

Microstructure and functional morphology of the Early Cambrian problematical fossil *Rhombocorniculum**

LI Guoxiang^{1**}, ZHU Maoyan¹ and Michael STEINER²

(1. Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, China; 2. Technische Universität Berlin, Sekr. ACK 14, Ackerstrasse 71 ~ 76, 13355 Berlin, Germany)

Received April 4, 2003; revised May 14, 2003

Abstract *Rhombocorniculum cancellatum* from the Lower Cambrian of southern Shaanxi Province (South China) is represented by the dextral and sinistral tooth-like sclerites (both in nearly equal numbers), indicating that the body plan of the organism with these sclerites probably was bilaterian. The main feature of the microstructure of the sclerites is the presence of longitudinally arranged, mutually contiguous hollow tubules—the shared walls consisting of microcrystalline apatite. In transverse cross sections, the sclerite wall mainly exhibits a spongy structure with pore size decreasing adapically. Functional morphological analysis indicates that the sclerites serve as a defensive rather than a grasping function.

Keywords: Early Cambrian, *Rhombocorniculum*, microstructure, functional morphology.

The abrupt appearance of diverse skeletal fossils near the base of the Cambrian System is a major piece of evidence for the Early Cambrian bioradiation event^[1]. Since these early skeletal fossils are generally small in size, they are commonly referred to as small shelly fossils, or abbreviated as SSFs. The SSFs include a number of extant phyla as well as extinct problematical groups of unknown phylogenetic affinities. Some of the problematical groups, including the phosphatic tooth-like fossils discussed in the present paper, are represented exclusively by isolated sclerites^[2,3], and their scleritomes are poorly known. The tooth-like fossils are a characteristic component of the earliest skeletal faunas, and are often present in acetic acid-etched residues from Lower Cambrian limestones. Because of their similarity to simple cone-like conodonts, tooth-like SSFs are also referred to as “conodont-like fossils”^[3,4]. Fossils assigned to this parataxonomic group include protoconodonts, paraconodonts, and several taxa, including *Fomitchella* and *Rhombocorniculum*, which have no affinity with conodonts and so are called pseudoconodonts^[3].

Rhombocorniculum Walliser, 1973, a typical representative of the tooth-like SSFs, consists of phosphatic hollow cones having a rhomboid sculpture and a single spine or node at the corners of the rhom-

boids. It has been reported mainly from the Early Cambrian (late Qiongzhusian to early Canglangpuian Age), and has a wide geographic distribution, occurring in such localities as China^[6,7], Mongolia and Siberia^[8], Kazakhstan^[9], England^[10,11], and North America^[5]. For these reasons, *Rhombocorniculum* has special significance for global biostratigraphic correlation^[3,12], especially for the correlation of the Qiongzhusian and Canglangpuian stages on the Yangtze platform with the Atdabanian and Botomian in Siberia. However, the function of *Rhombocorniculum* sclerites (defensive or grasping?) is still uncertain, and little is known about the phylogenetic affinities of this taxon.

The *Rhombocorniculum* sclerites here studied were recovered through acetic acid treatment of nodular limestones from the lower Shuijingtuo Formation at a section near the Xiaoyang Town, Zhenba County, Shaanxi Province. Biostratigraphic data of both trilobites and bradoriids indicate that the sclerites are from the Lower Cambrian Qiongzhusian stage^[13,14]. All specimens were examined and photographed under a scanning electronic microscope, and constitute a major sample important for analyzing the microstructure, functional morphology, and biological affinities of this organism.

* Supported by the National Natural Science Foundation of China (Grant Nos. 40172002 and 40232020), the Major State Basic Research Development Program of China (Grant No. G2000077700), and the Chinese Academy of Sciences (Grant No. KZCX2-116)

** To whom correspondence should be addressed. E-mail: gxi@nigpas.ac.cn

1 Description of the sclerites

Following the convention for the orientation of simple cone-like conodonts, the curved convex margin of a *Rhombocorniculum* sclerite is designated the anterior margin, while the curved concave margin is called the posterior margin. Oriented with the anterior margin facing the viewer and the base of the sclerite facing downward, the left side of the sclerite is designated the left one, while the opposite side is called the right side. Two sclerite morphotypes, one having a sulcus on the left side and the other having a sulcus on the right side, are termed the sinistral and the dextral morphotypes, respectively.

