animals from the fauna have been described and some new ones remain to be studied; others certainly remain to be found. Abundant macroscopic algae in the beds of the Chengjiang lagerstätte may constitute the most basic part of the food chain in the Chengjiang biota. They are often preserved as clumps on the bedding (Figure 6). The diversity of algae may be relatively low and a few species are present in the Chengjiang lagerstätte, being characterized by simple unbranched filaments.

Sponges.—There is an assemblage of demosponges and hexactinellid sponges including at least 20 species that form the second most diversified metazoan group, but the largest group of suspension-feeding sessile epifauna in the Early Cambrian sea. The body shows different outlines, such as spherical, radiate, ellipsoid, conical, sub-column-shaped. The smallest sponge is a few mm in diameter and the largest can reach 300 mm in length and over 120 mm in width. A majority of the sponges belong to the demosponges with a broad spectrum of morphological and size variation, including tubular *Leptomitella teretiusculus* (Figure 7.1) and *Paraleptomitella dictyodroma*, conical *Leptomitella conica*, cylindrical *Leptomitella confusa*, balloon-shaped *Paraleptomitella globula*, large ovate *Quadrolaminiella diagonalis* and *Q. crassa*, small discoidal

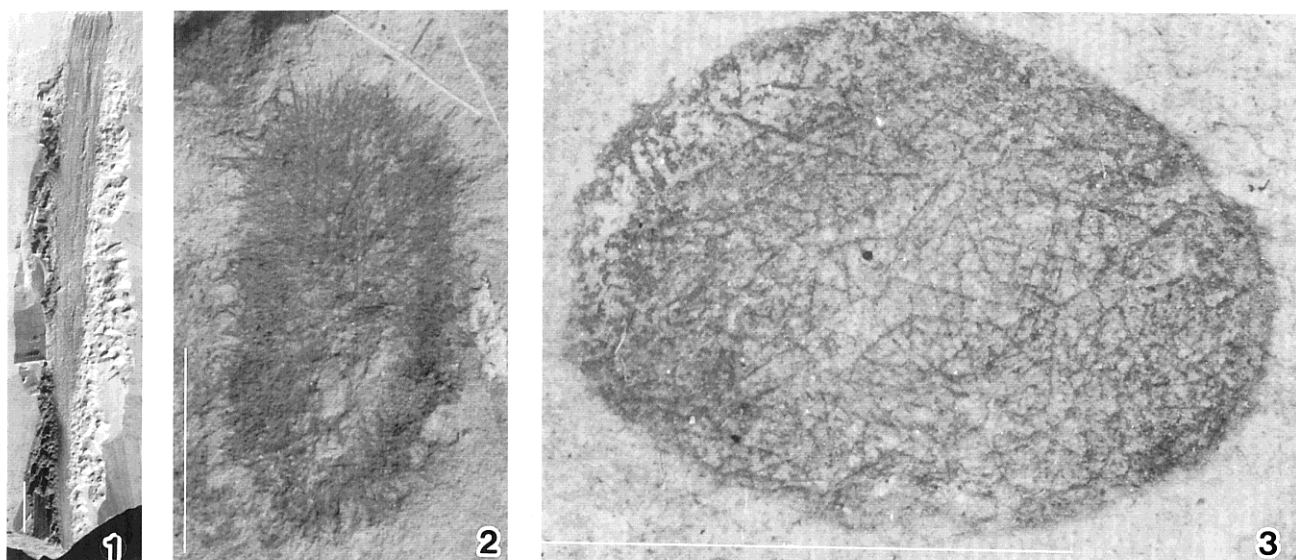


Figure 7. Examples of sponges. 1. *Leptomitrus teretiusculus*, from Maotianshan, Chengjiang. 2. *Allantospongia mica*, from Xiaolantian, Chengjiang. 3. *Triticispongia diagonata*, from Xiaolantian, Chengjiang. Scale bars: 5 mm.

