Epibionts on the lingulate brachiopod *Diandongia* from the Early Cambrian Chengjiang Lagerstätte, South China

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The classic Chengjiang Lagerstätte (Lower Cambrian, Atdabanian stage: Yu'an-shan Formation) Yunnan, southwestern China, has yielded, besides the exceptional and often controversial soft-bodied fossils, a fauna of primitive/early lingulid brachiopods. *Diandongia pista* (Rong 1974) is one of the commonest and most strongly mineralized of the phosphatic brachiopods from the Lagerstätte. The shells of this species have been found to commonly serve as a basibiont host. Epibionts comprise the coeval brachiopod *Longtancunella chengjiangensis* and the cone-shaped cnidarian-related *Archotuba conoidalis*, as well as rounded smaller-sized epizoans (lesser than 2 mm). A principle morphological analysis demonstrates that the ovoid and rounded organisms that often occur along the commissure of *D. pista* resemble small juvenile or immature brachiopods. Epibiont-bearing shells of *D. pista* with soft-tissue preservation demonstrate that the host brachiopods were overgrown while alive, and provide an argument for *D. pista* having a semi-infaunal life style with only the slim pedicle embedded in sediment. The epibiotic association sheds direct light on the ecology of Cambrian brachiopods in soft-substrate marine environments. The Chengjiang fossils demonstrate that the Early Cambrian brachiopods, as compared with recent lingulids, occupied different and a wider spectrum of ecological niches and tiers of space.

Keywords: Early Cambrian; Brachiopoda; lingulids; Chengjiang Lagerstätte; soft-tissue preservation; epibiosis

1. INTRODUCTION

Epibionts are organisms that lived on other organisms (e.g. Wahl 1989). Epibiont assemblages are often exceptionally good representations of 'biological communities'; they can provide ecological information that is usually lost in fossil assemblages, including competitive interactions, abundance, diversity, recruitment strategies, ecological succession and niche partitioning (Lescinsky 1997, 2000). Epibionts on brachiopods from the Lower Cambrian are, however, very rarely fossilized (Bassett *et al.* 2004), albeit post-Cambrian encrusted brachiopods have repeatedly been documented in the literature (e.g. Chang 1959; Pitrat & Rogers 1978; Sutton *et al.* 2005; Zapalski 2005).

The Early Cambrian Chengjiang Lagerstätte is well known for preserving one of the earliest examples and most abundant known faunas of Phanerozoic soft-bodied organisms (Chen & Zhou 1997; Hou *et al.* 2004). Many of these taxa have attracted considerable attention, and most of them have been intensely researched. Although extensive studies of the Chengjiang fauna have been carried out in the past two decades, few examples of epibiosis have been documented from these exceptional fossil beds (e.g. Hu 2005; Zhang *et al.* 2008). The phosphatic lingulate brachiopod (*Diandongia pista*) that was initially reported from the Lower Cambrian

Hongjingshao Formation of eastern Yunnan (Rong 1974), is one of the most common mineralized components of the Chengjiang fauna. Now, the species is known to be widely distributed in the Early Cambrian deposits, from exposures in a wide area of the Yangtze platform, South China (Luo *et al.* 1999; Zhang & Hua 2005).

The paper documents small rounded epibionts cemented on the shell margins of the brachiopod *D. pista* from the Lower Cambrian Chengjiang Lagerstätte. The zoological affinity of the small ovoid epizoans is also discussed herein. In addition, we present new data on the brachiopod *Longtancunella chengjiangensis* and the cone-shaped cnidarian *Archotuba conoidalis* (Hou *et al.* 2004), both of which are also ordinarily found attached to shells of *D. pista*. The study provides new insight into the autecology of host brachiopods and the ecology of Early Cambrian soft-substrate communities.

2. MATERIAL AND METHODS

To date, more than 400 specimens of the bostfordiid *D. pista* have been collected from the yellowish-green or greyish-green mudstone of the Chengjiang Lagerstätte at more than 10 localities around Kunming (Zhang *et al.* 2007b). The strata containing the Chengjiang fauna belongs to the Yu'an-shan member (*Eoredlichia* zone) of the Lower Cambrian Heilinpu Formation (Luo *et al.* 1999). This member was recently elevated to the status of a formation, and subdivided into three units, i.e. the Black Shale, the Maotianshan Shale member, and the Upper Siltstone

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One contribution to a Special Issue 'Recent advances in Chinese palaeontology'.

