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Cornulitid epibionts on brachiopod shells from the Late Ordovician (middle Ashgill) of East China

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Abstract. This is the first record of *Cornulites* sp. as an epibiont on brachiopods from the middle Ashgill, Late Ordovician, of the South China Palaeoplate. Twenty-one cornulitid specimens were found attached to the brachiopod shells of *Altaethyrella zhejiangensis* and *Ovalospira dichotoma*. Both the location of cornulitids and their orientation on the brachiopod shells indicate a possible commensal relationship between the cornulitids and their hosts.

Key words: cornulitids, brachiopods, Ordovician, South China.

INTRODUCTION

Traditionally, cornulitids constitute a family of tubicolous fossils with unknown zoological affinities (Fisher 1962), comprising four genera: *Cornulites* Schlotheim, 1820, *Cornulitella* (Nicholson, 1872a), *Conchicolites* Nicholson, 1872b, and *Kolihaia* Prantl, 1944. The last genus was later removed from cornulitids and placed among the cnidarians (Kříž et al. 2001). However, a new Devonian cornulitid genus with the reticulate ornamentation, *Reticornulites* Lardeux et al., 2003, has been described from the Armorican Massif. Recently also a new Silurian cornulitid genus, *Septalites* Vinn, 2005, was reported from the Silurian of Gotland, Sweden.

Cornulitids have been affiliated with annelids, tentaculitids, microconchids, cnidarians, molluscs, bryozoans, and phoronids (Fisher 1962; Bouček 1964; Blind 1972; Dzik 1991; Vinn & Mutvei 2005; Vinn 2005, 2006). Based on the bulbous egg-shaped morphology of the initial chamber of cornulitids, molluscan (Blind 1972) and bryozoan (Dzik 1991) affinities have been supposed alternatively. Dzik (1991) also described two new cornulitid genera, *Cornulitozoon* Dzik, 1991 and *Opatozoon* Dzik, 1991 from the Ordovician and Silurian of Poland, respectively. Data from recent studies of shell ultrastructure and cornulitid ontogeny suggest a tentaculitid, microconchid, or bryozoan rather than molluscan or annelid affinity (Vinn & Mutvei 2005; Vinn 2005, 2006). Presumably cornulitids were phylogenetically most closely linked to phoronids (Vinn 2005, 2006; Taylor & Vinn 2006).

Cornulitids commonly occur as encrusters on various invertebrate skeletons and shells in the Upper Ordovician of North America (Morris & Rollins 1971; Richards 1974; Morris & Felton 1993, 2003). The palaeoecology of Late Ordovician cornulitids has been well studied in North America (Morris & Rollins 1971; Morris & Felton 1993; Holland et al. 2001; Morris & Felton 2003). They have often been found on brachiopod shells and are thought to have benefited on the feeding currents of their hosts (Hoare & Steller 1967; Schumann 1967; Kesling & Chilman 1975; Sparks et al. 1980). Cornulitids first appeared in the late Middle Ordovician of North America (Richards 1974) and Baltoscandia (Öpik 1930; personal observations by O. Vinn), and became globally distributed in the Late Ordovician (Fisher 1962; Richards 1974). The youngest known cornulitids are of Carboniferous age (Fisher 1962; Richards 1974).

Cornulitids have hitherto been unknown in the Ordovician of China. A Late Ordovician brachiopod collection of close to 5000 specimens from the upper part of the Xiazhen Formation at Guanzhai of Xiazhen, Yushan County, northeastern Jiangxi Province, East China (Fig. 1) was examined here in search of encrusting cornulitids. The aim of this paper is to

