Soft-bodied fossils from the Shipai Formation, Lower Cambrian of the Three Gorge area, South China

XING LIANG ZHANG* & HONG HUA

Department of Geology and the Key Laboratory for the Continental Dynamics of the Education Ministry, Northwest University, Xian 710069, PR China

(Received 6 April 2004; accepted 3 February 2005)

Abstract – Mudstones and shales in the Lower Cambrian Shipai Formation in the Three Gorge area, Hubei, China, are richly fossiliferous, containing common shelly fossils and some soft-bodied fossils. The latter provide important new information about the nature and variety of Cambrian soft-bodied organisms. Identifiable, non-mineralized taxa include components of the Chengjiang fauna, such as *Vetulicola* Hou, 1987, a palaeoscolecidan referable to *Maotianshania* Sun & Hou, 1987, and a brachiopod *Diandongia pista* with pedicle preserved (not illustrated). *Cambrorhytium* Conway Morris & Robison, 1988, co-occurring both in the Burgess Shale and the Chengjiang Lagerstätte, was also recovered. Additionally, a new worm is described based on two specimens. This taxon, in common with many other fossil worms, has a slender, cylindrical body with annulations, but it is characterized by each annulus bearing an elevated ridge and lacking surface ornamentation. The occurrence of exceptional preservation in the Shipai Formation has likely been overlooked due to the relatively poor resolution of soft-bodied fossils; nevertheless, this occurrence is an important extension of the Burgess Shale-type biotas in China, over 1500 km northeast of the provenance of the Chengjiang Lagerstätte.

Keywords: Lower Cambrian, Burgess Shale, lagerstätten, Shipai Formation, soft-bodied fossils, South China.

1. Introduction

Cambrian Burgess Shale-type deposits have provided a major contribution to our knowledge of early animals without mineralized skeletons. These deposits have a worldwide distribution and appear to be over-represented in North America and Australasia (Conway Morris, 1985; Allison & Briggs, 1993). More exceptional preservations of this type have continued to be found in both regions (e.g. Zhao et al. 1999; Schwimmer & Montante, 2002; Lieberman, 2003). In the last decade, systematic investigation in the east-central Yunnan led to discoveries of over a dozen localities yielding Chengjiang fossils (Zhang et al. 2001). This, coupled with the very wide distribution of mudstones and shales of Cambrian age in South China, suggests that additional exceptional preservations remain to be found. The discovery of the Middle Cambrian Kaili fauna in Guizhou Province represents a very important geographic extension (Zhao et al. 1999). Here we report a new soft-bodied fauna from the Lower Cambrian of the Three Gorge area, Hubei Province, South China. Stratigraphy and palaeontology of Cambrian rocks in this area have been well studied (Wang et al. 1987), but no softbodied fossils have previously been reported. Initial excavation and study of material from the only known

locality has revealed a number of worms, vetulicolians, a brachiopod with pedicle preserved (not illustrated because of poor preservation), and some unidentifiable organisms, such as the cupulate creature shown in Figure 2e. This assemblage has some similarities with the older Chengjiang fauna and extends the geographic range of this faunal type to south-central China. Its diversity is limited compared with some well-known biota of similar age, such as the Burgess Shale and Chengjiang Lagerstätten. However, our investigation is at a preliminary stage. An intensive excavation has been underway and more exceptionally preserved fossils are expected to be found.

2. Geological setting, locality and stratigraphy

The Three Gorge area in the Hubei Province (Fig. 1a) lies in the centre of the Yangtze platform, where Sinian to Lower Palaeozoic strata are well known. Many sections here have been suggested as standard stratigraphic sections in China. Cambrian strata are superbly exposed because of deep erosion by the Yangtze River. Sequences of Cambrian strata are summarized in Figure 1b. The Middle–Upper Cambrian is dominated by thick dolostones, not suitable for exceptional fossil preservation and not, therefore, discussed further here. The Lower Cambrian is divided into four lithostratigraphic units, which in ascending order are: the top of Dengying Formation, Shuijingtuo

^{*} Author for correspondence: xlzhang@pub.xaonline.com



Figure 1. Locality and horizon of the soft-bodied fossils. (a) Sketch map of the People's Republic of China, showing the position of the collecting locality in the Hubei Province. (b) Stratigraphic sequences of Cambrian strata in the Three Gorge area, indicating the horizon where the soft-bodied fossils were collected. (c) Simplified geological sketch map of the Three Gorge area, Hubei Province, southern China, showing the outcrops of Cambrian strata and the fossil locality.