The sclerites here described are small, with a maximum length of 1.4 mm and a maximum width of 0.12 mm. The sclerites are laterally cultrate, curve posteriorly, and show a rounded anterior and a keeled posterior. They have a thick wall and a narrow internal cavity that extends from the base to the tip. One of the sides is slightly rounded or convex, while the other is concave and has a broad longitudinal sulcus. The basal cross-section is asymmetrically tear-shaped (Fig. 1, A₂) and becomes circular apically (Fig. 1, F). The surface exhibits a regular rhomboid sculpture with the longest diagonal of each rhomboid measuring about 20 μm long and extending longitudinally, and the short diagonal measuring about 15 μm long. The corners of the rhomboids bear a single spine (up to 20 μm long) or node. The sculpture is variable on a single specimen, being distinct on the convex side, faint on the concave side, and smooth around the tip (Fig. 1, A₁).

2 Dextral and sinistral sclerites

Based on the position of the sulcus, *R. cancellatum* sclerites from the Shuijingtuo Formation can be subdivided into two morphotypes, here called the dextral and sinistral forms. The present material includes 44 sclerites, of which 43 are slender and one is broad. The slender sclerites include 23 sinistral (Fig. 1, E) and 20 dextral specimens (Fig. 1, A₁ and B), while the single broad sclerite is sinistral and has a flattened transverse cross-section (Fig. 1, D₁ and D₂).

The fact that there are far more slender sclerites than broad ones is consistent with the results of previous results. Mambetov recovered sclerites of *R. cancellatum* from Kazakhstan with a slender/broad ratio

of 175 : 8^[4]. Landing^[5] subdivided sclerites from Canada into slender, broadly asymmetrical, and broadly symmetrical morphotypes and reported a ratio of 16 : 3 : 1. Hinz^[10] obtained a ratio of 34 (slender) : 1 (intermediate) : 3.2 (broadly symmetrical) : 1 (broadly asymmetrical); however, Hinz's intermediate sclerites are indistinguishable from her broad ones. Our examination of previously published figures revealed many examples of the two sclerite-morphotypes here recognized.

The existence of sinistral and dextral sclerites in nearly equal numbers indicates that the body plan of *R. cancellatum* probably was bilaterian. Although, unlike some previous collections^[5, 10], no symmetrical broad sclerites are examined from South Shaanxi, the absence or presence of symmetrical broad sclerites is consistent with this hypothesis. The symmetrical sclerites probably were located dorsally in the central part of the body, while the asymmetrical ones probably were located in or on the sides of the body.

3 Microstructures

R. cancellatum sclerites exhibit a three-layer structure^[5, 11, 12] consisting of thin, organic outer and inner layers and a thick middle layer composed of apatite rods arranged obliquely to the walls^[4, 3]. The inner layer was not examined in the present study. The 1 ~ 2 μm thick outer layer is phosphatic and massive in structure (Fig. 1, F), but the phosphatic composition may be secondary. The thickness of the middle layer is variable; thin at two lateral sides (minimum thickness 5 μm), and thick at the posterior end (maximum thickness 40 μm). The middle layer consists mainly of hollow tubules, the walls of which consist of microcrystalline apatite (commonly less than 0.2 μm). The tubule walls (less than 0.5 μm thick) are shared. In transverse sections, the wall of the sclerite is porous, and the pore diameter is larger in the basal cross-section (1 ~ 2 μm; Fig. 1, A₃) than in the distal cross-section (less 0.5 μm; Fig. 1, F). In longitudinal sections, the tubules parallel the longitudinal axis (Fig. 1, C₂ and C₃), and there are no septa or other structures within the tubules.

The present description of the microstructure of the middle layer is evidently different from that previously reported^[4, 5]. However, the previous conclusion was based primarily on examination of polished cross sections which commonly were etched with acids (possibly HCl) prior to examination under a SEM.

Acid etching can dissolve the original phosphatic structure, exposing secondary infillings that may appear fibrous and can be interpreted as the original microstructure. Our work shows that the sclerites consist mainly of longitudinally arranged hollow tubules

that may have housed organic matter. Following the decay of this organic matter, the tubules were filled with diagenetic cement. For this reason, the tubule-like structure is difficult to discern.

