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Morphology and palaeoecology of a new edrioblastoid from the Furongian of China

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A new edrioblastoid *Cambroblastus guolensis* is described from the Furongian (late Cambrian) Sandu Formation (South China). This represents the second occurrence of a Cambrian edrioblastoid, and the first ever reported from Asia, extending the palaeogeographic range of this very rare echinoderm grade. Surprisingly it preserves a complete stem and a distal holdfast suggesting edrioblastoids were hard substrate attachers living in soft bottom quiet environments.

Introduction

Edrioblastoids are an extremely rare grade of Lower Palaeozoic echinoderms known only from a limited number of species ranging from the late Cambrian to the Late Ordovician. They displayed a globular theca with five recumbent ambulacra constructed with large, biserial and exposed flooring plates and large, simple or complex cover plates. All known species have a polyplated stem to elevate the theca above the substrate, but their attachment mechanism is still unknown (Mintz 1970; Smith and Jell 1990; Guensburg and Sprinkle 1994; Guensburg et al. 2010).

The first edrioblastoid described in the literature was *Astrocystites ottawaensis* Whiteaves, 1897 from the Late Ordovician of North America. However, because of its unusual morphology, *Astrocystites* was successively interpreted as a primitive cystoid (Whiteaves 1897), an edrioasteroid (Bather 1900, 1914; Piveteau 1953), a blastoid (Hudson 1925), an intermediate form between eocrinoids and blastoids (Hudson 1927), or as a member of a separate class (Edrioblastoidea) closely related either to blastoids (Fay 1962, 1967), eocrinoids (Mintz 1970), or echinozoans (Sprinkle 1973). All recent cladistic analyses indicate that edrioblastoids are a derived group of edrioasterid edrioasteroids closely related to cyathocystids (Smith and Jell 1990; Guensburg and Sprinkle 1994; Sumrall et al. 2013).

Since the original description of *A. ottawaensis,* only few other occurrences of edrioblastoids have been reported. They include *Cambroblastus enubilatus* Smith and Jell, 1990 from the late Cambrian of Australia, and *Lampteroblastus hintzei* Guensburg and Sprinkle, 1994 from the early Floian (Early Ordovician) of Utah. Late Ordovician occurrences include *Astrocystites distans* from Australia, based on poorly preserved specimens (Webby 1968; Webby et al. 2000), as well as possible isolated remains from Virginia (Sprinkle 1973) and Sweden (Paul 1976).

Here, a new species of *Cambroblastus* is described from the Furongian of China. This record extends the palaeogeographic distribution of the first edrioblastoids. The aims of this brief report are to analyze and describe the morphology of *Cambroblastus* sp. nov., and for the first time, to provide evidences for attachment strategies in late Cambrian edrioblastoids.

Institutional abbreviations.—NIGPAS, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, China.

Geological setting and palaeoenvironment

The specimen was collected from mudstone and marl beds of the Sandu Formation, Guole Town, Jingxi County, Guangxi Province, southwest China (Fig. 1). Guole Town lies in Yangtze Area of South China Region. The Yangtze Area represented a shallow shelf during Cambrian time (Zhou and Zhen 2008). In addition to *Cambroblastus* sp. nov., the Sandu Formation has yielded a diverse associated fauna comprising aglaspidids, brachiopods (e.g., *Billingsella*, *Guoleella*, *Palaeostrophia*, *Plectotrophia*), other echinoderms (e.g., "*Phyllocystis*" *jingxiensis*), graptolites (e.g., *Callograptus*, *Dyctionema*), hyolithids, trilobites (e.g., *Akoldinioidia, Dictyella*, *Guangxiaspis*, *Shergoldia*, *Sinosaukia*, *Tamdaspis*), and undescribed palaeoscolecids (Han and Chen 2008; Zhan et al. 2010; Lerosey-Aubril et al. 2013). Co-occurring trilobites indicate an age equivalent to the *Probinacunaspis nasalis–Peichiashania hunanensis* Zone of northwestern Hunan, and thus part of the Furongian, Stage 9 (Zhu et al. 2007, 2010). Abundant articulated trilobites strongly suggest rapid burial, likely as the result of an obrution event (Zhu et al. 2010). These taphonomic conditions probably also explain the exquisite preservation of echinoderms.

Systematic palaeontology

Phylum Echinodermata Bruguière, 1791 (ex Klein, 1734)

Class Edrioasteroidea Billings, 1858

Order Edrioblastoida Fay, 1962

Genus *Cambroblastus* Smith and Jell, 1990

Type species: *Cambroblastus enubilatus* Smith and Jell, 1990; Chatsworth Limestone, Furongian; Queensland, Australia.