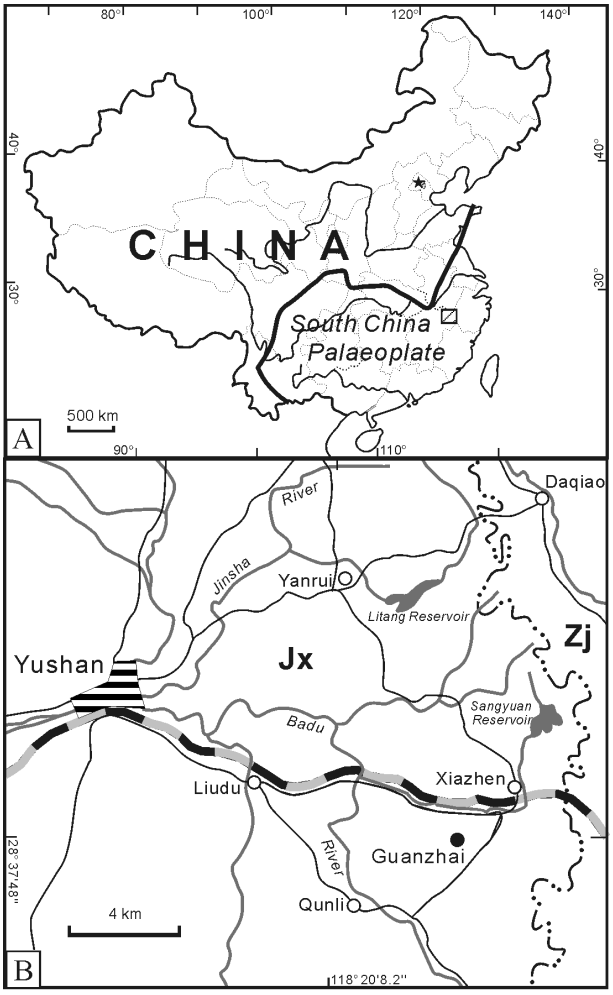

Fig. 1. Location map of the study area. (A) Map of China, with Beijing marked by a star and the study area in East China by a streaked square. (B) Enlarged map of the study area (Guanzhai of Xiazhen), Yushan County, northeastern Jiangxi Province, marked by a solid circle. Jx, Jiangxi Province; Zj, Zhejiang Province.

report the occurrence of encrusting cornulitids on the Ordovician brachiopods from the South China Palaeoplate, and to discuss the palaeoecological implications of their commensal relationship.

GEOLOGICAL SETTING AND THE MATERIAL

The study area of this paper is the northeastern Jiangxi Province, East China (Fig. 1). Its geology (e.g. Zhan & Fu 1994; Zhan & Cocks 1998; Wu 2000, 2003), palaeontology, and palaeoecology (e.g. Lin & Zou 1977; Liu et al. 1983; Rong et al. 1994; Zhan & Rong 1994, 1995; Rong & Zhan 1996; Zhan & Cocks 1998; Zhan et al. 2002) is well studied. The South China Palaeoplate was a peri-Gondwana terrane (Cocks & Torsvik 2004) in the Early and most of the Middle Ordovician. It is divided into the Yangtze Platform, the Jiangnan Transitional Belt, and the Zhujiang Basin in northwest to southeast direction. The study material has been collected from the calcareous mudstones of the upper part of the Xiazhen Formation near Guanzhai village (Collection YS), Xiazhen (Fig. 2). The collection includes 4786 loose, complete shells of brachiopods: *Altaethyrella zhejiangensis* Wang, 1964 (Wang & Jin 1964) (4508 specimens), *Sowerbyella sinensis* Wang, 1964 (Wang & Jin 1964) (103 specimens), *Mimella zhejiangensis* Liang, 1983 (Liu et al. 1983) (102 specimens), *Ovalospira dichotoma* Fu, 1982 (34 specimens), *Antizygospira liquanensis* Fu, 1982 (26 specimens), *Triplesia zhejiangensis* Liang, 1983 (Liu et al. 1983) (6 specimens), *Strophomena* sp. (6 specimens), and *Eospirigerina yulangensis* Liang, 1983 (Liu et al. 1983) (1 specimen). Careful inspection of all the specimens under a stereomicroscope revealed 21 specimens of cornulitids encrusting the brachiopod shells: two associated with *Ovalospira dichotoma* (e.g. Fig. 3D) and the others with *Altaethyrella zhejiangensis* (e.g. Fig. 3A–C).

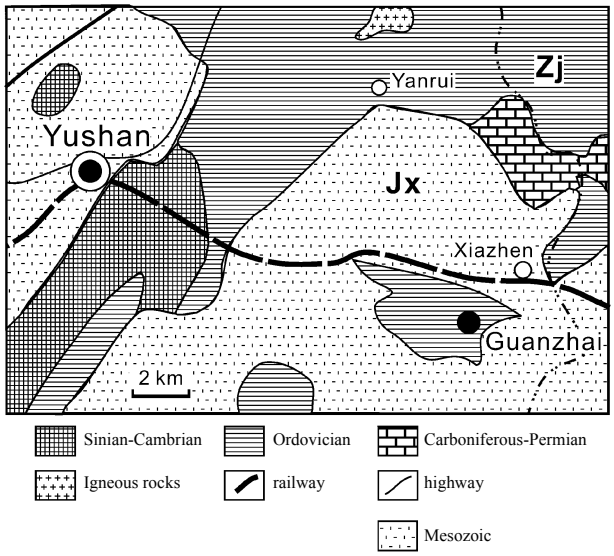

Fig. 2. Simplified geological map of the study area in eastern Yushan County, northeastern Jiangxi Province (Zhan et al. 2002). Jx, Jiangxi Province; Zj, Zhejiang Province.