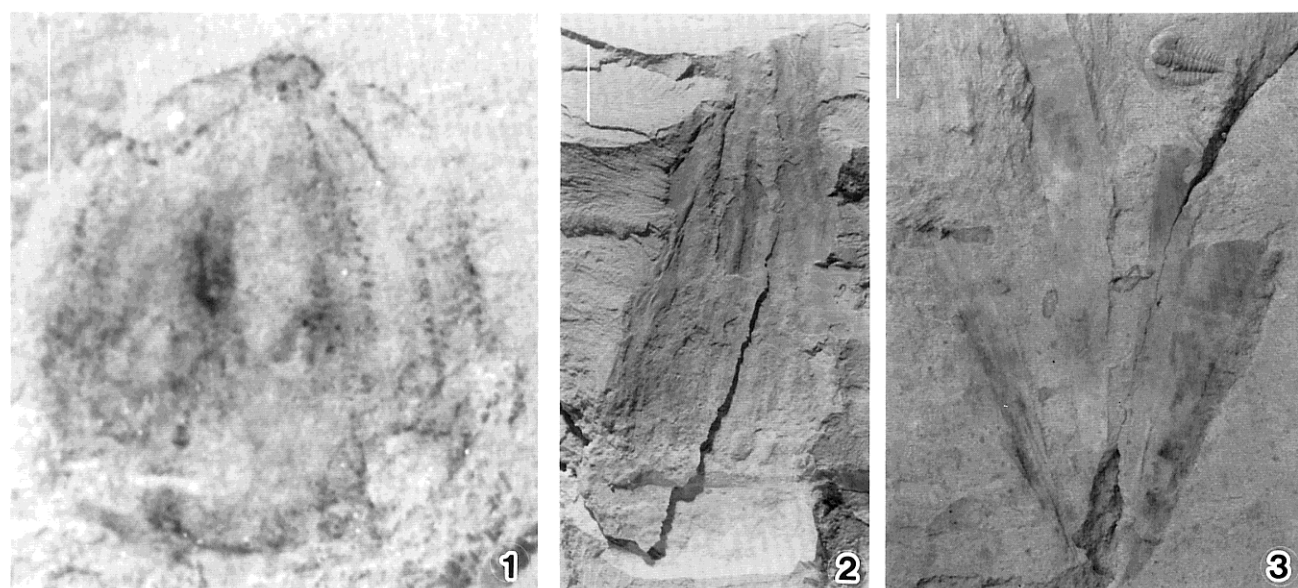


Figure 8. Representative ctenophore and cnidarians. 1. Ctenophore *Maotianoascus octonarius*, from Maotianshan, Chengjiang. 2. Cnidarian, *Xianguangia sinica*, from Maotianshan, Chengjiang. 3. ?Cnidarian *Archotuba conoidalis*, from Ma'anshan, Chengjiang. Scale bars: 5 mm.

Choiaella radiata, small sausagelike *Allantospongia mica* (Figure 7.2), and cape-shaped *Choia xiaolantianensis* with radially arranged long spicules. There are two hexactinellid sponges described; namely, small rounded *Triticispongia diagonata* (Figure 7.3) and *Saetaspongia densa*.

Ctenophores.—Ctenophores, also known as comb jellies, constitute the Phylum Ctenophora. *Maotianoascus octonarius* (Figure 8.1), considered to be a globular ctenophore, bears eight comblike rows of petaloid lobes that are arranged longitudinally and are equally spaced, meeting aborally into a spherical structure.