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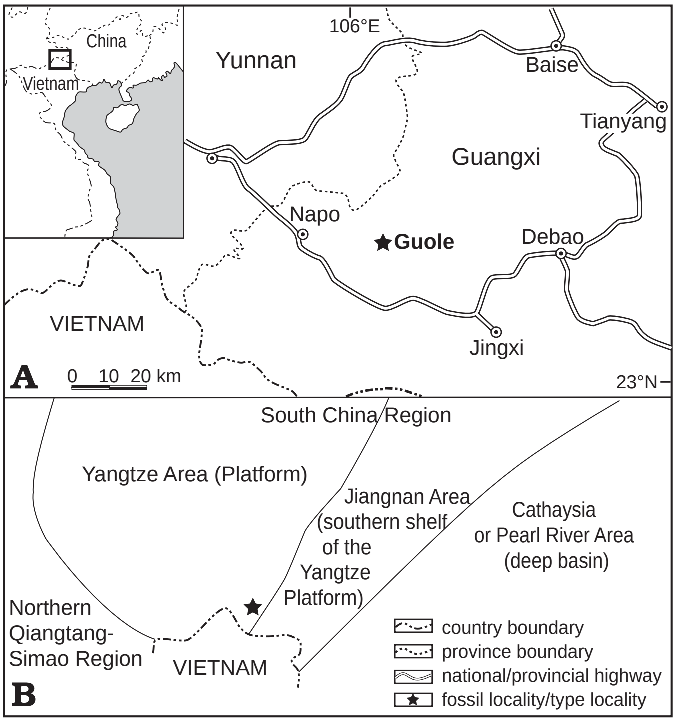


Fig. 1. Location (**A**) and geological setting (**B**) of the studied site (modified from Zhou et al. 2008).

Emended diagnosis.—An edrioblastoid with irregular, polyplated stem, distal polyplated and expanded holdfast, 3–4 irregular circlets of strongly ornamented thecal plates, ambulacra composed of large, exposed flooring plates and complex cover plates.

Discussion.—*Cambroblastus enubilatus* was originally described based on poorly preserved material from the Furongian of Australia, which prevented the detailed observation of several aspects of its morphology (Smith and Jell 1990). The specimen described herein from the Furongian of South China shows many similarities with *C. enubilatus*, and is thus assigned to the same genus: same plating patterns for the stem and theca, comparable morphology and extent of ambulacra, similar arrangement and size of ambulacral elements (flooring plates and primary cover plates). Moreover, the exquisite preservation of the Chinese material of *Cambroblastus* makes it possible to modify the original diagnosis of the genus, so as to accommodate additional information both on the structure of ambulacra and the morphology of the holdfast. For example, Smith and Jell (1990) suggested that ambulacra were roofed by only two series (left and right) of large, alternating cover plates. The better preserved Chinese material allows the identification, perradially, of two additional series of smaller (secondary) cover plates.

The improved knowledge of the morphology of *Cambroblastus* makes it possible to compare it with unprecedented details with the two other known genera of edrioblastoids: *Astrocystites* and *Lampteroblastus*. *Cambroblastus* differs from *Astrocystites* in both ambulacral construction and stem morphology. In *Cambroblastus*, ambulacra are made of a reduced number of large, distinct flooring plates roofed by multiple series of cover plates, whereas in *Astrocystites*, ambulacra comprise numerous, tightly sutured flooring plates and one single biseries of elongate primary cover plates. In *Cambroblastus*, stem meres are almost as high as wide, whereas they are more elongate and much wider than high in *Astrocystites*. Main differences between *Cambroblastus* and *Lampteroblastus* concern the shape and ornamentation of the theca, the extent and structure of ambulacra, and the stem morphology. In *Cambroblastus*, the theca is globular, and composed of numerous plates ornamented with multiple delicate ridges. In *Lampteroblastus*, the theca is more cylindrical, and composed of a reduced number of plates, each ornamented with strong primary ridges. The ambulacra are significantly more extensive in *Cambroblastus* than in *Lampteroblastus*, and they comprise four series of cover plates (instead of two in *Lampteroblastus*). Finally, the stem is short and tapering in *Lampteroblastus*, whereas it is long and cylindrical, with a distal expanded holdfast in *Cambroblastus*.

