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Cyrtinoides Yudina and Rzhonsnitskaya, 1985, an aberrant Middle Devonian ambocoeliid brachiopod genus from China

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Abstract

Here we redescribe and reillustrate specimens of an ambocoeliid brachiopod previously described as *Echinocoelia guangsiensis* Sun, 1992 from the late Eifelian–earliest Givetian Mingtang Formation of the Liujing section in Guangxi Autonomous Region. The internal structure of the species, and especially the presence of a spondylium with tichorhinum in the ventral valve indicates that the species represents the aberrant genus *Cyrtinoides* Yudina and Rzhonsnitskaya, 1985. It seems probable that the anterior part of the tichorhinum in *Cyrtinoides* accommodated the diductor attachments. Geographic distribution of *Cyrtinoides* is restricted to the Northern Hemisphere and shows a disjunct pattern. This genus has not hitherto been identified from China.

Keywords: Ambocoeliidae; *Cyrtinoides*; Palaeoecology; South China; Middle Devonian

1. Introduction

The Ambocoeliidae constitute a group of about 36 genera of commonly small- and smooth-shelled Silurian to Triassic spiriferides. They are especially common and characteristic of the Devonian brachiopod faunas. Within the family Ambocoeliidae the Eifelian–Givetian genus *Cyrtinoides* Yudina and Rzhonsnitskaya, 1985 is especially interesting because it is distinguished from all members of the group by some aberrant features in the shell internal structure. The unusual nature of the *Cyrtinoides* shell interior is marked by the presence of a spondylium with tichorhinum in the ventral valve. As a matter of fact, *Cyrtinoides* is the only known genus with a tichorhinum not only within Ambocoeliidae, but in the whole order Spiriferida. It is worth noting that the tichorhinum was originally described as a characteristic structure for the Cyrtinidae (Oehlert, 1901; Williams et al., 1997), the family of punctate spirolophous brachiopods belonging to the order Spiriferinida. There is, however, a difference in the structure of the tichorhinum of *Cyrtinoides* and that of the Cyrtinidae. The latter has a tichorhinum with a median partition completely developed in the majority of species whereas in *Cyrtinoides* the hollow of the tichorhinum is not divided.

In this study we redescribe internal shell structure and systematic position of the species originally described as *Echinocoelia guangsiensis* Sun, 1992 (= *Cyrtinoides guangsiensis*) from the late Eifelian–earliest Givetian Mingtang Formation of the Liujing section in Guangxi Autonomous Region (Sun, 1992; Xian, 1998). It is worth noting that the generic affinities of some ambocoeliids with a tichorhinum were previously poorly understood and have been associated with species representing *Echinocoelia*. The silicification of the brachiopod material from Liujing, although usually coarse and frequently with additional silica deposition obliterating some details, enabled study of the internal shell structure as well as growth variability. The presence of a well preserved tichorhinum in the ventral valve of the studied form shows that the species should be transferred to the genus *Cyrtinoides*. The brachiopod fauna that co-occurs with this ambocoeliid species was described by Sun (1992) and Xian (1998).