Formation, Shipai Formation and Tianheban Formation (Fig. 1b).

The deposits that yield soft-bodied fossils belong to the middle part of the Shipai Formation. The single locality is situated in the section along the road passing Wangjiaping village, about 20 km west of Yichang (Fig. 1c).

The absolute age of this fauna is presently unknown, but regional and intercontinental correlations indicate that it is Early Cambrian. The top of the Dengying Formation is composed of varicoloured dolostones, containing small shelly fossils and generally accepted as Meishucunian in age. The overlying Shuijingtuo Formation is a sequence of black shales containing large carbonate concretions, approaching 2 m in diameter. The black shales yield trilobite *Hupeidiscus*, recently correlated with the *Abadiella huoi* Zone in Australia, the *Nevadella* Zone in Laurentia, the lower part of the Holmia Zone in Baltica, and the Antatlasia Zone in Morocco (Geyer & Shergold, 2000), and thus may correlate with late Atdabanian. The Shipai Formation where the soft-bodied fossils were collected is a mudstone-dominated unit interbedded with siltstones (Fig. 1b). It was correlated with the lower part of the Canglangpu Formation (old spelling: Tsanglangpu) in eastern Yunnan on the basis of trilobite faunas (Zhang et al. 1980). The uppermost unit of the Lower Cambrian, the Tianheban Formation, is characterized by oolitic limestones and was correlated with the upper part of the Canglangpu Formation (Zhang et al. 1980). From this evidence, the Canglangpuan age of this softbodied fauna is firmly established. Coeval deposits containing soft-bodied fossils may be the Emu Bay Shale in South Australia, which was also correlated to the Canglangpuan Stage with the occurrence of the trilobite Redlichia takooensis (Zhang et al. 1980;

Nedin, 1995). Contemporary South Australia faunas correlate with the Botomian of Siberia (Bengtson *et al.* 1990). Therefore, the present fauna is slightly younger than the famous Chengjiang fauna, which is Qiongzhusian (Chiungchussuan) in age, equivalent to the late Atdabanian in the Siberian sequence (Zhang *et al.* 2001; Babcock, Zhang & Leslie, 2001).

3. Systematic palaeontology

The figured specimens are in the repository of either the Department of Geology, Northwest University based in Xian, People's Republic of China (NWU), or the U.S. National Museum of Natural History (USNM), Washington D.C.

Phylum uncertain Genus Cambrorhytium Conway Morris & Robison, 1988 Cambrorhytium cf. C. major Walcott, 1908, emend. Conway Morris & Robison, 1988 Figure 2a, b

Description. Two slabs were obtained, each showing several tubes arranged with their apices emanating from shells of brachiopods (Fig. 2a, b) similar to Diandongia pista also known from the Chengjiang Lagerstätte (Zhang et al. 2003). Five tubes in Figure 2a and seven in Figure 2b have been preserved. Tubes are incomplete, most lacking apex. The maximum preserved length is about 20 mm, within the size range of the type material. Neither surface ornamentation nor annulations have been observed. Information on soft parts is limited. A dark axial structure along the middle part of a tube in NWU 041001 (Fig. 2a) may indicate the trace of the intestine. A similar structure is visible in USNM 198638 (Conway Morris & Robison, 1988, fig. 12.4) and has been reported from the Chengjiang material (Hou et al. 1999, fig. 70; Hou et al. 2004, fig. 12.6a).