Figure 1. (a–b) The brachiopod *L. chengjiangensis* (represented by stout pedicles marked by numbers) attached to the ventral valve of the lingulid brachiopod *Diandongia pista*, in some cases with fine preservation of slim pedicles (arrows). (a) ELI BD-089, note the three epibiont individuals indicated by numbers. (b) ELI BD-502B, note the impressions of mantle canals. (c) A complete specimen of *L. chengjiangensis*, attached by a pedicle on the hyolith shell. (d–g) The cone-shaped *A. conoidalis* attached to the brachiopod *D. pista*. (d–e) ELI BD-063. (d) Note the cluster of epibiont individuals indicated by numbers. (e) Close-up view of D, showing the proximal pedicle of *D. pista*. (f) ELI BD-068A, also note the four individuals. (g) ELI BD-110, two individuals with dark central intestinal lineation. Scale bars, 5 mm except (e). See figure 3 for some interpretations.

member (Zhu *et al.* (2005) and references therein). The fossils with soft-part preservation are mainly derived from the Maotianshan Shale member.

In our collection, 50 specimens of *Diandongia* shells were affected by epizoan cementation (figures 1 and 2); of these, 20 shells have the brachiopod *L. chengjiangensis* attached by a pedicle (figure 1a–c); 6 have attached solely or populosly the cone-shaped cnidarian *A. conoidalis*; 24 are cemented with small epizoans (figure 2). All the material discussed herein was collected by the work-team of the Early Life Institute (prefix: ELI) and all the specimens are deposited at ELI, Northwest University, Xi'an, PR China.

3. EPIZOANS ON SHELLS OF *D. PISTA*

As mentioned above, the epibionts present on *D. pista* shells belong to the following genera and species. *Longtancunella chengjiangensis*: Hou *et al.* (1999). *Archotuba conoidalis*: Hou *et al.* (1999); and ovoid epizoans preserved as variably rounded or ovoid impressions (less than 2 mm) sometimes with some relief along the shell commissure.

(a) The epibiontic brachiopod *Longtancunella*

Longtancunella chengjiangensis is one of the few linguliform brachiopods in the Chengjiang fauna, which is characterized by subcircular, poorly mineralized shell valves, a stout pedicle, and notably by gregarious fossil occurrences

(Zhang *et al.* 2007a). There are four specimens of *L. chengjiangensis* attached by their pedicles to a single ventral valve of *D. pista*. The pedicles of three of the *L. chengjiangensis* appear to bend deeply into the basal sediment, and then attach on the shell surface of *D. pista*. Examination of these attached specimens of *L. chengjiangensis* reveals that the attachment occurs six times more often on the ventral valve than on the dorsal valve. In *D. pista*, the ventral valve lies on the muddy seafloor. The pattern of attachment might, thus, be related to the sessile life of both brachiopod species and can be interpreted as an epibiosis. Furthermore, the ventral valve of *D. pista* represented a kind of hard debris on which *L. chengjiangensis* anchored by its pedicle.

On average, two *Longtancunella* individuals occur on any *D. pista* shell. *Longtancunella* also used other hard substrates on which to anchor by its stout pedicle, e.g. exoskeletons of hyoliths and trilobites (figure 1c; Zhang *et al.* 2008).

(b) The cone-shaped *A. conoidalis*

Archotuba conoidalis (Hou *et al.* 2004) has also been found attached to the anterolateral margin of the shell of *D. pista*, either separately or in clusters (figure 1d,f,g) with an average of four occurrences per shell. *Archotuba* has also been recorded on skeletal fragments of hyoliths and on the shell of the brachiopod *Heliomedusa orientalis* (Jin & Wang 1992). *Archotuba* fossils are usually unornamented, but a dark axial lineation along the middle part of some tubes

Figure 2. Putative brachiopod larvae cemented on the marginal commissure of the botsfordiid brachiopod *D. pista* from the Early Cambrian Chengjiang Lagerstätte, South China. Scale bars, 5 mm except for those indicated. (a,c,e,i) general view, ELI BD-005, 031A, 093A, 0069. (b,d,f,j) detailed view of the marginal epizoans, indicated by a box, respectively in (a,c,e,i), showing concentric growth lines. (f) Note paired putative baculate mantle canals preserved in the three-dimensional juvenile brachiopod. (g) ELI BD-0134, a non-adult *D. pista* with bifurcate imprints of the dorsal mantle canals. (h) BSEM of (f) showing details of the probable larval brachiopod. See figure 3 for some interpretations.

might represent a putative intestine (figure 1g). *Archotuba* has been interpreted as an epibenthic suspension-feeder related to cnidarians (Chen & Zhou 1997; Chen 2004).