The presence of multiple cover plates series in *Cambroblastus* is probably a plesiomorphic feature shared with other primitive edrioasteroids (e.g., *Cambraster*, *Edriodiscus*, *Kailidiscus*, *Stromatocystites*).

Cambroblastus guolensis sp. nov.

Figs. 2, 3.

Etymology: Referring to the town of Guole (China), where the holotype was collected.

Holotype: NIGPAS156159, a single specimen with both part and counterpart preserved as natural mould in a yellow brownish mudstone. All parts are well preserved with the exception of the summit and anal pyramid.

Type locality: Daba Village, Guole Town, Jingxi County, Guangxi Province, southwest China.

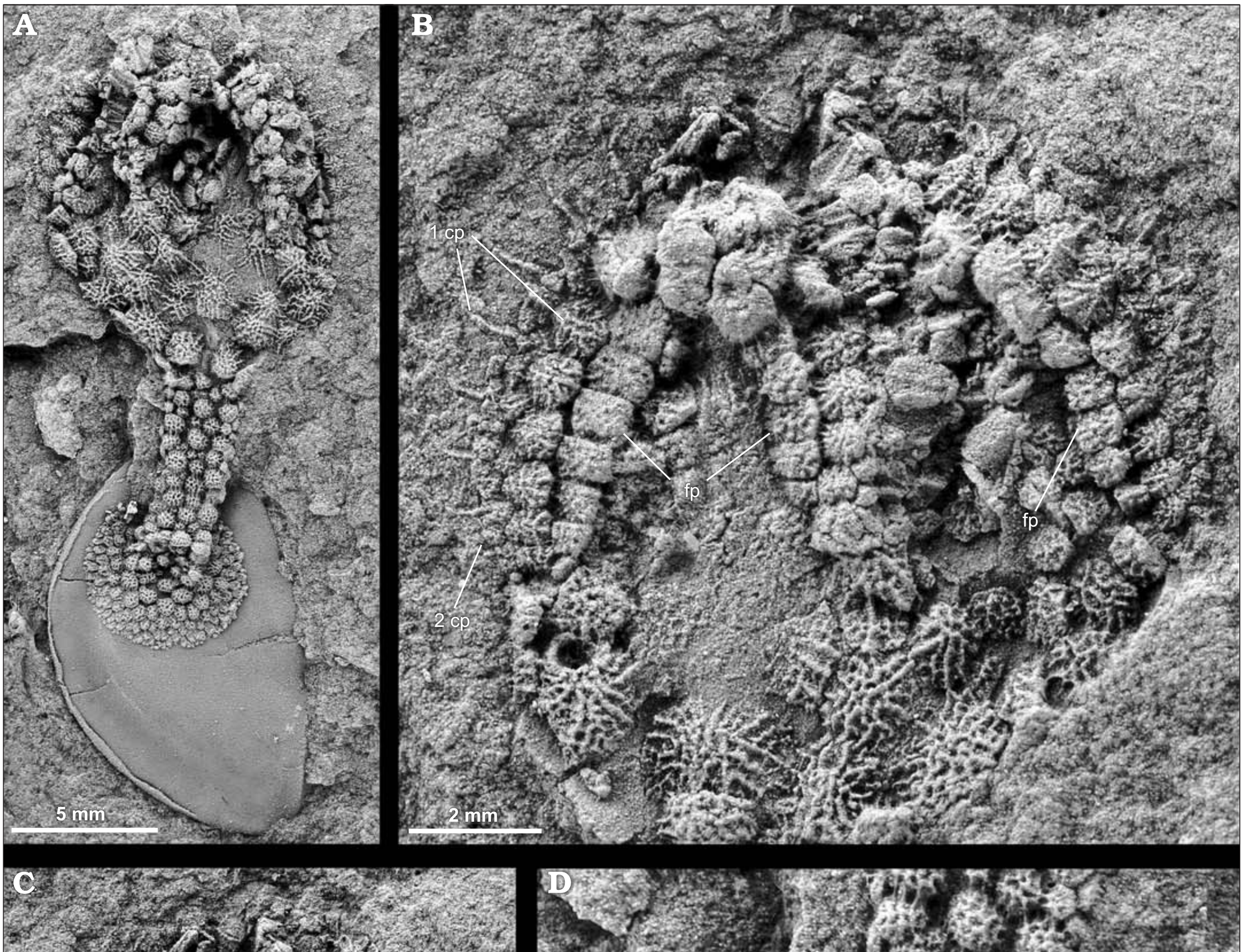
Type horizon: Sandu Formation, Furongian, late Cambrian.