Discussion. Tubes from the Stephen Formation (North America) were originally attributed to Selkirkia by Walcott (1911). Subsequently, they were separated from Selkirkia and assigned to a genus of their own, Cambrorhytium, because they lacked typical characters of the Priapulida, and were tentatively considered as cnidarians given the occurrence of possible tentacles (Conway Morris & Robison, 1988). Strikingly similar tubes from the Chengjiang fauna have been treated differently. Chen & Zhou (1997; see also Chen et al. 1996) briefly described their material under the genus Cambrorhytium as a new species. They also interpreted this species as a sessile benthic cnidarian and depicted tentacles in the reconstruction. In contrast, similar fossils were placed in a separate taxon, Archotuba conoidalis (Hou et al. 1999). At the same time, these authors claimed that there was no evidence for the presence of tentacles and interpreted these fossils as tubes of priapulid worms (Hou et al. 2004).

Present material provides no new diagnostic information. Some of the Chengjiang tubes have been found attached to skeleton of various animals, such as brachiopods, hyolithids and trilobites (Hou et al. 1999, 2004). In this respect, the new material resembles the Chengjiang specimens. Annulations are visible on the external surface of some specimens of the Burgess Shale but lacking in others (Conway Morris & Robison, 1988, fig. 12). The same applies in the case of the Chengjiang specimens (Hou et al. 2004). Additionally, in one of the specimens from the Burgess Shale, fine annulations only occur in the axial region under highangle illumination (Fig. 2d). It is likely that annulations occasionally occurring on the external surface of a tube are impressions of an internal body with annulations. Accordingly, Cambrorhytium may be tubes of wormlike creatures with annulations.

Phylum ?NEMATOMORPHA Class PALAEOSCOLECIDA Conway Morris & Robison, 1986 Order uncertain Family MAOTIANSHANIIDAE Hou *et al.* 1999 Genus *Maotianshania* Sun & Huo, 1987 *Maotianshania cylindrica* Figures 3e–g, 4

Description. Thousands of specimens of this monospecific genus are known from the Chengjiang Lagerstätte (Hou *et al.* 2004). Recently, it has also been reported from the Middle Cambrian Kaili fauna (Zhao *et al.* 1999). New material includes a single specimen, with part and counterpart. The specimen is incomplete, lacking the proboscis and the terminal hooks. The animal is 2.2 mm wide, a width that is maintained along the length of the body. The preserved portion as measured along the curvature of the trunk is about 33 mm, comparable to an average-sized specimen from the Chengjiang Lagerstätte. Annulations and surface ornamentation are clearly preserved, identical to the type material (comparing Fig. 3g with Hou & Bergström, 1994, fig. 3B).

Discussion. Maotianshania was originally described from the Chengjiang fauna as a possible priapulid on account of its priapulid-like features, including the retractable spiny proboscis and a cylindrical annulated body with terminal hooks (Sun & Hou, 1987). This viewpiont appears to be followed by Chen et al. (1996) and Chen & Zhou (1997). Subsequently, the pioneer researcher Xianguang Hou, joined by Jan Bergström, reconsidered it as a palaeoscolecidan given its surface ornamentation, that is, 'irregularly scattered sclerites'. However, SEM studies for the Chengjiang material are still lacking and a microscopic comparison to those taxa with well-documented ornamentation, for example, a number of genera from the Middle Cambrian of Australia (Müller & Hinz-Schallreuter, 1993), Palaeoscolex piscatorum (Conway Morris, 1997) and other



Figure 2. *Cambrorhytium major* Walcott (a–d) and an unknown form (e). Scale bars, 1 cm in (a–c) and (e), 5 mm in (d). (a, b) tubes attached to shells of *Diandongia pista*, both from the Shipai Formation, Wangjiaping, NWU 041001 and 041002, respectively; (c), (d) from the phyllopod bed of the Burgess Shale, Stephen Formation, British Columbia, (c) USNM198636, photographed under low-angle radiation, (d) USNM 200455, photographed under high-angle illumination; (e) NWU 040001, a cupulate creature with unknown affinities, from the Shipai Formation, Lower Cambrian, Wangjiaping.

species recently described from the Lower Cambrian of eastern Siberia (Ivantsov & Wrona, 2004), is presently not possible. The systematic position of the Palaeoscolecida is controversial. Conway Morris (1997) cited evidence for linking palaeoscolecidans with priapulids. Other authors placed them in Nematomorpha (Hou & Bergström, 1994; Hou *et al.* 1999, 2004) or in the Aschelminthes in the broad sense (Müller & Hinz-Schallreuter, 1993; Ivantsov & Wrona, 2004).