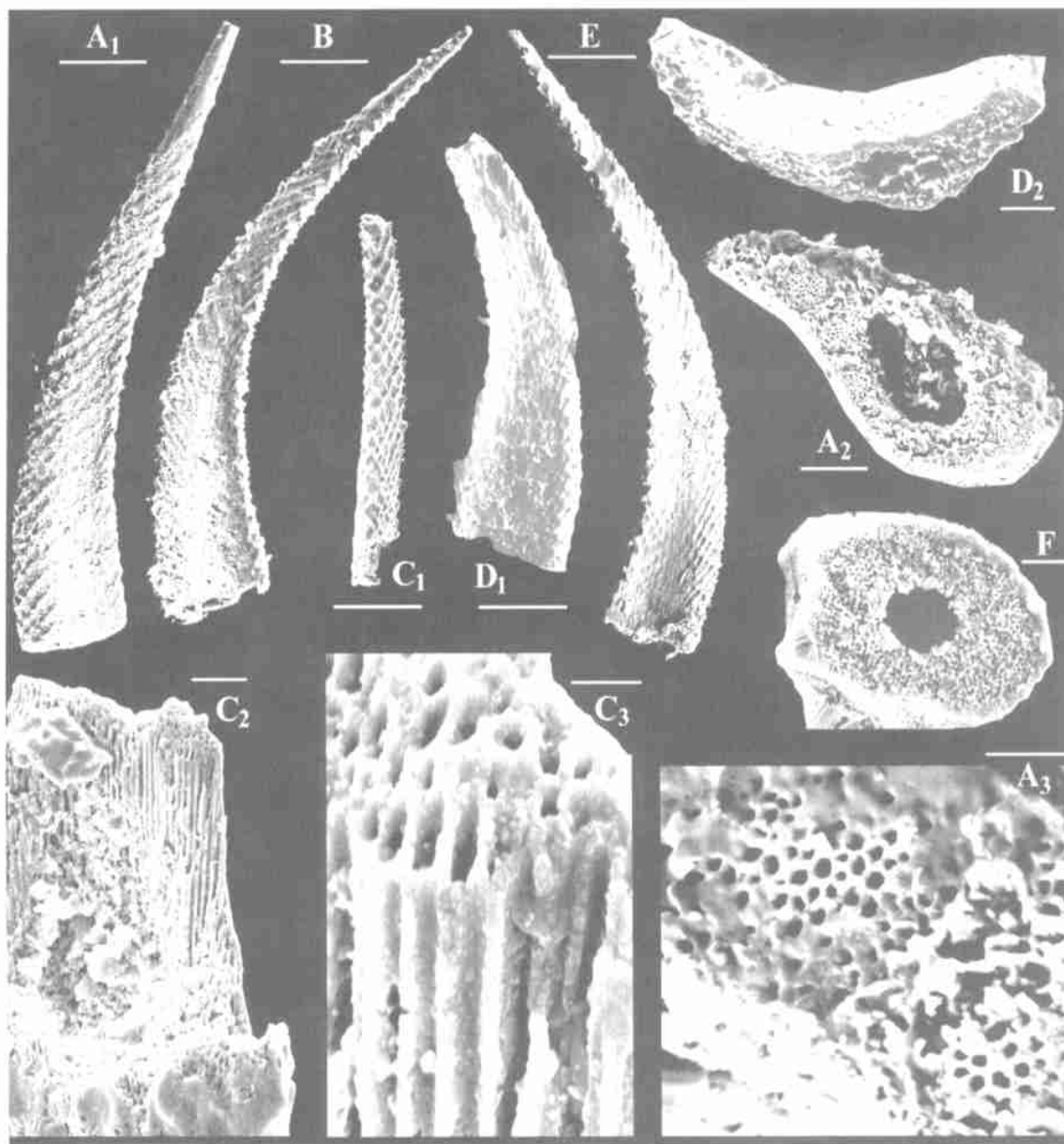


Fig. 1. SEM photographs of *Rhombocorniculum cancellatum* from the Lower Cambrian Shuijingtuo Formation of southern Shaanxi. Scale bar is $100\mu\text{m}$ for A₁, B, C₁, D₁, E; $20\mu\text{m}$ for A₂, D₂; $10\mu\text{m}$ for C₂, F; $5\mu\text{m}$ for A₃; $2\mu\text{m}$ for C₃. A₁, right lateral view, cat. No. 135540; A₂, basal transversal section; A₃, spongy structure; B, right lateral view, cat. No. 135541; C₁, a fragment, cat. No. 135542; C₂, basal part in detail; C₃, fibrous tubules; D₁, left lateral view, cat. No. 135543; D₂, basal transversal section; E, left lateral view, cat. No. 135544; F, distal transversal section, cat. No. 135545.