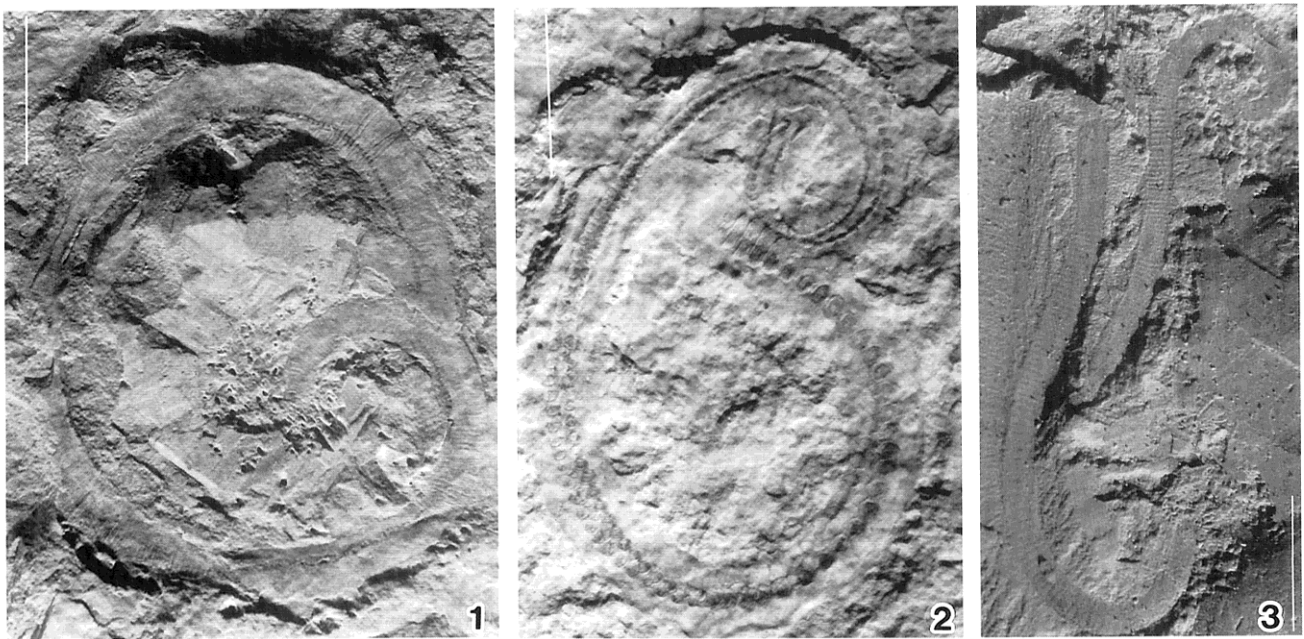


Figure 9. Nematomorphs. 1. *Palaeoscolex sinensis*, from Maotianshan, Chengjiang. 2. *Cricocosmia jinningensis*, from Meishucun, Jinning. 3. *Maotianshanian cylindrica*, from Maotianshan, Chengjiang. Scale bars: 5 mm.

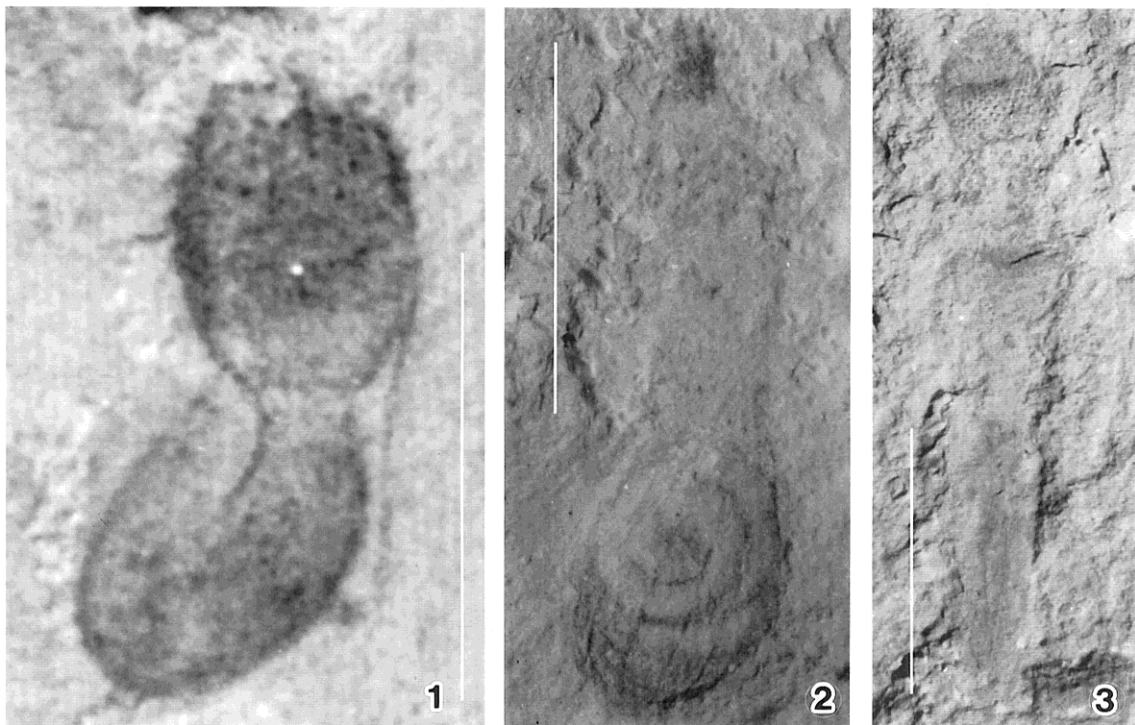


Figure 10. Examples of priapulids. 1. Bag-shaped priapulid, *Palaeopriapulites parvus*, from Maotianshan, Chengjiang. 2. Bag-shaped priapulids *Protopriapulites haikouensis*, from Haikou, Kunming. 3. Tubicolous priapulid *Paraselkirkia jinningensis*, from Haikou, Kunming. Scale bars: 5 mm.

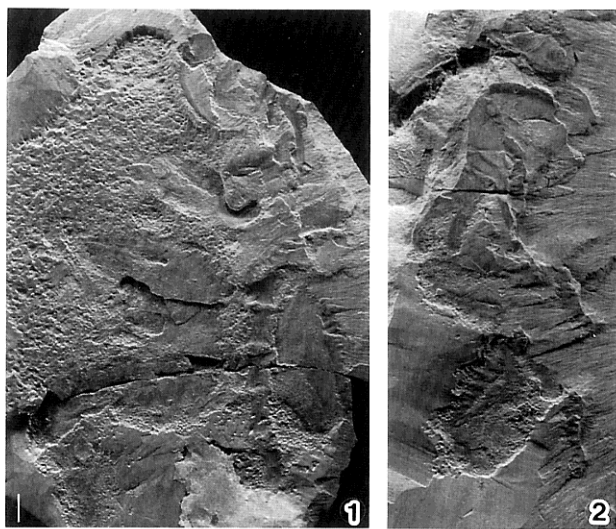


Figure 11. Anomalocaridid with the robust paired ventral legs, *Parapeytoia yunnanensis*, part (1) and counterpart (2), from Maotianshan, Chengjiang. Scale bar: 5 mm.