Phylum Uncertain *Goettingenia* n. g.

Derivation of name. From *Göttingen*, a university town in Germany where specimens were studied.

Diagnosis. The vermiform body is elongate, with annulations throughout but lacking surface ornamentation. The middle zone of each annulus is marked by a transverse ridge. Full length reaches 120 mm.



Figure 3. Fossil worms from the Shipai Formation, Lower Cambrian, Wangjiaping. Scale bars, 1 cm in (a) and (c), 2 mm in (b) and (d), 5 mm in (e) and (f). (a) *Goettingenia wangjiapingensis* n. g. et n. sp., NWU 042001; (b) magnification of the marked region in (a), showing details of annulations; (c) *Goettingenia wangjiapingensis*, NWU 042002; (d) detailed view of annulations the marked region of (c); (e) *Maotianshania cylindrica* Sun & Hou, NWU 042003; (f) counterpart of (e); (g) detailed view of the marked region in (e), showing surface ornamentation.



Figure 4. *Maotianshania cylindrica* Sun & Hou, Explanatory drawing of NWU 042003, composition of part and counterpart.

Type species. Goettingenia wangjiapingensis n. sp.

Goettingenia wangjiapingensis n. sp. Figures 3a-d, 5

Derivation of name. From Wangjiaping, the village where the fossils were found.

Types. Holotype, NWU 042001. The other available specimen, lacking traverse ridges but identical to the holotype in other respects, is here referred to as paratype (NWU 042002).

Occurrence. Shipai Formation, Lower Cambrian of Three Gorge area, Hubei Province, P. R. China. Specimens were collected from the section along the road passing through Wangjiaping village.

Diagnosis. As for the genus (only known species).

Description. Two available specimens are preserved in yellowish green mudstone as flattened compressions. Both worms are folded upon themselves in a way similar to those worms from the Chengjiang Lagerstätte (Hou *et al.* 2004) and other palaeoscolecidans from the Burgess Shale-type deposits (Glaessner, 1979; Conway Morris & Robison, 1986), and incomplete, lacking what is interpreted as the anterior end. The unfolded length of the preserved portion of the holotype exceeds 120 mm (Figs 3a, 5a). The body tapers only slightly from a maximum width of 4.3 mm. Annulations are clearly visible throughout the preserved portion of this specimen, about 20 annuli in 10 mm, uniform in shape. Annulus boundaries are marked by depressions between the raised central ridges of the annuli (Fig. 3b). The paratype (Figs 3c, d, 5b) is slightly more slender than the holotype. The unfolded length of the preserved portion is about 80 mm and the maximum width is approximately 3 mm. Annulations are evident, defined by a series of transverse depressions (Fig. 3d). The raised ridge through the middle zone of each annulus is invisible in this specimen, probably for a taphonomic reason. No surface ornamentation can be observed in either of the specimens.

Discussion. The specimens resemble palaeoscolecidans in vermiform body with annulations, more similar to *Palaeoscolex sinensis* (Hou & Sun, 1988) in body size. However, *Goettingenia* is naked, lacking any surface equipment like sclerites, which are diagnostic characters in palaeoscolecidans. They are readily distinguishable from those priapulid worms from the Burgess Shale or other deposits (Conway Morris, 1977; Conway Morris & Robison, 1986) by more elongated body and unique ridges in the annuli. The systematic position remains unclear because of the lack of anatomical details.