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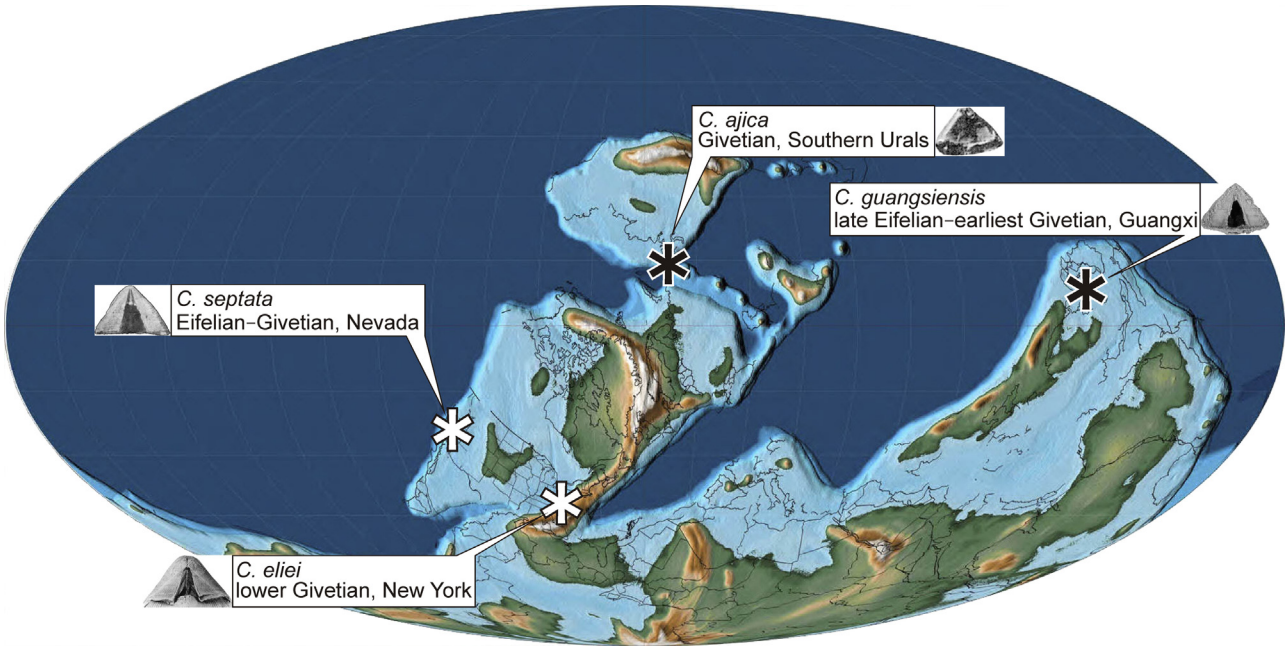

Fig. 1. Distribution of *Cyrtinoides* against the Middle Devonian palaeogeography (adapted from Scotese, 2014). Asterisks denote occurrences of *Cyrtinoides* species with recumbent (white) and well developed (black) crural plates.

The geographic distribution of *Cyrtinoides* is restricted to the Northern Hemisphere and shows a disjunct pattern (Fig. 1). Previously, it was reported from the western slope of the Southern Urals (eastern Europe), Nevada (western North America) and western New York (eastern North America). Stratigraphically the genus ranges from the Eifelian up to the upper Givetian (Yudina and Rzhonsnitskaya, 1985; Johnson and Blodgett, 1993). The presently studied material of *Cyrtinoides* comes from the late Eifelian–earliest Givetian of the South China Palaeoplate. This genus has not hitherto been identified from China.

2. Geological background

2.1. Geological setting and stratigraphy

Liujing area, located at about 60 km east of Nanning City, Guangxi Autonomous Region (Fig. 2A), is one of the classic type localities of the marine Devonian in China with a continuous and complete sequence ranging from the Lochkovian to the lower Famennian including seven formations (Lower Devonian Lianhuashan, Nagaoling, Yujiang, and Moding formations, the Middle Devonian Najiao and Mintang formations, and the Upper Devonian "Rongxian" Formation). The complete sedimentary sequence and rich and diversified fossils had attracted many researchers to work there (Bai et al., 1982, 1994; Kuang et al., 1984; Su and Wang, 1985; Wang and Rong, 1986; Sun, 1992; Zhong et al., 1992; Xian, 1998; Jiang et al., 2000).

The Mintang Formation is about 90–110 m thick in Liujing area and consists mainly of dark gray platy limestone intercalated with light gray massive bioclastic limestone (Fig. 2B). The platy limestone contains abundant pelagic tentaculites (*Nowakia* and *Viriatellina*) and is considered to have been deposited in a relatively deep water setting. The bioclastic limestone interbeds are rich of benthic fossils (brachiopods, corals, stromatoporids, etc.) and probably represent debris flows derived from the nearby stromatoporid bioherms. The conodont biostratigraphic work revealed that the formation spans from the uppermost Eifelian *kockelianus* Zone to the Givetian Upper *hermanni-cristatus* Zone (Su and Wang, 1985; Bai et al., 1994; Jiang et al., 2000). According to Bai et al. (1994), the Eifelian–Givetian boundary, marked with the first appearance of the conodont *Polygnathus hemiansatus*, is situated 12.7 m above the base of the formation at the Liujing section (Fig. 2B).