4 Functional morphology

Rhombocorniculum sclerites have been interpreted as having served as a grasping function^{4,5} similar to that of the grasping apparatuses of proto-

conodonts (chaetognaths). However, this interpretation is based mainly on morphological similarity (analogy) with no compelling independent evidence. Indeed, the microstructure and surface sculptures of the sclerites suggest that they served as a defensive

rather than a grasping function.

Rhombocorniculum sclerites differ histologically from protoconodonts. As noted above, the wall of *Rhombocorniculum* sclerites consists mainly of hollow, mutually contiguous tubules. In transverse sections the sclerite wall is porous, and in longitudinal sections the hollow tubules are somewhat coaxial. In contrast, the walls of protoconodont elements consist mainly of fibrous lamellae with a basal-internal growth model^[4], a microstructure that is very similar to that of the grasping spines of chaetognaths^[16, 18]. Moreover, whereas *Rhombocorniculum* sclerites have a thick wall and a narrow internal cavity that does not extend to the tip, protoconodonts are thin-walled, and the internal cavity extends to the apex. In short, histological evidence refutes the hypothesis of a close phylogenetic relationship between *Rhombocorniculum* and protoconodonts (chaetognath grasping spines^[18]).

The spinose sculpture of *Rhombocorniculum* sclerites is also inconsistent with the hypothesis of a grasping function. Skovsted and Peel^[19] argued that the presence of scale-like processes on *Mongolitubulus* spines ruled out a grasping function for these structures, and we think that a similar argument can be applied to *Rhombocorniculum* sclerites. The spinose ornamentation could not have facilitated the seizing/grasping of prey, but rather would have hampered such activity. The grasping spines of chaetognaths usually are enclosed by a hood^[18], and retraction of this hood exposes the spines for prey capture. The spinose ornamentation of *Rhombocorniculum* sclerites would undoubtedly have obstructed the retraction of a chaetognath-like hood and thus hindered prey capture. The fact that some *Rhombocorniculum* sclerites are strongly twisted^[5, 10] also is inconsistent with a grasping function. Therefore, *Rhombocorniculum* sclerites are not comparable to the grasping spines of chaetognaths, and may instead have served as a defensive function.

Rhombocorniculum has variously been assigned to the Cambroscleritida^[15, 20], the Halkieriidae^[8], the protoconodonts^[21], or the paraconodonts^[22]. However, assignments of this fossil to the Cambroscleritida or the Halkieriidae are arbitrary^[4, 5]. Moreover, assignment to the Paraconodontida by Müller^[22] has been shown to be untenable through histological investigations^[23]. Histological analysis also indicates that *Rhombocorniculum* cannot be as-

signed to the protoconodonts^[5]. However, because *Rhombocorniculum* sclerites were thought to be similar in function to protoconodonts, the descriptive term “pseudoconodonts” was introduced by Landing et al.^[5] for *Rhombocorniculum* sclerites. Later, the hypothesis of a grasping function became widely accepted^[4, 10].

As noted above, *Rhombocorniculum* sclerites differ markedly from grasping spines and may have served as a defensive function. Indeed, when Meshkova assigned *Rhombocorniculum* to the Cambroscleritida^[20], she interpreted the spine-like fossils as external, defensive sclerites. Unfortunately, however, Meshkova's Cambroscleritida is an invalid taxon that includes phylogenetically unrelated fossils such as *Protohertzina*, tomotüids, and *Sachites*^[5]. Although the existence of dextral and sinistral sclerites indicates that the body plan of *Rhombocorniculum* was bilaterian, very little is known about the details of its anatomy including the arrangement of the sclerites in or on the soft body. Presumably these questions and the problem of the affinities of this organism will be resolved by the discovery of soft-bodied specimens.

Acknowledgements We are grateful to Dr. H. Van Iten for comments and improving the manuscript, to Zhang Junming for assistance in the field and Mao Yongqiang for SEM photography.