Phylum ?VETULICOLIA Shu *et al.* 2001 Class VETULICOLIDA Chen & Zhou, 1997 Order VETULICOLIDA Hou *et al.* 1999 Family VETULICOLIDAE Hou *et al.* 1999 Genus *Vetulicola Hou*, 1987 *Vetulicola* sp. Figures 6–7

Type species. Vetulicola cuneatus Hou, 1987

General Morphology. Vetulicola is a fairly common animal in the Early Cambrian Chengjiang Lagerstätte. More than 1000 specimens have been known from many localities in east-central Yunnan, China, and these specimens are deposited in different institutes. Unfortunately, it was only briefly described, although illustrations are frequently present in scientific publications or public displays (Hou, 1987; Chen et al. 1991; Chen et al. 1996; Chen & Zhou, 1997; Shu et al. 2001; Hou et al. 1999, 2004). The animal consists of a large bag-shaped anterior section and a paddle-like posterior section with seven segments. The anterior section is composed of four elongate subrectangular plates (a dorsal pair and a ventral pair), which are tightly fused along the dorsal, ventral and posterior margins, forming fin-like marginal bands. The anterior margins of each of these four plates are strongly convex-forward, therefore, the animal is 'B'shaped in lateral view and with long doublures directing backward. The longitudinal connection between the dorsal and ventral plates is along the mid-line of the



Figure 5. *Goettingenia wangjiapingensis* n. g. et n. sp. from the Shipai Formation, Lower Cambrian, Wangjiaping. (a) Explanatory drawing of NWU 042001 showing the outline of the worm and details of annulations, dotted lines representing ridges; (b) Explanatory drawing of NWU 042002.

body, by means of soft membranes, which bend inside and form a pair of vascular-like structures. These two tubes expand partially into five pairs of sac-like structures. On the inner wall of each sac there is an opening, interpreted as a gill slit and comparable with that of some deuterostomes (Shu et al. 2001). The posterior section consists of seven segments, connected to each other by articulating membranes. The last four segments each have a pair of lateral flaps. This section was previously considered as a limbless abdomen of a bivalved arthropod and was therefore described as protruding from the 'carapace' (Hou, 1987). However, close examination of hundreds of specimens indicates that the posterior section connects to the posterodorsal margins of the anterior section by a membrane similar to that between adjacent segments of the posterior section. Gut is more often preserved in the posterior section, occasionally occurring in the posterodorsal of the anterior section.

Description. New material includes five specimens on two slabs, NWU 043001-043002, each including part of the material. NWU 043001 has four specimens (Fig. 6a-e) indicated in numbers in Figures 6a and 7a, and NWU 043002 (Figs 6f, 7b) shows a single specimen. None of them is complete. Figure 7 represents our interpretations of these specimens. Number 1 of NWU 043001 (Fig. 6b) is probably dorsoventrally compacted, showing the lateral flaps of the last four segments of the posterior section. Segmentation is clear and the dark linear impression is interpreted as gut (Fig. 6b). Number 2 of NWU 043001 is a fragment of the ventral plates of the anterior section, which is compacted in lateral aspect and parallel to the bedding. The anterior portion is absent and the dark band indicates where the ventral and posterior margins are fused. (Fig. 6c). The compaction of number 3 of NWU043001 (Fig. 6d) is oblique, showing an almost complete posterior section. Segmental rings are more clearly preserved



Figure 6. *Vetulicola sp.* from the Shipai Formation, Lower Cambrian, Wangjiaping. Scale bars, 1 cm. (a) Slab NWU 043001, four specimens indicated in number 1–4; (b–e) detailed view of Number 1–4 of NWU 043001; (f) NWU 043002.

than articular membranes, probably more resistant to decay. A longitudinal dark line, representing the gut, is visible throughout the preserved portion (number 3 of Fig. 7a). Number 4 of NWU043001 (Fig. 6e) preserves most of the posterior section, dorsoventrally compressed and parallel to the bedding. Lateral flaps of the last four segments are better revealed in this specimen. Like those from the Chengjiang Lagerstätte, the outline of the lateral flaps is asymmetrical (Fig. 6e). This led them to be alternatively interpreted as vertical tail fins (Shu *et al.* 2001) rather than horizontal propulsive flaps (Hou *et al.* 2004). NWU043002 shows the posterior margin of the anterior section and almost the whole of the posterior section (Figs 6f, 7b). Overall, it is laterally compacted parallel to the bedding but the posterior portion of the posterior section is preserved



Figure 7. Vetulicola sp., explanatory drawings of Figure 6. (a) Slab NWU 043001, four specimens are indicated; (b) NWU 043002.

at an angle to the bedding. Therefore, the posterior section may be rotated somewhat whether the tail fins of the living creature were vertical or horizontal. The gut impression is also present in this specimen (Fig. 7b).