(c) *New cementing brachiopods*

The specimen ELI-BD 005 of *D. pista* is a ventral valve with a slim pedicle (figure 2a). The anterior and anterolateral commissural margins of the ventral valve are covered by seven small reddish-brown protuberances with some relief (figure 2a), which range in size from 1.8 to 2.4 mm, and vary slightly in general contour possibly because of sediment compaction. As illustrated in figure 2c,d, the anterior commissural, marginal portion of the shell was nearly overgrown by such ovoid epizoans.

This organism is the most common epizoan on *D. pista*, occurring along the anterior and lateral commissure. The average number of small ovoids per specimen is five, with a maximum of seven individuals. The majority of the cemented organisms are strongly compressed specimens, composed of part and counterpart, preserved as distorted indentions or protuberances, respectively (figure 2). These larval animals seem poorly mineralized and their shell might be randomly preserved, either laterally or dorsoventrally, showing no signs of brittle breakage. Close observation of several individuals cemented on *D. pista* shells (figure 2b,d,f) suggests that they appear to be

bilaterally symmetrical, with concentric growth increments on their shell surface. This bisymmetrical nature is clearly revealed in the individual specimen ELI-D093B (figure 2e,f), which shows a pronounced three-dimensional relief, reflecting its original convexity and rounded outline. The bilateral symmetry of the epibiontic organisms and their probable concentric growth (figure 2b,d,e,f) suggests that these animals are brachiopods or related to brachiopods that are very common in the Lower Cambrian of southern China (Li & Holmer 2004); the epibionts settled after metamorphosis showing then their bilaterally symmetrical shells with concentric growth lines. In addition, in specimen ELI-D 093B, two symmetrical arcuate impressions present in the postero-lateral portion of the epizoan shell (figure 2f) are reminiscent of the paired main trunks of the mantle canals in brachiopods. The brachiopod nature is, thus, endorsed further by these inferred mantle trunks.

Studies of development and settlement of living brachiopods demonstrate that brachiopod larvae settle mainly around the edges of parental shells and prefer to live conspecific to dead shells (for e.g. Davidson 1888; Brice & Mistiaen 1992; Pennington *et al.* 1999; Peck *et al.* 2001). It is thus possible that these Cambrian ovoids may be non-adult (infant/juvenile) *D. pista*. Nevertheless, it is hard to imagine that *Diandongia* juveniles could have acted

as epibionts on adult forms, when taking into account the slim type of pedicle possessed by the adult *D. pista* (figure 1a–c). Juveniles of *D. pista* are assumed to have had a typical triangular delthyrium as seen in the juvenile *Botsfordia minuta* etched from the coeval Lower Cambrian (Atdabanian) carbonate of Southern Shaanxi province China (Li & Holmer 2004), but this characteristic cannot be verified in our fossils. Furthermore, some isolated similarly sized (lesser than or equal to 2 mm) juveniles of *D. pista* were also recovered from the muddy Chengjiang deposits. Their shell surface is ornamented with regularly distributed pustules or pits (figure 2g). Thus, we consider it unlikely that the ovoids cemented along the commissure of *D. pista* are juveniles of *D. pista*. The cementation on shell margin demonstrates that the ovoids probably belong to small cementing brachiopods, such as those known to attach on the dichotomous branches of green algae from the Chengjiang mudstones in Malong County, Yunnan Province (Hu 2005, plate 18, figs. 1 and 7; Jin 2005). However, it seems hardly assured that all of these small ovoid epibionts belong to the same brachiopod species, because *Longtancunella* is also epizoic on *Diandongia*. Also, similar epibionts are found on the cuticle of Chengjiang priapulid worms (J. Han 2003, unpublished thesis), where they were provisionally named *Inquilinus haikouensis* (also see Han *et al.* 2004), and on eldonioid discs from the Lower-Middle Cambrian Kaili biota (Yuan & Huang 1994; Dzik *et al.* 1997). The ovoids on the Middle Cambrian eldonioid discs were initially interpreted as bradoriid ostracodes, i.e. *Chuandianella? subovata*: Yuan & Huang (1994) and *C? linguiformis*: Yuan & Huang (1994).