2.2. Faunal succession

The lower part of the Mintang Formation in Liujing area contains abundant brachiopod faunas (Xian, 1982, 1998; Sun, 1992; Bai et al., 1994). Xian (1998), on the basis of brachiopods collected on the west bank of the Yunjiang River (ca. 1.5 km west of the section from which the present material was collected; see Sun, 1992) remarked that the brachiopod fauna can be subdivided into a lower fauna and an upper fauna. He named the lower one as *Geranocephalus-Pentamerella* Fauna and the upper one as *Stringocephalus-Changtangella* Fauna (Xian, 1998). At the Xian's section the lower fauna is restricted to the interval about 1.5–2.2 m above the dolostone of Najiao Formation (Fig. 2B) and consists of at least 35 genera, but none of them appears to be endemic. The fauna is dominated by small sized atrypid and ambocoeliid brachiopods. *Pentamerella nanningensis*, *Davidsonia sinensis*, and *Echinocoelia guangsiensis* (= *Cyrtinoides guangsiensis*) also occur in abundance. *Geranocephalus sinensis* described by Xian (1998) from the lower fauna is a junior synonym of *Stringocephalus*

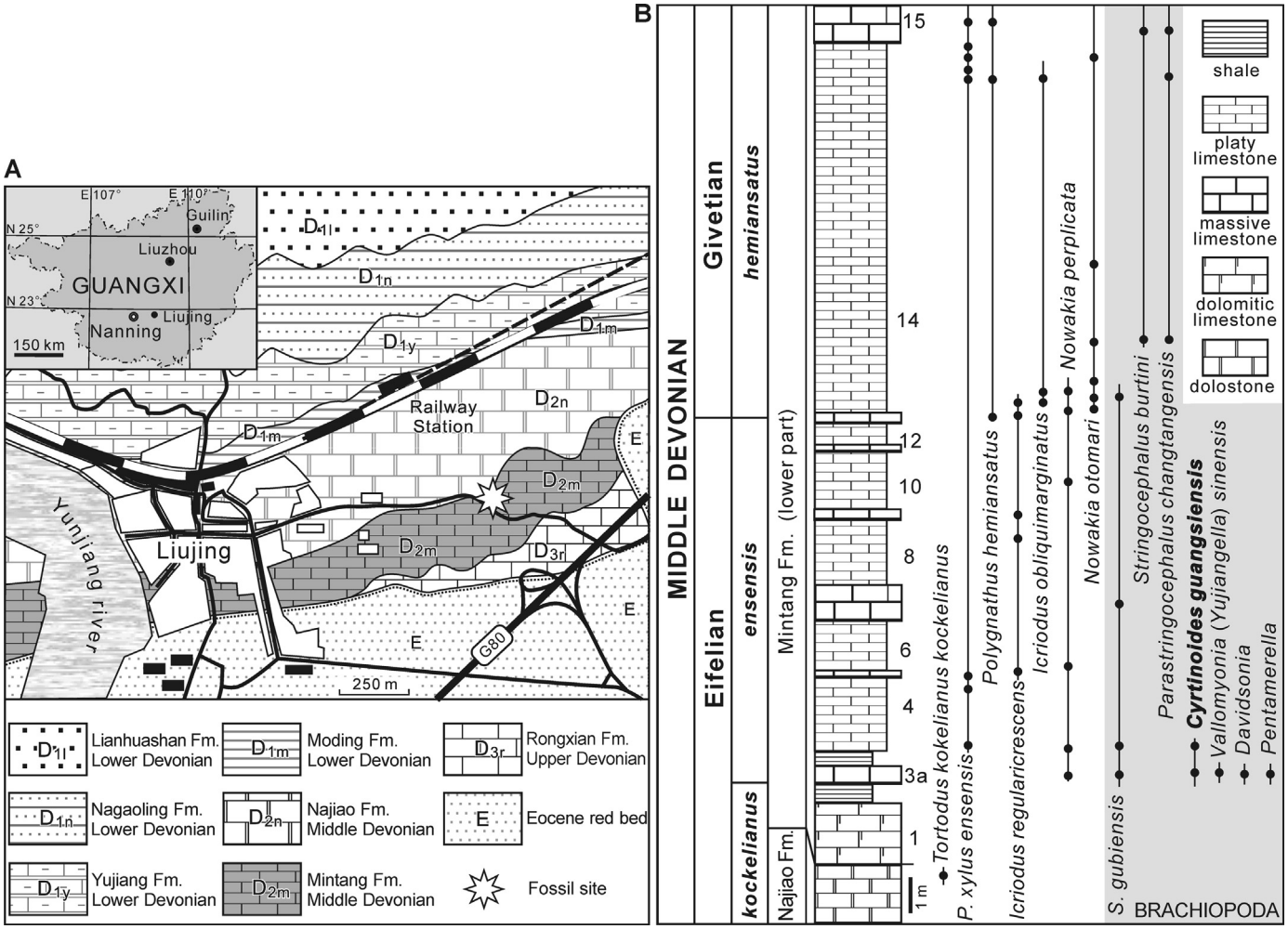

Fig. 2. Location and geological map of the Liujing area near Nanning City, Guangxi Autonomous Region (A) and stratigraphic column of the Eifelian–Givetian sequence showing distribution of conodonts and brachiopods (B).

gubiensis Sun, 1994, which is the oldest (Eifelian) known occurrence of *Stringocephalus* (Sun and Bai, 1995) and its ontogeny provides valuable information about the phylogeny of the genus (Sun and Boucot, 1999; see also Balinski et al., 2000). Conodonts