Discussion. Vetulicola is represented by two species, V. cuneata Hou (1987) and V. rectangulata Luo et al. (1999), both of which are from the Chengjiang Lagerstätte. V. rectangulata differs from the type species in its straight anterior margin of the anterior section. New material is preserved in fragments and it is difficult to assign the material to either species. The occurrence of a fused marginal band in NWU043001 distinguishes the material from a number of other vetulicolians: Pomatrum (Luo et al. 1999), Xidazoon (Shu et al. 1999), Didazoon (Shu et al. 2001) and Yuyuanozoon (Chen, Feng & Zhu, 2003).

Vetulicola was originally described as a bivalved arthropod by Hou (1987), based on a few specimens from the classic Maotianshan section of the Chengjiang Lagerstätte. This view was widely accepted by a number of authorities (Hou & Bergström, 1991; Chen et al. 1991; Delle Cave & Simonetta, 1991; Chen et al. 1996; Chen & Zhou, 1997; Hou et al. 1999). Although Chen & Zhou admitted that the bivalved carapace could not open up, they considered V. cuneatus as a unique arthropod and erected a new class Vetulicolida including Vetulicola and Banffia (Chen & Zhou, 1997). Shu et al. (2001) considered the similarities to arthropods to be a result of convergent evolution and proposed a distinct phylum, the Vetulicolia within deuterostomes, based in a large part on lateral openings that were interpreted as gill slits. Since this work was published, a few comments have emerged. Lacalli (2002) questioned the interpretation of vetulicolians as a basal group of deuterostomes. Butterfield (2003) insists that they are better interpreted as arthropods. There is currently no agreement about the systematic position of this animal.

Since a detailed description is still lacking, anatomical characters with phylogenetic importance may have not been recovered. Overall, *Vetulicola* resembles arthropods in many aspects but no eyes or appendages are known. New material provides no new information on its phylogeny.

Acknowledgements. The '211' project of Northwest University funded initial collection and investigation of softbodied fossils in the Three Gorge area. This work subsequently supported by the Natural Science Foundation of China and a Foundation for the Author of National Excellent Doctoral Dissertation of PR China (FANEDD). We would like to thank Yong Li, Hongxiang Guo, Wei Bai, Bin Zhou and ten students at the Chang'an University for their participation in the field trips, and Jian Han for discussion. XZ also gratefully acknowledges the Alexander von Humboldt Foundation for the financial support for a oneyear research stay in the Department of Geobiology, Center of Geosciences, University of Göttingen (GZG, Germany). Special thanks are given to Professor Joachim Reitner for access to numerous facilities in the GZG. Thanks also go to D. H. Erwin for the access to examine Cambrorhytium specimens in the U.S. National Museum of Natural History (NMNH), Smithsonian, Washington, D.C.