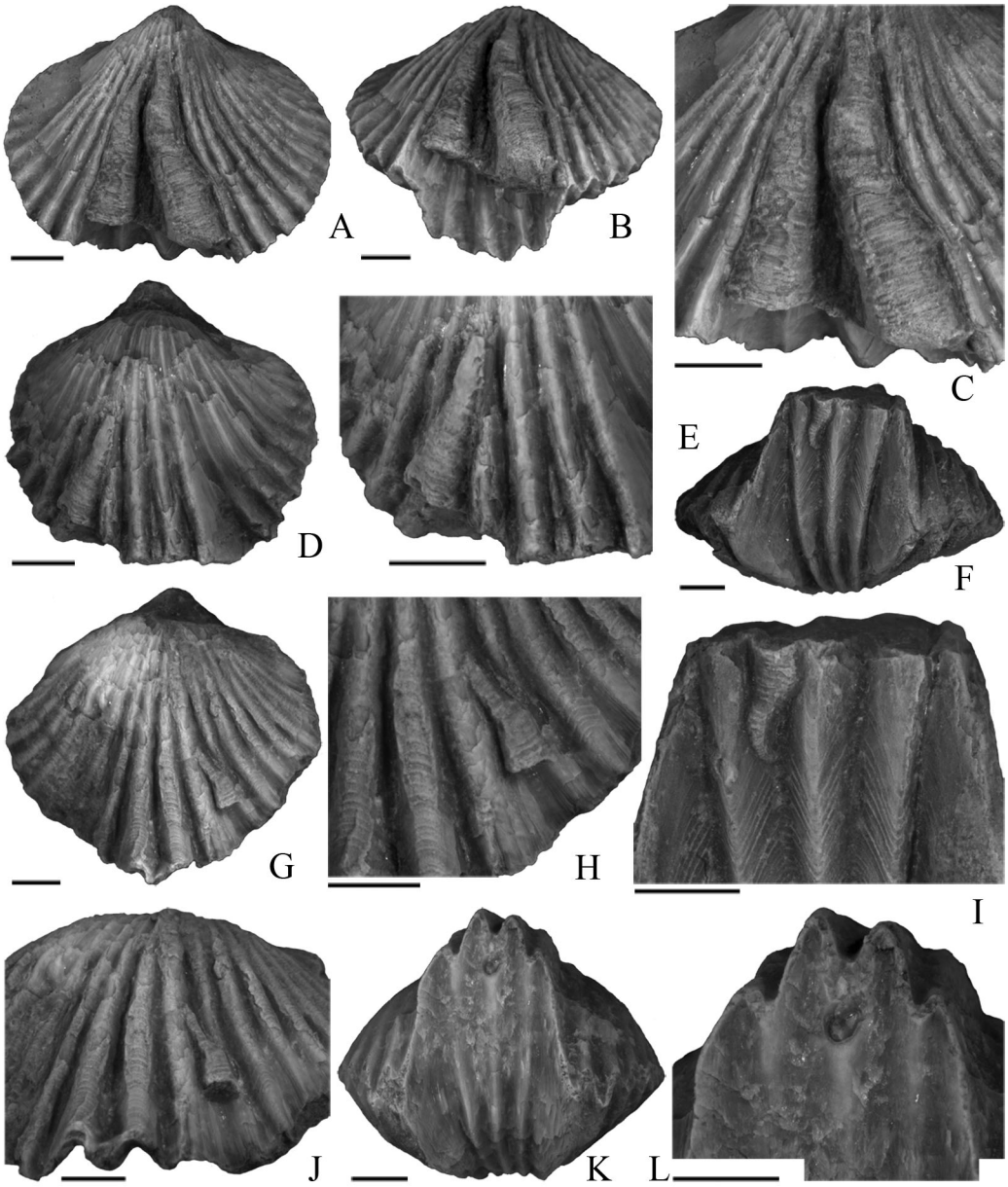

Fig. 3. A–J, *Cornulites* sp., upper Xiazhen Formation, middle Ashgill (Upper Ordovician), Guanzhai of Xiazhen, Yushan County, northeastern Jiangxi Province: A–C, NIGP 140560, two specimens oriented towards the anterior commissure in the ventral sulcus of the brachiopod *Altaethyrella zhejiangensis* Wang, 1964 (Wang & Jin 1964); D, E, NIGP 140561, one specimen on the left side of the dorsal fold of *Altaethyrella zhejiangensis*, oriented towards the anterior commissure; F, G, NIGP 140562, one smaller specimen in the ventral sulcus of *Altaethyrella zhejiangensis*, oriented towards and close to the brachiopod anterior commissure; H–J, NIGP 140563, one small specimen on the right side of the dorsal fold of the brachiopod *Ovalospira dichotoma* Fu, 1982, oriented towards the anterior commissure. **K**, **L**, *Oichnus* boring in the ventral sulcus near the anterior commissure of *Altaethyrella zhejiangensis* Wang, 1964 (Wang & Jin 1964), NIGP 140564, upper Xiazhen Formation, middle Ashgill (Upper Ordovician), Guanzhai of Xiazhen, Yushan County, northeastern Jiangxi Province. Scale bars = 2 mm.

PALAEOECOLOGICAL IMPLICATIONS

The brachiopod collection studied here (Collection YS) has already been recognized as the *Altaethyrella zhejiangensis* community and assigned to a relatively shallow-water environment (BA2) based on a synecological analysis (Zhan et al. 2002, p. 461). Ziegler et al. (1968) found that cornulitids are common in the late Llandovery *Lingula* community in Britain, Norway, and North America, which indicates a near-shore, shallow-water environment, corresponding to lower BA1 to upper BA2 (Boucot 1975). Thus, the discovery of cornulitids in the locality of the *Altaethyrella zhejiangensis* community could serve as a further support for the palaeoecological concept of Zhan et al. (2002).

Cornulitids were found on shells of both *Altaethyrella zhejiangensis* (19 specimens) and *Ovalospira dichotoma* (two specimens), which shows that they may have favoured coarsely ribbed shells because none occurred on finely costellate (e.g. *Mimella zhejiangensis*, *Sowerbyella sinensis*) or smooth shells (e.g. *Triplesia zhejiangensis*). However, the shells of *Antizygospira liquanensis* are also coarsely ribbed but lack cornulitids, probably because of their very small sizes (normally <5–6 mm, Zhan & Cocks 1998). The frequency of *Cornulites* sp. on *Altaethyrella zhejiangensis* (one *Cornulites* per 237 brachiopod specimens) and *Ovalospira dichotoma* (one *Cornulites* per 17 brachiopod specimens) varies by over a magnitude. Despite the very different sizes of the *Altaethyrella zhejiangensis* (4508 specimens) and *Ovalospira dichotoma* (34 specimens) collections, this may reflect host specificity of *Cornulites* sp.