References

- 1 Conway Morris S. The search for the Precambrian-Cambrian boundary. *American Scientist*, 1987, 75: 156.
- 2 Bengtson S. The cap-shaped Cambrian fossil *Maikhanella* and the relationship between coeloscleritophorans and mollusks. *Lethaia*, 1992, 25: 401.
- 3 Qian Y. et al. Taxonomy and biostratigraphy of small shelly fossils in China. Beijing: Science Press, 1999, 1~247.
- 4 Bengtson S. The early history of the Conodonta. *Fossils and Strata*, 1983, 15: 5.
- 5 Landing E. et al. A microfauna associated with Early Cambrian trilobites of *Callavia* Zone, northern Antigonish Highlands, Nova Scotia. *Canadian Journal of Earth Sciences*, 1980, 17: 400.
- 6 Xie Y. S. Early Cambrian conodont fossils from Zhenba County, Shaanxi Province. *Journal of Chengdu College of Geology*, 1990, 17(4): 16.
- 7 Yue Z. et al. Palaeontology and biostratigraphy of the Early Cambrian protoconodonts and other skeletal microfossils from Aksu-Wushi Region, Xinjiang, China. *Bulletin of Geology Institute of Chinese Academy of Geological Sciences*, 1992, 23: 133.
- 8 Missarzhevsky, V. V. Conodonts(?) and phosphatic problematica from the Cambrian of Mongolia and Siberia. In: Tatarinov L P et al. eds. *Bespozvonochnye Paleozoya Mongolii*. Moscow: Nauka, 1977, 10.

- 9 Missarzhevsky, V. V. Conodont-shaped organisms from the Precambrian-Cambrian boundary beds of the Siberian Platform and Kazakhstan. *Trudy Inst Geol Geofiz Sib Otd*, 1973, 49; 53.
- 10 Hinz, I. The Lower Cambrian microfaua of Comley and Rushton, Shropshire, England. *Palaeontographica*, 1987, A 198; 41.
- 11 Walliser, G. H. *Rhomboorniculum comleyense* n. gen. n. sp. incertae sedis Unter Kambrium, Shropshire. *Palaontologische Zeitschrift*, 1958, 32; 176.
- 12 Brasier, M. D. Toward a biostratigraphy of the earliest skeletal biotas. In: Cowie J W, Brasier M D eds. *The Precambrian-Cambrian Boundary*. Oxford: Clarendon Press, 1989, 117.
- 13 Xie, Y. S. Small shelly fossils in Qiongzhusi Stage of Lower Cambrian in Zhenba County, Shaanxi Province. *Journal of Chengdu College of Geology*, 1988, 15(4); 21.
- 14 Shu, D. G. Cambrian to Ordovician bradoriids from western Zhejiang, western Hunan, and southern Shaanxi. Xi'an: Northwest University Press, 1990, 1~95.
- 15 Mambetov, A. M. On revision of the genus *Helenia*. *Paleontological Journal*, 1977, 10; 90.
- 16 Szaniawski, H. Chaetognath grasping spines recognized among Cambrian protoconodonts. *Journal of Paleontology*, 1982, 56; 806.
- 17 Szaniawski, H. Structure of protoconodont elements. *Fossils and Strata*, 1983, 15; 21.
- 18 Szaniawski, H. New evidence for the protoconodont origin of chaetognaths. *Acta Palaeontologica Polonica*, 2002, 47; 405.
- 19 Skovsted, C. B. et al. The problematic fossil *Mongolitubulus* from the Lower Cambrian of Greenland. *Bulletin of Geological Society of Denmark*, 2001, 48; 135.
- 20 Meshkova, V. V. Cambroscleritida incertae sedis — new kind of Cambrian fossils. In: Zhuravleva I T, Rozanov A Yu eds. *Biostratigraphy and Palaeontology of the Early Cambrian of Europe and Northern Asia*. Moscow: Nauka, 1974, 190.
- 21 Brasier, M. D. The succession of small shelly fossils (especially conoidal microfossils) from English Precambrian-Cambrian boundary beds. *Geological Magazine*, 1986, 123(3); 237.
- 22 Müller, K. J. Supplement to systematics of conodonts. In: Moore R C ed. *Treatise on Invertebrate Paleontology, Pt. W, Miscellaneous*. Lawrence: Geol. Soc. Amer. and Univ. Kansas Press, 1962, 246.
- 23 Müller, K. J. et al. Ueber den Feinbau der Conodonten. *Mem. Fac. Sci. Kyoto Univ. Ser. Geol. Min.*, 1971, 38; 1~88.