4. THE EARLY CAMBRIAN BRACHIOPOD COMMUNITY ON MUD SUBSTRATUM

The structure of fossil communities cannot be fully understood without understanding how the animals that lived together in these communities interacted. One of the major regions of potential interaction is competition for food and life habitat. Recognizing epibiosis is of key importance in describing and explaining the autecology of basibiont and epibiont species and their correlations. Despite the importance of epibionts in palaeoecology, their role in Cambrian ecosystems is poorly understood. This reflects a lack of information about their fossil record, and especially how they interacted with other organisms during the ‘Cambrian explosion’ interval. Whether such epibionts represent examples of parasitism or commensalism should then be investigated.

The fossils from the Chengjiang Lagerstätte provide some direct data on this ecological niche during the rapid radiation of metazoans. Soft-part preservation (for e.g. of pedicle and mantle canals) in *D. pista* (figures 1 and 2) indicates that the host shells represent whole animals buried alive, rather than accumulated and winnowed valves. Additionally, the cementation of epizoans on shells unquestionably signifies their original life position. It is, therefore, assumed that the host brachiopods were alive, or at least in their life position during epibiont recruitment, and that the host-epibiont assemblages are close approximations of the original biological community.

Chatterton (1975) recognized a response in the skeletal growth of a brachiopod clearly related to the presence of an epizoan (also see Bassett *et al.* 2004). With the exception of some circular scars on shell surface (figure 2e,i), few reactions of *D. pista* to its epizoans have been identified with certainty in our fossil collection. It seems that there was little or no physical reaction from the host to epibiont settlement, as there are no apparent morphologic modifications to the shell valves of *D. pista*. Nevertheless, the macro-epibiontic cementation could have been a great disadvantage to the opening and closing of the shells, decreasing the gape of *D. pista* so as to stir or reduce water currents for respiration of oxygen and release of faeces. However, this question seems to be solved by the preferential attachment on ventral valves rather than dorsal valves of *D. pista*. Hence, a mutualism between the macroscopic animals, such as *L. chengjiangensis* and *A. conoidalis*, and the host *D. pista* can be proposed: the shell of *D. pista* was clearly used by the epibionts as a firm substrate, and the association with the large epizoans *Longtancunella* and *Archotuba* might have given the host animal protection from predators.

The exclusive distribution of cementing brachiopods along the commissure of *D. pista* suggests that *I. haikouensis* preferred to cement or attach on a living brachiopod rather than on any dead skeletal debris. This is because all brachiopods are passive suspension feeders that use the lophophore for water and food uptake, and thus the larval/juvenile brachiopods prefer to use water currents produced by the host brachiopod’s lophophore for their own food collection. Therefore, the presence of such small epizoans on shell of *D. pista* might have had detrimental effects on the growth and normal life of the basibiont brachiopod, until the epizoans grew enough to detach therefrom (figures 2i and 3g).

Fossil lingulid brachiopods could be assumed to be infaunal burrowers comparable with their recent representatives (Emig 2000), but this is an unlikely mode of life for *L. chengjiangensis* because of its moderately biconvex rounded shell (rather than elongate and streamlined; as in *Lingula*), and the extremely stout pedicle. The clustering occurrence of *L. chengjiangensis* in the fossil, with its pedicle end attached on shells (figure 1a–c), demonstrates that this brachiopod taxon represented a sedentary suspension feeder (Zhang *et al.* 2007a).

In conjunction with earlier studies of Chengjiang brachiopods (Zhang *et al.* 2005, 2006, 2007a,b), this study demonstrates that in the shore-face to proximal offshore muddy seafloor environments (Zhu *et al.* 2001), Early Cambrian brachiopods have occupied distinct tiers of space and trophic niches on the soft-substratum (figure 3h), as compared with the lingulids from the Middle Cambrian Burgess Shale (Holmer & Caron 2006; Pettersson Stolk *et al.* in press). In the Chengjiang brachiopod assemblage, the brachiopod *Xianshanella haikouensis* (Zhang *et al.* 2006) tended to elevate its feeding structure through its elongated pedicle to the highest possible level above the sea bottom; this upper biotope level was also occupied by the epibenthic, fixosessile *L. chengjiangensis* (Hou *et al.* 1999) and *Kutorgina chengjiangensis* (Zhang *et al.* 2007b). Then we might surmise that *D. pista* (Rong 1974; Zhang *et al.* 2003, 2008) and *H. orientalis* (Jin & Wang 1992) could have occupied the lowest ecological niche near