revealed from the *Geranocephalus-Pentamerella* Fauna indicate the uppermost Eifelian *kockelianus-ensensis* zones. The upper fauna (i.e., *Stringocephalus-Changtangella* Fauna) is dominated by stringocephalid and large-sized ambocoeliid brachiopods and characterized by the abundant occurrence of *Stringocephalus*, *Parastringocephalus*, *Rhynchospirifer*, and *Changtangella*. Generally, the two faunas characterized by Xian (1998) from the section on the west bank of the Yunjiang River can be distinguished in the presently studied section, although in the latter they are less clearly delineated. The inventory of the brachiopod faunas from the lower part of the Mintang Formation led Xian (1998) to the conclusion that they are characteristic for Benthic Assemblage 3.

Whole studied materials have been extracted from the limestone by acid digestion. All specimens are housed in the Geological Museum of Peking University, Beijing, China (abbreviated as PKUM).

3. Systematic palaeontology

The classification of Spiriferida adopted herein follows Carter et al. (2006).

Order SPIRIFERIDA Waagen, 1883
Family AMBOCOELIIDAE George, 1931
Subfamily Ambocoeliinae George, 1931
Genus *Cyrtinoides* Yudina and Rzhonsnitskaya, 1985
(= *Mucroclipeus* Goldman and Mitchell, 1990)

Type species: *Cyrtinoides ajica* Yudina and Rzhonsnitskaya, 1985; Middle Devonian (Givetian), western slope of Southern Urals, Russia.

Cyrtinoides guangsiensis (Sun, 1992) new comb.
(Figs. 3–5)

1992 *Echinocoelia guangsiensis*–Sun, p. 718, pl. 3, figs. 1–9, 16, 18, 22, 26.
1998 *Echinocoelia guangsiensis* Sun–Xian, pl. 2, figs. 16–21, 23, 33, 34.