Cnidarians.—*Xianguangia sinica* (Figure 8.2), approximately cylindrical and up to 70 mm high and 25 mm wide, possesses 16 long and flexible tentacles extending distally from the distal disc and is compared to living sea anemones. Tubicolous *Archotuba conoidalis* (Figure 8.3) is similar to *Cambrorhytium* from the Burgess Shale in Canada and the Marjum Formation in Utah (Conway

Morris and Robison, 1988). The Chinese *Archotuba* was a sessile benthic organism, and one to five individuals can be seen attached on animal shells. No tentacles are seen in *Archotuba*.

Nematomorphs.—The long, slender worms of this group are common elements in the Chengjiang fauna. They used to be considered as possible annelids. This kind of worm is characterized by the presence of an armed proboscis, paired posterior hooks and sclerites on the body surface. Compared with the Nematoda, Priapulida and Nematomorpha, they are closest to the latter although the latter are parasitic. *Palaeoscolex sinensis* (Figure 9.1) differs from other long worms in its regularly placed papillae on the body surface, *Maotianshania cylindrica* (Figure 9.3) in its irregularly placed papillae on the body surface and *Cricocosmia jinningensis* (Figure 9.2) in its two conical sclerites on each body ring.

Priapulids.—The bag-shaped Chengjiang priapulids include a few species, such as *Palaeopriapulites parvus* (Figure 10.1) and *Protopriapulites haikouensis* (Figure 10.2). They generally are between 7 and 10 mm long and both proboscis and trunk are oval as preserved. Similarly fat priapulids were found only in the Pennsylvanian of Illinois (Schram, 1973). The tubicolous priapulid *Paraselkirkia jinningensis* (Figure 10.3) is common in Jinning county and Haikou, Kunming but rare or absent in Chengjiang. Most specimens possess well-preserved soft parts in association with tubes and a few specimens are represented only by empty tubes. The tube is less than 20

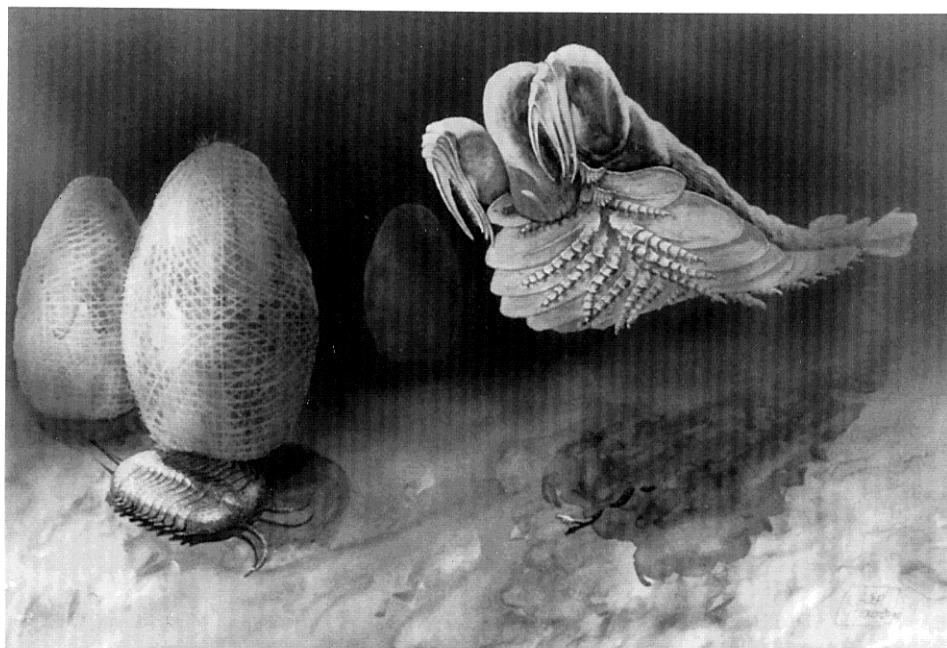


Figure 12. Reconstruction of *Parapeytoia yunnanensis* in ventral view.