Figure 3. (a–g) Graphic drawings of epibionts attached to shells of the lingulid brachiopod *D. pista* from the Lower Cambrian Chengjiang Lagerstätte fauna, Yunnan, southwestern China. (h) Sketch reconstruction of the proposed ecological picture of Chengjiang brachiopods. (a) Sketch of figure 2a. (b) Sketch of figure 2b. (c) Sketch of figure 2c. (d) Sketch of figure 2c. (e) Sketch of figure 2e. (f) Sketch of figure 2f. (g) Sketch of figure 2i. Abbreviations: Lo, the brachiopod *L. chengjiangensis* represented by stout pedicles; Pd, Pedicle of the basibiont brachiopod *D. pista*; Ep, probable epibiontic larval brachiopods; Oa, other organisms preserved together with *Diandongia*; Dc, putative discarded cicatrices from attachment of epizoans; Ma, main mantle canals of *D. pista*.

the sediment–water interface, as evidenced by the overgrowth with its epibionts. ‘*Lingulella*’ *chengjiangensis* and *Lingulellotretra malongensis* apparently had thin, long pedicles with only the distal termination embedded into soft sediments (Zhang *et al.* 2005). In conjunction with their small, slightly mineralized shell valves, it can therefore be assumed that these two species rose above any turbulence at the sediment–water interface, akin to kites, tethered by long and thin pedicles. Comparatively, the cementing brachiopods probably had a more variable tier of trophic niche by cementing at different heights on the macroscopic host animals (figures 2 and 3) and large algae (see Hu 2005, plate 18, figs. 1 and 7).

To summarize, gregarious epibionts found on undegraded shell valves of animals with preservation of soft parts, demonstrate that the host brachiopod *D. pista* was invaded and overgrown while alive. The position of the miniature epizoans invariably along the commissure of the brachiopod shells provides insight into how epibionts preferred to cement on a live host. Thus, they probably

represent epibiont suites that settled, lived and interacted in the increasingly complex ecological communities in the time during the initiation of the Cambrian. As a result, the fossils illustrated in this paper provide an unusual and immediate opportunity to observe the autecology of host brachiopods and their epizoans, and shed light upon the ecological structure of Early Cambrian soft-substrate communities (figure 3h).

We are grateful to Prof. Rong Jiayu (Institute of Palaeontology, Nanjing) for his kind invitation to contribute a paper to this special issue. This work was financed by the National Natural Science Foundation of China (grant 40702005 and 04062003, 40332016), MOST special Fund from the State Key Laboratory of Continental Dynamics, Northwest University, the National Basic Research Programme of China (grant 2006CB806401), and the grant (07YYB01) for excellent PhD dissertation of Northwest University, Xi’an (to Z.Z.). We also thank Prof. Lars Holmer (Uppsala) very much for detailed discussion, and to Dr Susan Turner (Brisbane) for linguistic assistance; to Y. C. Yao for help with fieldwork; to J. P. Zhai and M. R. Cheng for

preparation of the fossils; and to Dr H. J. Gong for SEM photographs. Our appreciation is extended to the editors and anonymous referees for their suggestions to improve this manuscript.