References

- ALLISON, P. A. & BRIGGS, D. E. G. 1993. Exceptional fossil record: Distribution of soft-tissue preservation through the Phanerozoic. *Geology* 21, 527–30.
- BABCOCK, L. E., ZHANG, W.-T. & LESLIE, S. A. 2001. The Chengjiang Biota: record of the Early Cambrian diversification of life and clues to exceptional preservation of fossils. *GSA Today* 11, 4–9.
- BENGTSON, S., CONWAY MORRIS, S., COOPER, B. J., JELL, P. A. & RUNNEGAR, B. N. 1990. Early Cambrian Fossils from South Australia. *Memoir of the Association of Australasian Paleontologists* 9, 364.
- BUTTERFIELD, N. J. 2003. Exceptional fossil preservation and the Cambrian explosion. *Integrative and Comparative Biology* **43**, 166–77.
- CHEN, A.-L., FENG, H.-Z. & ZHU M.-Y. 2003. A new vetulicolian from the Early Cambrian Chengjiang fauna in Yunnan of China. *Acta Geologica Sinica* 77, 281–87.
- CHEN, J.-Y., BERGSTRÖM, J., LINDSTRÖM J. & HOU, X.-G. 1991. Fossilized soft-bodied fauna. *National Geo*graphic Research & Exploration 7, 8–19.
- CHEN, J.-Y. & ZHOU, G.-Q. 1997. The Biology of the Chengjiang fauna. *Bulletin of the National Museum of Natural Science* **10**, 11–106.
- CHEN, J.-Y., ZHOU, G.-Q., ZHU, M.-Y. & YEH, K. 1996. The Chengjiang Biota – A Unique Window of the Cambrian Explosion. Taichung, Taiwan: The National Museum of Natural Science, 222 pp. (in Chinese).
- CONWAY MORRIS, S. 1977. Fossil priapulid worms. *Special Papers in Palaeontology* **20**, 1–95.
- CONWAY MORRIS, S. 1985. Cambrian Lagerstätten: their distribution and significance. *Philosophical Transactions of the Royal Society of*London **B 311**, 49–65.
- CONWAY MORRIS, S. 1997. The cuticular structure of the 495-Myr-old type species of the fossil worm *Palaeoscolex*, *P. piscatorum* (?Priapulida). *Zoological Journal of the Linnean Society* **119**, 69–82.
- CONWAY MORRIS, S. & ROBISON, R. A. 1986. Middle Cambrian priapulids and other soft-bodied fossils from Utah and Spain. *The University of Kansas Paleontological Contributions* **Paper 117**, 1–22.
- CONWAY MORRIS, S. & ROBISON, R. A. 1988. More softbodied animals and algae from the Middle Cambrian of Utah and British Columbia. *The University of Kansas Paleontological Contributions* **Paper 122**, 1–48.

- DELLE CAVE, L. & SIMONETTA, A. M. 1991. Early Paleozoic arthropods and problems of arthropod phylogeny: with some notes on taxa of doubtful affinities. In *The Early Evolution of Metazoa and the Significance* of Problematic Taxa (eds A. M. Simonetta and S. Conway Morris), pp. 189–244. Cambridge: Cambridge University Press.
- GEYER, G. & SHERGOLD, J. 2000. The Quest for Internationally Recognized Divisions of Cambrian Time. *Episodes* 23, 188–95.
- GLAESSNER, M. F. 1979. Lower Cambrian Crustacea and annelid worms from Kangaroo Island, South Australia. *Alcheringa* 3, 21–31.
- HOU, X.-G. 1987. Early Cambrian large bivalved arthropods from Chengjiang, eastern Yunnan. *Acta Palaeontologica Sinica* 26, 286–98.
- HOU, X.-G., ALDRIDGE, R. J., BERGSTRÖM, J., SIVETER, D. J., & FENG, X.-H. 2004. *The Cambrian Fossils of Chengjiang*, China: *the Flowering of Early Animal Life*. Oxford: Blackwell Science, 233 pp.
- HOU, X.-G. & BERGSTRÖM, J. 1991. The arthropods from the Lower Cambrian Chengjiang fauna, with relationship and evolutionary significance. In *The Early Evolution of Metazoa and the Significance of Problematic Taxa* (eds A. M. Simonetta and S. Conway Morris), pp. 179–87. Cambridge: Cambridge University Press.
- HOU, X.-G. & BERGSTRÖM, J. 1994. Palaeoscolecid worms may be nematomorphs rather than annelids. *Lethaia* 27, 11–17.
- HOU, X.-G., BERGSTRÖM, J., WANG, H.-F., FENG, X.-F. & CHEN, A.-L. 1999. *The Chengjiang Fauna – Exceptionally Well-preserved Animals from 530 Million Years Ago*. Kunming: Yunnan Science and Technology Press, 170 pp. (in Chinese with English summary).
- HOU, X.-G. & SUN, W.-G. 1988. Early Cambrian worms from Chengjiang, Yunnan, China: *Maotianshania* gen. nov. *Acta Palaeontologica Sinica* 27, 1–12.
- IVANTSOV, A. Y. & WRONA, R. 2004. Articulated palaeoscolecid sclerite arrays from the Lower Cambrian of eastern Siberia. Acta Geologica Polonica 54, 1–22.
- LACALLI, T. 2002. Vetulicolians—are they deuterostome? Chordates? *BioEssays* 24, 208–11.
- LIEBERMAN, B. S. 2003. A new soft-bodied fauna: the Pioche Formation of Nevada. *Journal of Paleontology* 77, 674– 90.
- LUO, H.-L., HU, S.-X., CHEN, L.-Z., ZHANG, S.-S. & TAO, Y.-H. 1999. Early Cambrian Chengjiang Fauna from the Kunming Region, China. Kunming: Yunnan Science and Technology Press, 129 pp.
- MÜLLER, K. J. & HINZ-SCHALLREUTER, I. 1993. Palaeoscolecid worms from the Middle Cambrian of Australia. *Palaeontology* 36, 549–92.
- NEDIN, C. 1995. The Emu Bay Shale, a Lower Cambrian fossil Lagerstätte, Kangaroo Island, South Australia. In APC94: Papers from the First Australian Palaeontological Convention (ed. P. A. Jell), pp. 31–40. Association of Australiasian Palaeontologists Memoir no. 18.
- SCHWIMMER, D. R. & MONTANTE, W. M. 2002. Exceptional fossil preservation in the Conasauga Formation, Middle Cambrian of Western Georgia. *Annual Meeting of GSA*, *Abstracts with Program, Session no. 31*, 65.
- SHU, D.-G., CONWAY MORRIS, S., HAN, J., CHEN, L., ZHANG, X.-L., ZHANG, Z.-F., LIU, H.-Q., LI, Y. & LIU, J.-N. 2001. Primitive deuterostomes from the Chengjiang Lagerstätte (Lower Cambrian, China). *Nature* **414**, 419– 24.