Figure 13. Anomalocaridid *Anomalocaris saron*, from Haikou, Kunming. Scale bar: 5 mm.

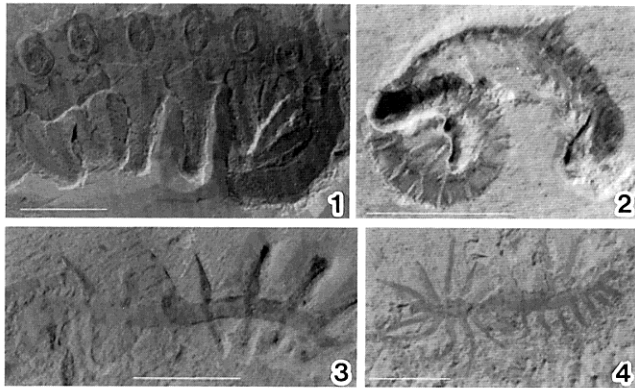


Figure 14. Examples of lobopods. 1. *Microdictyon sinicum*, from Maotianshan, Chengjiang. 2. *Cardiodictyon catenulum*, from Maotianshan, Chengjiang. 3. *Hallucigenia fortis*, from Maotianshan, Chengjiang. 4. *Luolishania longicruris*, from Haikou, Kunming. Scale bars: 5 mm.

mm in length and less than 3 mm in width at the opening. Annulations on the outer wall of the tube are distinct and regularly placed. It is similar to *Selkirkia* from the Middle Cambrian (e.g. Conway Morris and Robison, 1986), but has not been studied in detail.

Anomalocaridids.—There are four anomalocaridid genera and species in the fauna, such as *Parapeytoia yunnanensis* (Figures 11, 12) and *Anomalocaris saron*

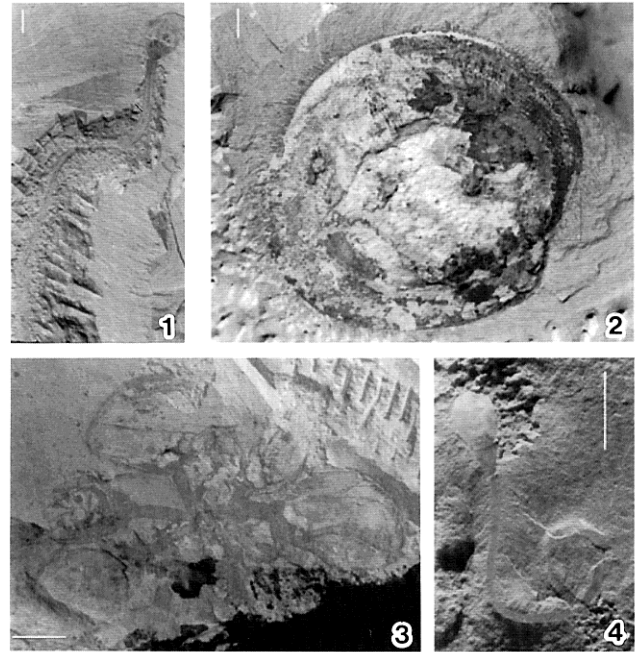


Figure 15. Examples of brachiopods. 1. *Lingulella chengjiangensis*, from Haikou, Kunming. 2. *Heliomedusa orientalis*, from Haikou, Kunming. 3. *Longtancunella chengjiangensis*, from Maotianshan, Chengjiang. 4. *Lingulepis malongensis*, from Maotianshan, Chengjiang. Scale bars: 5 mm.

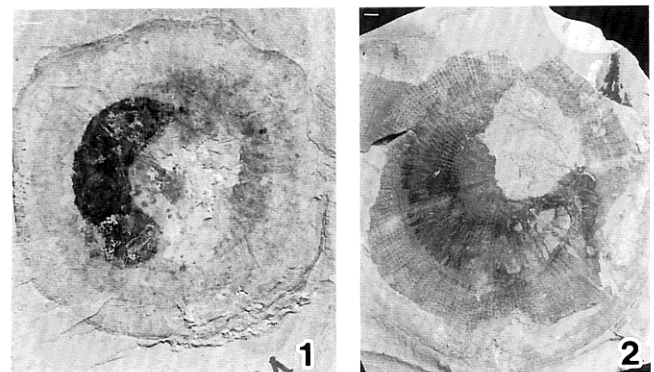


Figure 16. Discoidal animals (echinoderms). 1. Sea cucumber *Eldonia eumorpha*, from Xiaolantian, Chengjiang. 2. Sea cucumber *Rotadiscus grandis*, from Xiaolantian, Chengjiang. Scale bars: 5 mm.