REFERENCES

- Bassett, M. G., Popov, L. E. & Holmer, L. E. 2004 The oldest-known metazoan parasite? *J. Palaeontol.* **78**, 1214–1216. (doi:10.1666/0022-3360(2004)078<1214:TOMP>2.0.CO;2)
- Brice, D. & Mistiaen, B. 1992 Épizoaires des brachiopodes Frasnien de Ferques (Boulonnais, Nord de la France). *Geobios* **14**, 45–58.
- Chang, S. H. 1959 Note on the palaeoecological relation between *Aulopora* and *Mucrospirifer*. *Acta Palaeontol. Sin.* **7**, 502–504.
- Chatterton, B. D. 1975 A commensal relationship between a small filter feeding organism and Australian Devonian spiriferid brachiopods. *Paleobiology* **1**, 371–378.
- Chen, J. Y. 2004 *The dawn of the animal world*. Nanjing, China: Jiangsu Science and Technology Press p. 366. [In Chinese.]
- Chen, J. Y. & Zhou, G. Q. 1997 Biology of the Chengjiang fauna. *Bull. Natl Mus. Nat. Sci.* **10**, 11–106.
- Davidson, T. 1888 A monograph of recent Brachiopoda. *Trans. Linn. Soc. Lond. (Ser. 2, Zool.)* **4**, 183–248. (doi:10.1111/j.1096-3642.1888.tb00657.x) pl 26–30.
- Dzik, J., Zhao, Y. L. & Zhu, M. Y. 1997 Mode of life of the Middle Cambrian Eldonoid lophophorate *Rotadiscus*. *Palaeontology* **40**, 385–396.
- Emig, C. C. 2000 Ecology of inarticulated brachiopods. In *Treatise on invertebrate paleontology. Part H. Brachiopoda, revised*, vol. 1 (ed. P. A. Selden), pp. 2580–2590. Boulder, CO: The Geological Society of America; Lawrence, KS: The University of Kansas.
- Han, J., Zhang, Z. F. & Liu, J. N. 2004 Taphonomy and ecology of the introverts in Chengjiang fauna. *J. Northw. Univ. (Natural Science edition)* **34**, 207–212.
- Holmer, L. E. & Caron, J. B. 2006 A spinose stem group brachiopod with pedicle from the Middle Cambrian Burgess Shale. *Acta Zool.* **87**, 273–290. (doi:10.1111/j.1463-6395.2006.00241.x)
- Hou, X. G., Bergström, J., Wang, H. F., Feng, X. H. & Chen, A. L. 1999 *The Chengjiang fauna: exceptionally well-preserved animals from 530 million years ago*, p. 80. Kunming, China: Yunnan Science and Technology Press. [In Chinese with English summary.]
- Hou, X. G., Aldridge, R. J., Bergström, J., Siveter, D. J., Siveter, D. J. & Feng, X. H. 2004 *The Cambrian fossils of Chengjiang, China: the flowering of early animal life*, p. 233. Malden, MA: Blackwell.
- Hu, S. X. 2005 Taphonomy and palaeoecology of the Early Cambrian Chengjiang Biota from eastern Yunnan, China. *Berliner Paläobiologische Abhandlungen* **7**, 1–197.
- Jin, Y. G. 2005 Life styles of Early Cambrian brachiopods on mud substrate. *Acta Micropalaeontol. Sin.* **22**, 77.
- Jin, Y. G. & Wang, H. Y. 1992 Revision of the Lower Cambrian brachiopod *Helimedusa* Sun and Hou, 1987. *Lethaia* **25**, 35–49. (doi:10.1111/j.1502-3931.1992.tb01790.x)
- Lescinsky, H. L. 1997 Epibiont communities: recruitment and competition on North American Carboniferous brachiopods. *J. Paleontol.* **71**, 34–52.
- Lescinsky, H. L. 2000 Epibionts. In *Palaeobiology II* (eds D. E. G. Briggs & P. R. Crowther), pp. 460–464. Oxford, UK: Blackwell Scientific Publications.
- Li, G. & Holmer, L. E. 2004 Early Cambrian lingulate brachiopods from the Shaanxi Province, China. *GFF* **126**, 193–211.
- Luo, H. L., Hu, S. X., Chen, L. Z., Zhang, S. S. & Tao, Y. H. 1999 *Early Cambrian Chengjiang fauna from Kunming region, China*. p. 129. Kunming, China: Yunnan Science and Technology Press. [In Chinese with English summary.]
- Peck, L. S., Meidlinger, K. & Tyler, P. A. 2001 Developmental and settlement characteristics of the Antarctic brachiopod *Lithyrella uva* (Broderip 1833). In *Brachiopods past and present* (eds C. H. C. Brunton, L. R. M. Cocks & S. L. Long), pp. 80–90. London, UK: Taylor & Francis.