Material.— Holotype only.

Diagnosis.—A species of *Cambroblastus* with widely exposed flooring plates, and a distal holdfast composed of numerous elements, smaller than those of the stem.

Description.—Theca of holotype slightly flattened, about 11 mm high and 10 mm large (at widest diameter). Theca bulb-shaped, with large oral area and very wide ambulacra. About 80 polygonal thecal plates exposed on both part and counterpart. Thecal plates large (1 to 1.5 mm in diameter), with central elevated area, ornamented with a series of prominent ridges connecting adjacent plates. Ridges about 4 to 5 per plate side, relatively straight across plate sutures, more irregular towards central elevated areas of thecal plates. Hexagonal "deltoid" plates in interambulacral position, in contact and along adjoin-

Fig. 2. Holotype of edrioblastoid edrioasteroid *Cambroblastus guolensis* sp. nov. (NIGPAS156159) from the Furongian (late Cambrian) of China. **A**, **C**. General view of the specimen attached to a trilobite pygidium, showing the division of the body into theca, stem, and expanded distal holdfast. **B**. Detail of the upper part of theca showing three ambulacra. Note the disposition of large exposed flooring plates and multiple cover plates. **D**. Detail of the distal stem and polyplated holdfast. All photographs are from latex casts whitened with NH_4Cl sublimated. Abbreviations: fp, flooring plates; 1cp, primary cover plates; 2cp, secondary cover plates. →


A
B
C
D
5 mm
2 mm
2 mm
2 mm
1 cp
2 cp
fp
fp

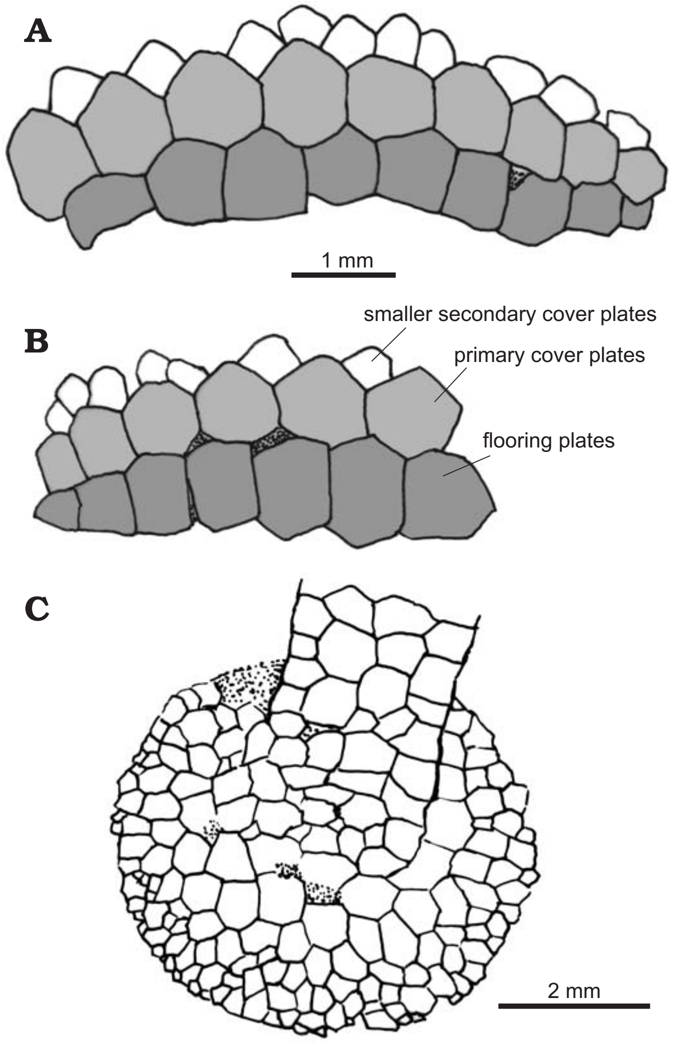


Fig. 3. Camera lucida drawings of ambulacra and distal stem and holdfast. **A**, **B**. Ambulacral construction of *Cambroblastus guolensis* sp. nov. showing flooring plates, primary cover plates, and smaller secondary cover plates. **C**. Distal part of the polyplated stem that ends in a distal expanded holdfast composed of minute elements cemented to a trilobite fragment.

ing ambulacra. Deltoids with straight adoral region and wider distally. At stem insertion, aboral part of theca comprising at least five modified plates, each with aborally invaginated borders and a facet for insertion of stem plates.