All specimens (21) described here are attached to the central part of the brachiopod shell, particularly within the ventral sulcus (14 out of 21, Table 1). However, in fossil material one can study only the recruitment patterns, and not settlement patterns. For example, the apparent preferential settlement of *Cornulites* larvae in

Table 1. Location of *Cornulites* sp. on brachiopods and their measurements (length of the shell and the diameter at the aperture). AC – *Cornulites* at the anterior commissure of the brachiopod; NAC – *Cornulites* not at the anterior commissure of the brachiopod

Cornulites specimen	Length of the shell, mm	Diameter at the aperture, mm	Location of the shell aperture	Shell cemented to the dorsal valve D, to the ventral valve V (in sulcus S)
1	8.0	2.0	AC	V (S)
2	9.5	2.1	AC	V (S)
3	2.5	0.9	AC	D
4	2.5	1.0	NAC (but oriented to the commissure)	D
5	2.1	0.9	AC	V (S)
6	3.0	1.0	AC	D
7	–	2.0	AC	V (S)
8	4.0	1.2	AC	V (S)
9	–	–	AC	V (S)
10	–	1.1	AC	D
11	–	1.9	AC	D
12	–	–	AC	V (S)
13	3.0	1.0	NAC	D
14	2.0	0.6	AC	V (S)
15	–	2.0	AC	V (S)
16	–	–	AC	V (S)
17	2.3	0.6	NAC	V (S)
18	2.0	0.7	NAC	D
19	3.2	0.9	NAC	V (S)
20	–	0.8	AC	V (S)
21	2.6	1.0	AC	V (S)

–, no data.

the sulcus of brachiopods may actually result from early loss of those specimens that settled on more exposed locations (see Taylor & Wilson 2003). The *Cornulites* specimens studied have a regular orientation: apertures opened towards the anterior of the brachiopod. Based of the ecological study of various modern brachiopods, it is now commonly accepted that brachiopods have a separated inhalant and exhalant feeding mechanism (Chuang 1956; LaBarbera 1984). The inhalant water streams are located on both sides of the shell, and the exhalant water stream is in the central part of shell. This enhances greatly the feeding efficiency of a brachiopod (Peck et al. 1997). The larvae of Chinese Late Ordovician cornulitids were presumably attached to the shells of living brachiopods and had a commensal relationship with their host because of their common orientation and location near the brachiopod anterior commissure. Their location in the middle of the brachiopod shells along coarse ribs was advantageous because: (1) the brachiopod sulcus or folds served as a shelter to resist the relatively strong water current, (2) cornulitids could have fed on nutrient remnants from the host or even on the brachiopod excrement in the rhythmic excurrent water stream.