- Pennington, J. T., Tamburri, M. N. & Barry, J. P. 1999 Development, temperature tolerance, and settlement preference of embryos and larvae of the articulate brachiopod *Laqueus californianus*. *Biol. Bull. Woods Hole* **196**, 245–256. (doi:10.2307/1542949)
- Pettersson Stolk, S., Holmer, L. E. & Caron, J. B. In press. First record of the brachiopod *Lingulella waptaensis* with pedicle from the Middle Cambrian Burgess Shale. *Acta Zool.*
- Pitrat, C. W. & Rogers, F. S. 1978 Spinocyrtia and its epibionts in the Traverse Group (Devonian) of Michigan. *J. Paleontol.* **52**, 1315–1324.
- Rong, J. Y. 1974 Cambrian brachiopods. In *Nanjing Institute of Geology, Academia Sinica, Handbook of Palaeontology and Stratigraphy of Southwest China*, pp. 113–114. Beijing, China: Sciences Press.
- Sutton, M. D., Briggs, D. E. G., Siveter, D. J. & Siveter, D. J. 2005 Silurian brachiopods with soft-tissue preservation. *Nature* **436**, 1013–1015. (doi:10.1038/nature03846)
- Wahl, M. 1989 Marine epibiosis. I. Fouling and antifouling—some basic aspects. *Mar. Ecol. Progr. Ser.* **58**, 175–189. (doi:10.3354/meps058175)
- Yuan, J. L. & Huang, Y. Z. 1994 Preliminary report on non-trilobite arthropods from Lower-Middle Cambrian Kaili Formation of southeastern Guizhou, South China. *Acta Palaeontol. Sin.* **33**, 329–334.
- Zapalski, M. K. 2005 Paleocology of Auloporina: an example from the Devonian of the Holy Cross Mts, Poland. *Geobios* **38**, 677–683. (doi:10.1016/j.geobios.2004.05.002)
- Zhang, X. L. & Hua, H. 2005 Soft-bodied fossils from the Shipai Formation, Lower Cambrian of the Three-Gorge area, South China. *Geol. Mag.* **142**, 699–709. (doi:10.1017/S0016756805000518)
- Zhang, Z. F., Han, J., Zhang, X. L., Liu, J. N. & Shu, D. G. 2003 Pediculate brachiopod *Diandongia pista* from the Lower Cambrian of South China. *Acta Geol. Sin. (English Edition)* **77**, 288–293.
- Zhang, Z. F., Shu, D. G., Han, J. & Liu, J. N. 2005 Morpho-anatomical differences of the Early Cambrian Chengjiang and recent lingulids and their implications. *Acta Zool.* **86**, 277–288. (doi:10.1111/j.1463-6395.2005.00211.x)
- Zhang, Z. F., Shu, D. G., Han, J. & Liu, J. N. 2006 New data on the rare Chengjiang (Lower Cambrian, South China) linguloid brachiopod *Xianshanella haikouensis*. *J. Paleontol.* **80**, 203–211. (doi:10.1666/0022-3360(2006)080[0203:NDOTRC]2.0.CO;2)
- Zhang, Z. F., Shu, D. G., Han, J. & Liu, J. N. 2007a A gregarious lingulid brachiopod *Longtancunella chengjiangensis* from the Lower Cambrian, South China. *Lethaia* **40**, 11–18.
- Zhang, Z. F., Shu, D. G., Emig, C. C., Zhang, X. L., Han, J., Liu, J. N., Li, Y. & Guo, J. F. 2007b Rhynchonelliformean brachiopods with soft-tissue preservation from the Lower

- Cambrian Chengjiang Lagerstätte of South China. *Palaeontology* **50**, 1391–1402. (doi:10.1111/j.1475-4983.2007.00725.x)
- Zhang, Z. F., Robson, S. P., Emig, C. C. & Shu, D. G. 2008 Early Cambrian radiation of brachiopods: a perspective from South China. *Gondwana Res.* **14**, 241–254. (doi:10.1016/j.gr.2007.08.001)
- Zhu, M. Y., Zhang, J. & Li, G. 2001 Sedimentary environments of the Early Cambrian Chengjiang biota: sedimentology of the Yu'an-shan Formation in Chengjiang Country, eastern Yunnan. *Acta Palaeontol. Sin.* **40**, 80–105.
- Zhu, M. Y., Li, G. X., Hu, S. X. & Zhao, F. C. 2005 Ediacaran–Cambrian boundary stratigraphy at Meishucun, Jinning County, and fossil quarries of the Early Cambrian Chengjiang Biota near Haikou, Kunming city, Yunnan, China. In *Cambrian system of China and Korea* (eds S. C. Peng, L. E. Babcock & M. Y. Zhu), pp. 30–36. China: University of Science and Technology of China Press.