(Figure 13), at least two of which are preserved with paired robust ventral legs. Although the ventral legs of anomalocaridids are biramous, they differ notably from the biramous legs of arthropods in their structure since the flat lateral “swimming” lobe is the main proximal part in the

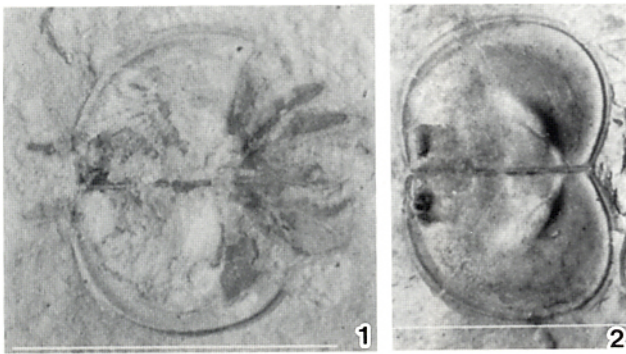


Figure 17. Bradoriid arthropod. 1. Bradoriid with soft parts, *Kunmingella douvillei*, from Xiaolantian, Chengjiang. 2. Carapace, *Kunmingella douvillei*, from Xiaolantian, Chengjiang. Scale bars: 5 mm.

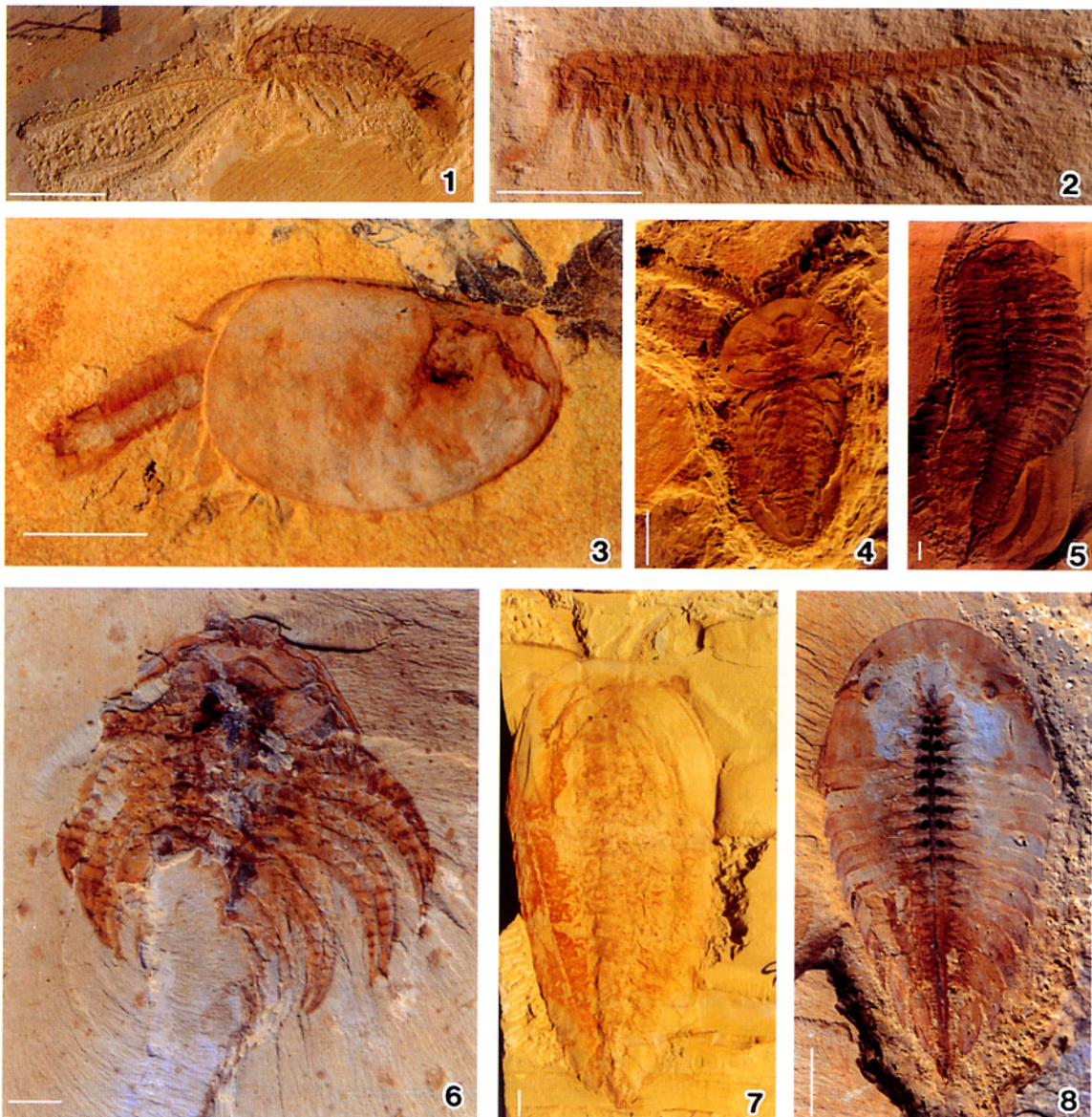


Figure 18. Examples of miscellaneous arthropods. 1. *Leanchoilia illecebrosa*, from Dapotou, Chengjiang. 2. *Jianfengia multisegmentalis*, from Maotianshan, Chengjiang. 3. Bivalved arthropod *Canadaspis laevigata*, from Maotianshan, Chengjiang. 4. *Naraolia longicaudata*, from Maotianshan, Chengjiang. 5. *Fuxianhuia protensa*, from Maotianshan, Chengjiang. 6. *Chengjiangocaris longiformis*, from Xiaolantian, Chengjiang. 7. *Cindarella eucalla*, from Haikou, Kunming. 8. *Xandarella spectuculum*, from Haikou, Kunming. Scale bars: 5 mm.



Figure 19. Vetulicolian *Vetulicola cuneata*, from Maotianshan, Chengjiang. Scale bar: 5 mm.



Figure 20. Agnathan fish *Myllokunmingia fengjiaoa*, from Haikou, Kunming. Scale bar: 5 mm.

former, but a lateral branch in the latter. There are some isolated biramous legs that obviously do not belong to arthropods, but to anomalocaridids.

Lobopods.—They are onychophore- and tardigrade-like animals. Six lobopod animals from the Chengjiang fauna have been described (see Figure 14. 1–14.4 for examples). The fauna has taught us that the lobopods were not only present but also unexpectedly varied in the beginning of the Phanerozoic.

Brachiopods.—There are five brachiopod taxa in the fauna. Most of them are lingulids preserved with long pedicles (Figure 15.1, 15.4). *Longtancunella chengjiangensis* (Figure 15.3) is seen in a cluster of ten individuals attached to the shell of an unknown animal.

Hyoliths.—There are four genera and species in the fauna. The largest one reaches a length of 35 mm and is 15 mm wide at the aperture, whereas the smallest is 4.5 mm long and 1.3 mm wide at the aperture. The relationship of hyoliths is uncertain; mostly they are regarded as mollusks or as a separate group.

