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

Zhifei Zhang1,*, Jian Han1, Yang Wang1, Christian C. Emig2 and Degan Shu1

1Early Life Institute, State Key Laboratory of Continental Dynamics, Northwest University, Xi’an 710069, People’s Republic of China
2Brachnet 20, Rue Chaix, 13007 Marseille, France

The classic Chengjiang Lagerstätte (Lower Cambrian, Atdabanian stage: Yu’anshan 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 botsfordiid *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’anshan member (*Boreodichnia* zone) of the Lower Cambrian Helinpu 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
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 populously 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, North West 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 (lesser than 2 mm) sometimes with some relief along the shell commissure.

(a) The epibiotic 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 Holomeda orienta (Jin & Wang 1992). Archotuba fossils are usually unornamented, but a dark axial lineation along the middle part of some tubes
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 posterolateral 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 *Diandogia* 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 *Botsoforia 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 (less 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 *Inquilius haikouensis* (also see Han et al. 2004), and on eldoionid discs from the Lower-Middle Cambrian Kaili biota (Yuan & Huang 1994; Dzik et al. 1997). The ovoids on the Middle Cambrian eldoionid discs were initially interpreted as bradoriid ostracodes, i.e. *Ghuandianella? 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 autocology 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 2c), 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-epibiotic 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 sedimentary 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 tropic 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. orienta* (Jin & Wang 1992) could have occupied the lowest ecological niche near
the sediment-water interface, as evidenced by the overgrowth with its epibionts. ‘Lingulella’ chengjiangensis and Lingulellotreta 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 (07YB01) 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

![Figure 3](http://rsbp.royalsocietypublishing.org/)

**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 2e. (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.
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


Chen, J. Y. 2004 The dawn of the animal world. Nanjing, China: Jiangsu Science and Technology Press p. 366. [In Chinese.]


Li, G. & Holmer, L. E. 2004 Early Cambrian lingulate brachiopods from the Shaanxi Province, China. GFF 126, 193–211.