Five wide ambulacra made of two series of large, exposed flooring plates and multiple sets of large cover plates. Flooring plates hexagonal, transversally elongate proximally, more massive and progressively decreasing in size distally. Perradial suture between opposite series of flooring plates forming a zigzag pattern. Two series of primary cover plates, abradially in contact with underlying flooring plates. Each primary cover plate articulated to one flooring plate. Primary cover plate and associated flooring plate approximately of same size. Longitudinal rib of unknown function on internal side of each (primary?) cover plate. Adradially, two series of small, secondary cover plates alternating with primary cover plates. Secondary cover plates about twice smaller than primary ones. Perradial contact between opposite series of secondary cover plates forming a zigzag pattern. Both cover and flooring plates coarsely ornamented.

Transition between theca and stem relatively sharp, with large, polygonal, aboral thecal plates directly in contact with small, proximal-most stem elements. Stem relatively elongate, cylindrical, with expanded holdfast for attachment at distal extremity. Stem and holdfast both made of numerous, small, similar, polygonal, undifferentiated plates, about as wide as long. Stem elements showing no clear organisation proximally, but longitudinally aligned into vertical rows distally. Adjacent stem elements showing no clear transverse pattern (e.g., rows). New (smaller) stem plates added mainly in proximal region, apparently anywhere along sutures between larger elements. Holdfast circular in shape, wide (5.5 mm), cemented to trilobite fragment in holotype. Holdfast elements rapidly decreasing in size distally, and forming a tesselate, unorganised pavement.

Epispires (and other respiratory structures) absent. Periproct, gonopore, and hydropore not observed. Precise arrangement of oral plates also poorly documented on single available specimen.

Discussion.—A proper comparison of *Cambroblastus guolensis* with *C. enubilatus* is difficult, because of their different types of preservation. The Australian material is silicified and preserved in three dimensions in limestone, whereas the Chinese specimen is mouldic, flattened, slightly collapsed, and preserved in shale. Consequently, the original shape of the theca is better captured in the Australian material, but finer details (e.g., precise plate pattern, ornamentation) are obscured by the silicification. In contrast, in spite of a strong flattening, the exquisite preservation of the Chinese specimen makes it possible to document most aspects of its anatomy, including very minute features, such as the reticulate stereom microstructure. As far as can be compared, *C. guolensis* appears very similar to *C. enubilatus*, thus justifying its assignment to the same genus. However, *C. guolensis* shows at least two differences with *C. enubilatus*: flooring plates are abradially largely exposed in *C. guolensis*, whereas they are almost hidden in *C. enubilatus*; and holdfast elements are smaller than those of the stem in *C. guolensis*, whereas they are much larger than stem plates in *C. enubilatus*.

Attachment strategies in Cambrian edrioblastoids

All edrioasteroids were sessile, epibenthic organisms permanently attached by the aboral, imperforate extraxial part of their body (Bell 1976; Sumrall and Zamora 2011). In various edrioasteroid grades, the flexible aboral region was modified into a stem, so as to elevate the theca above the substrate (e.g., cyathocystids, pyrgocystids, rhenopyrgids). Rhenopyrgids probably evolved in deep, outer shelf, environments, where they attached directly on the sea floor, introducing their coraceous sac into the sediment (Smith and Jell 1990). In contrast, cyathocystids were cemented on hard substrates (Bell 1982). The stem-like structures of all edrioblastoids are remarkably convergent with the stems acquired, independently, in several pelmatozoan groups (Guensburg et al. 2010).

However, in all groups, stems were developed from the same, imperforate region of the body wall. In all edrioblastoids known so far, the distal part of the stem was missing, and their attachment strategy was thus unknown. The new Chinese specimen described herein shows a complete stem with a distal holdfast for attachment. The stem is polyplated and clearly less organized than the aboral appendages of more derived edrioblastoids (e.g., *Astrocystites*). The holdfast is also polyplated, relatively wide, and very gogiid-like (see Sprinkle 1973; Parsley 2012). The holdfast of the holotype of *C. guolensis* is attached to a trilobite pygidium, suggesting that edrioblastoids were living as skeletal cementers on soft substrates in quiet environmental conditions. The same strategy was documented in many other Cambrian sessile echinoderms living on soft substrates, such as gogiids (Sprinkle 1973; Lin et al. 2008; Zamora et al. 2009), early isorophids (Zamora and Smith 2010), and basal solutans (Daley 1996; Lefebvre and Fatka 2003).

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