Arthropods.—This is the predominant group and shows the largest number of species variety in the fauna. Of the total of 120 described animal species, more than 50 are arthropods, such as *Leancoilia illecebrosa* (Figure 18.1), *Jianfengia multisegmentalis* (Figure 18.2), *Canadaspis laevigata* (Figure 18.3) and *Naraoia longicaudata* (Figure 18.4). The Chengjiang arthropods, ranging from 1 mm to over 400 mm long, generally show primitive characters. For example, legs of a primitive design greatly outnumber the segmental tergites in *Fuxianhuia protensa* (Figure 18.5) and *Chengjiangocaris longiformis* (Figure 18.6); the compound eyes were commonly ventral, as seen in *Cindarella eucalla* (Figure 18.7), but tended to shift to a dorsal position in *Xandarella spectuculum* (Figure 18.8); there are many short podomeres (segments) in the leg endopods, and the exopods were simple. Other primitive characters include the absence of labrum, a semipendant stance of ventral appendages, and a low degree of tagmosis. Perhaps the most surprisingly, many of them were deposit feeders. This mode of feeding is unknown in extant arthropods and indicates the mode of feeding in worm ancestors. This mode of feeding goes along with the absence of specific mouthparts and other specialized appendages.

Echinoderms.—The common element of echinoderms may be discoidal animals *Eldonia eumorpha* (Figure 16.1). It and *Rotadiscus grandis* (Figure 16.2) were originally described as jellyfish. They possess a large disclike body (more than 10 cm in diameter) that enveloped the coiled gut. There are oral tentacles adjacent to the mouth (Figure 16.2). The affinities of *Eldonia* have been the subject of considerable controversy. The new study suggests that *Eldonia* is a holothurian (sea cucumber), supporting Walcott's original view (Briggs *et al.*, 1994).

Vertebrates.—There are three complete, jawless “fish” specimens found in the same bed at Haikou, Kunming. A study of an additional specimen indicates that all three specimens may belong to a single species, *Myllokunmingia fengjiaoa* (Figure 20).