A symbiotic association of *Cornulites*, gastropods, and crinoids is also known from the Upper Ordovician of North America (Morris & Felton 1993). Ectoparasitic or commensal *Cornulites* on Devonian brachiopods (Hoare & Steller 1967; Schumann 1967; Kesling & Chilman 1975; Sparks et al. 1980) are located similarly to the Upper Ordovician Chinese *Cornulites*. Some Silurian cornulitids have rather consistent radial orientation and marginal positioning on rhynchonellid brachiopods and could represent the early stage of evolving parasitic behaviour (Richards 1974). *Cornulites* attached to the Late Ordovician brachiopod *Zygospira* are commonly oriented from the pedicle-beak area towards the anterior commissure, and their relationship has been interpreted as symbiotic in which *Cornulites* may have utilized the feeding currents set up by the host (Morris & Rollins 1971). A similar relationship between *Cornulites* and the host brachiopod presumably existed also in the Late Ordovician (middle Ashgill) of the South China Palaeoplate.

In addition to the cornulitid encrustation, two specimens of *Altaethyrella zhejiangensis* have *Oichnus* borings penetrating the pedicle valves at 90 degrees close to the anterior commissure (Fig. 3E), and two specimens of the same brachiopod species are encrusted by bryozoans.

Late Ordovician cornulitids have been hitherto known from the palaeocontinents of Laurentia, Baltica, Avalonia, and Gondwana (Fisher 1962; Richards 1974; Gabbott 1999; personal observations by O. Vinn). The discovery of *Cornulites* in the mid Ashgill of the South China Palaeoplate adds new evidence of global distribution of cornulitids in the Late Ordovician at least at low latitudes.

SYSTEMATIC PALAEONTOLOGY

Phylum *incertae sedis*
Class TENTACULITA Bouček, 1964
Order CORNULITIDA Bouček, 1964
Family CORNULITIDAE Fisher, 1962
Genus *Cornulites* Schlotheim, 1820

Cornulites sp.
Figure 3A–J; Table 1

Description. Minute straight or slightly curved conical shells attached to the substrate in their whole length. Shells slowly increasing in diameter anteriorly. External surface covered by thin but prominent perpendicular ridges formed by the annuli, moderately developed longitudinal striae are present with the interval of 0.05–0.06 mm in the adult portion of the shell. Annuli of the shell are relatively irregular in shape. Five to six perpendicular ridges are counted per one mm. Shells have a relatively thin wall, 0.1–0.2 mm thick at the diameter of 2.0 mm. Cross-section of the shell is circular. Internal surface covered by the annuli. Maximum shell length of the shells is 9.5 mm and maximum width 2.1 mm.

Material examined. 21 specimens (figured specimens are stored in the Nanjing Institute of Geology and Palaeontology, NIGP140560–NIGP140564, and all the spare ones are kept by Renbin Zhan).

Discussion. This Chinese cornulitid species is assigned to *Cornulites* because of the presence of longitudinal striae characteristic of the genus (Fisher 1962; Vinn & Mutvei 2005). *Cornulites* sp. is somewhat similar to *C. semiapertus* Öpik, 1930 (p. 9, figs 5–7, pl. 1, fig. 1) from the lower Upper Ordovician (Caradoc) of Estonia,

but differs in having finer and less regular perpendicular ridges. It differs also in having faint longitudinal striae, which seem to be lacking in *C. semiapertus* (personal observations by O. Vinn). The sculpture of the studied specimens is not well enough preserved. Additional material should be studied to assign the described *Cornulites* sp. to any particular species of *Cornulites* or to establish a new species.

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Kornuliitidest epibiondid Ida-Hiina Ülem-Ordoviitsiumi käsijalgsetel

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On kirjeldatud esmakordselt kornuliitidest epibionte Hilis-Ordoviitsiumi vanustel käsijalgsetel Lõuna-Hiina paleokontinendilt (Jiangxi provintsist Ida-Hiinast). Kornuliidid kinnitusid tõenäoliselt elusate käsijalgsete *Altaethyrella zhejiangensis* ja *Ovalospira dichotoma* karbi kaanele, mida tõestab nende orienteeritus.