- SHU, D.-G, CONWAY MORRIS, S., ZHANG, X.-L., CHEN, L., LI, Y. & HAN, J. 1999 A Pipiscus-like fossil from the Lower Cambrian of South China. *Nature* 400, 746–9.
- SUN, W.-G. & HOU, X.-G. 1987. Early Cambrian worms from Chengjiang, Yunnan, China: *Maotianshania* gen. nov. Acta Palaeontologica Sinica 26, 299–305.
- WALCOTT, C. D. 1908. Mount Stephen rocks and fossils. *Canadian Alpine Journal* 1, 232–48.
- WALCOTT, C. D. 1911. Cambrian geology and paleontology II, no. 5 – Middle Cambrian annelids. *Smithsonian Miscellaneous Collections* 57, 107–44.
- WANG, X.-F., NI, S.-Z., ZENG, Q.-L., XU, G.-H., ZHOU, T.-M., LI, Z.-H., XIANG, L.-W. & LAI, C.-G. 1987. *Biostratigraphy of the Three-gorge area*. Early Palaeozoic. Beijing: Geological Publishing House.
- ZHANG, W.-T., LU, Y.-H., ZHU, Z.-L., QIAN, Y., LIN, H.-Z., ZHOU, Z.-Y., ZHANG, S.-G. & YUAN, J.-L.

1980. Cambrian trilobite faunas of Southwest China. *Palaeontologica Sinica* **159**(16), 1–497 (in Chinese with English summary).

- ZHANG, X.-L., SHU, D.-G., LI, Y. & HAN, J. 2001. New sites of Chengjiang fossils: crucial windows on the Cambrian explosion. *Journal of the Geological Society*, London 158, 211–18.
- ZHANG, Z.-F., HAN J., ZHANG, X.-L. et al. 2003. Pediculate brachiopod *Diandongia pista* from the Lower Cambrian of South China. *Acta Geologica Sinica* 77, 288– 94.
- ZHAO, Y.-L., YUAN, J.-L., ZHU, M.-Y., YANG, R.-G., GUO, Q.-J., QIAN, Y., HUANG, Y.-Z. & PAN, Y. 1999. A progress reports on research on the Early Middle Cambrian Kaili Biota, Guizhou, P. R. C. Acta Palaeontologica Sinica 38 (supplement), 1–15 (in Chinese with English summary).