Miscellaneous animals.—There are about 11 animals in the fauna that cannot be easily placed in any recognized phylum. For example, vermicular animals *Yunnanozoon lividum* (Figure 21.4), *Farcivermis yunnanensis* (Figure 21.2), *Dinomischus venusta* (Figure 21.1), *Maanshanian crusticeps* and cancelloriid *Allonnia phrixothrix* (Figure 21.3). *Y. lividum* was considered to be a chordate (Chen *et al.*, 1995) or hemichordate (Shu *et al.*, 1996), or neither a chordate nor a hemichordate (Bergström, 1997; Bergström *et al.*, 1998).

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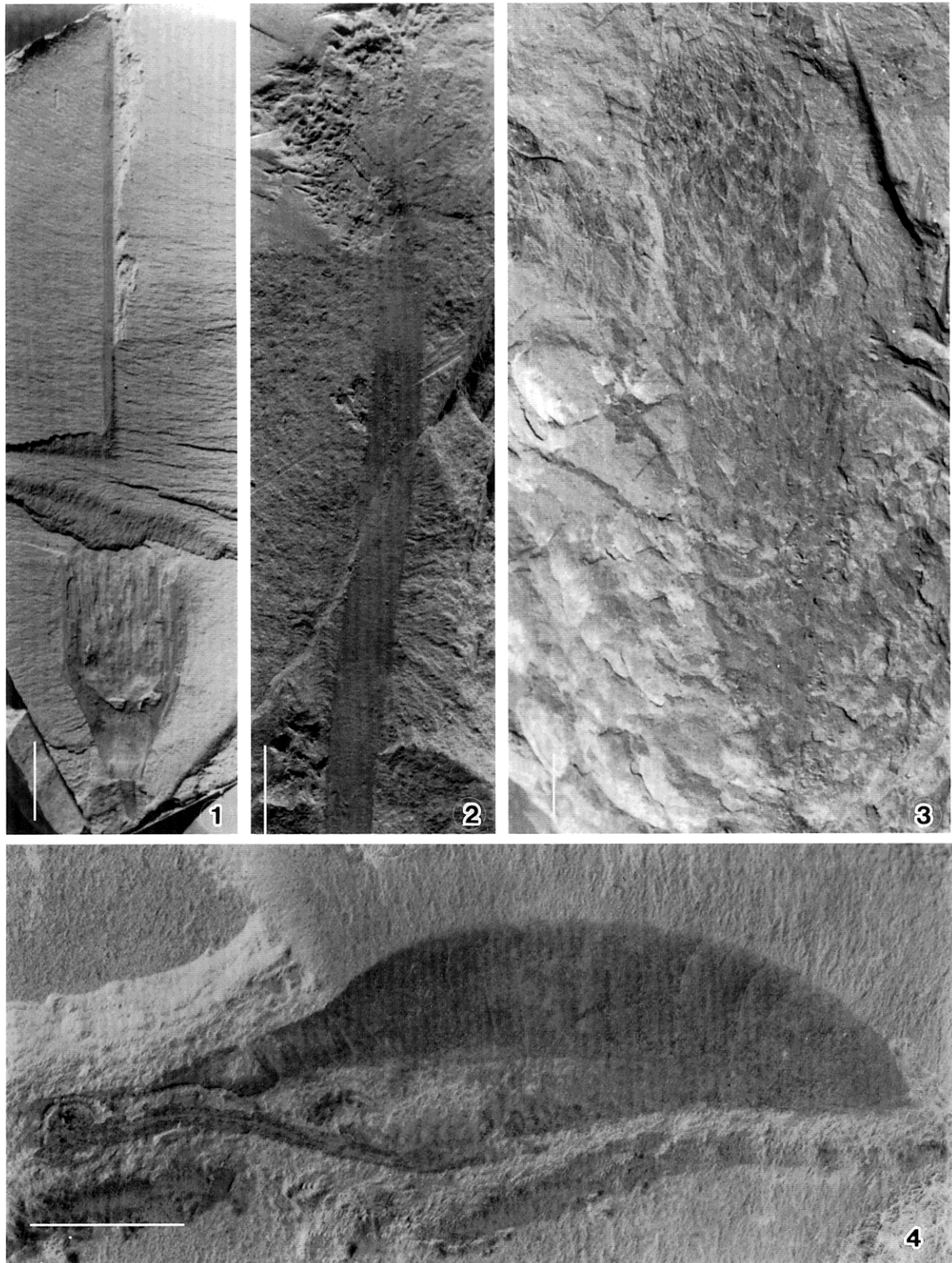


Figure 21. Examples of miscellaneous uncertain taxa. 1. *Dinomischus venusta*, from Maotianshan, Chengjiang. 2. *Facivermis yunnanicus*, from Maotianshan, Chengjiang. 3. Chancelloriid *Allonnia phrixothrix*, from Haikou, Kunming. 4. Holotype of *Yunnanozoon lividum*, from Maotianshan, Chengjiang. Scale bars: 5 mm.

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