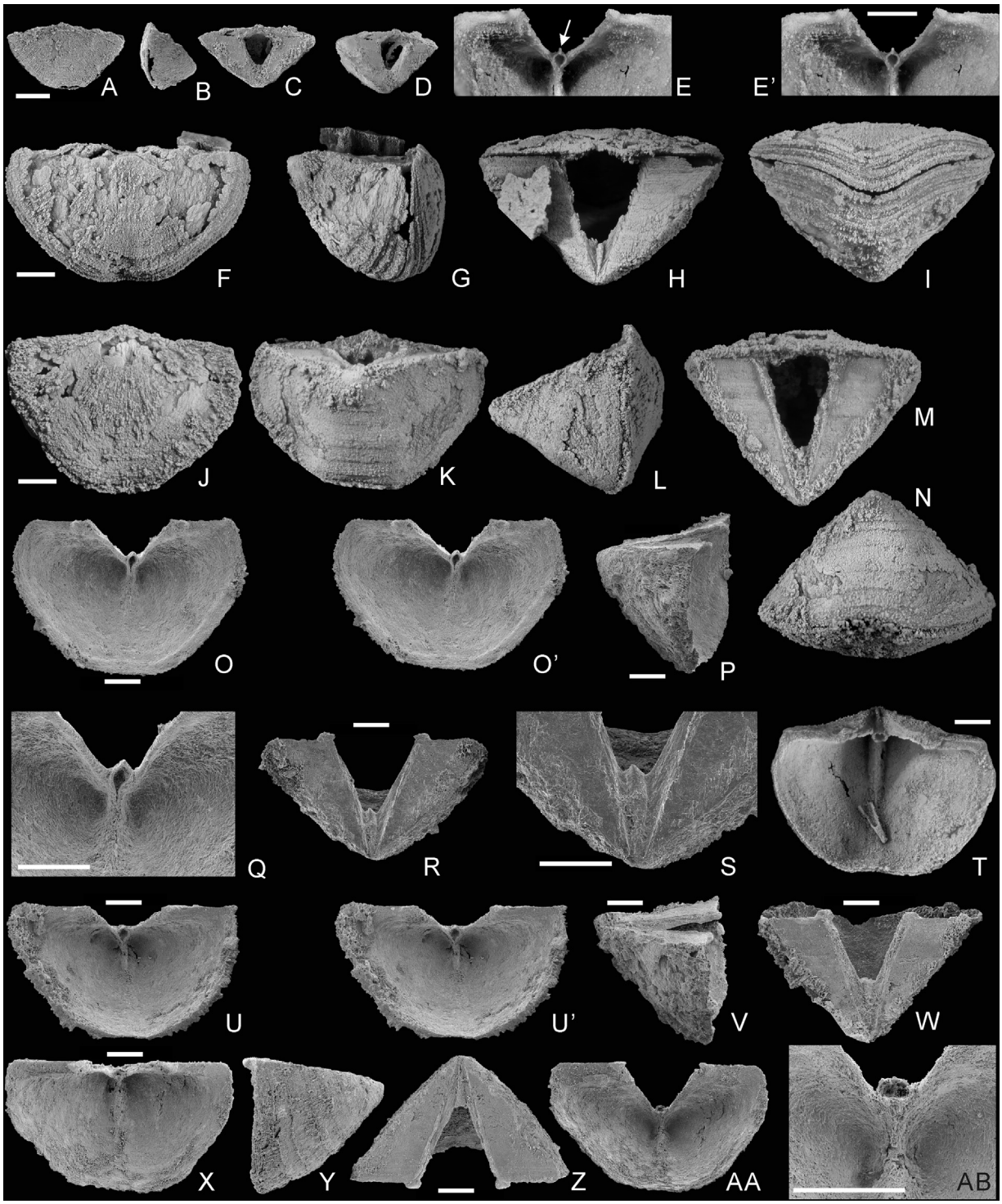

Fig. 3. *Cyrtinoides guangsiensis* (Sun, 1992) from the Mintang Formation, Liujing area, Guangxi Autonomous Region. (A–D) SEM micrographs of a small shell in dorsal, lateral, posterior, and oblique posterior views (PKUM02-660); note crus visible in (D). (E, E′) Interior of postero-umbonal region of ventral valve (stereopair); note a median ridge on the tichorhinum (arrowed) (PKUM02-661). (F–I) Large shell in dorsal, lateral, posterior, and anterior views (PKUM02-662). (J–N) Complete shell in dorsal, ventral, lateral, posterior, and anterior views (PKUM02-663). (O–S) SEM micrographs of ventral valve (O, O′ stereopair) in five views (PKUM02-664). (T) Ventral valve interior (PKUM02-665). (U–W) SEM micrographs of ventral valve (U, U′ stereopair) in three views (PKUM02-666). (X–AB) SEM micrographs of ventral valve in five views (PKUM02-667); note the enlargement of the tichorhinum in (AB). Scale bar = 1 mm.

Material examined: Ten more or less complete and 2 fragmentary shells, 157 ventral and 91 dorsal valves.

Description: Shell small-sized, attaining up to 6.6 mm in width, strongly ventribiconvex, hemi-pyramidal in lateral view, transversely subtrapezoidal to sub-semielliptical in outline, wider than long; hinge line wide, slightly shorter than the maximum shell width, the latter situated near cardinal extremities; cardinal angles acute to obtuse, lateral margins weakly rounded

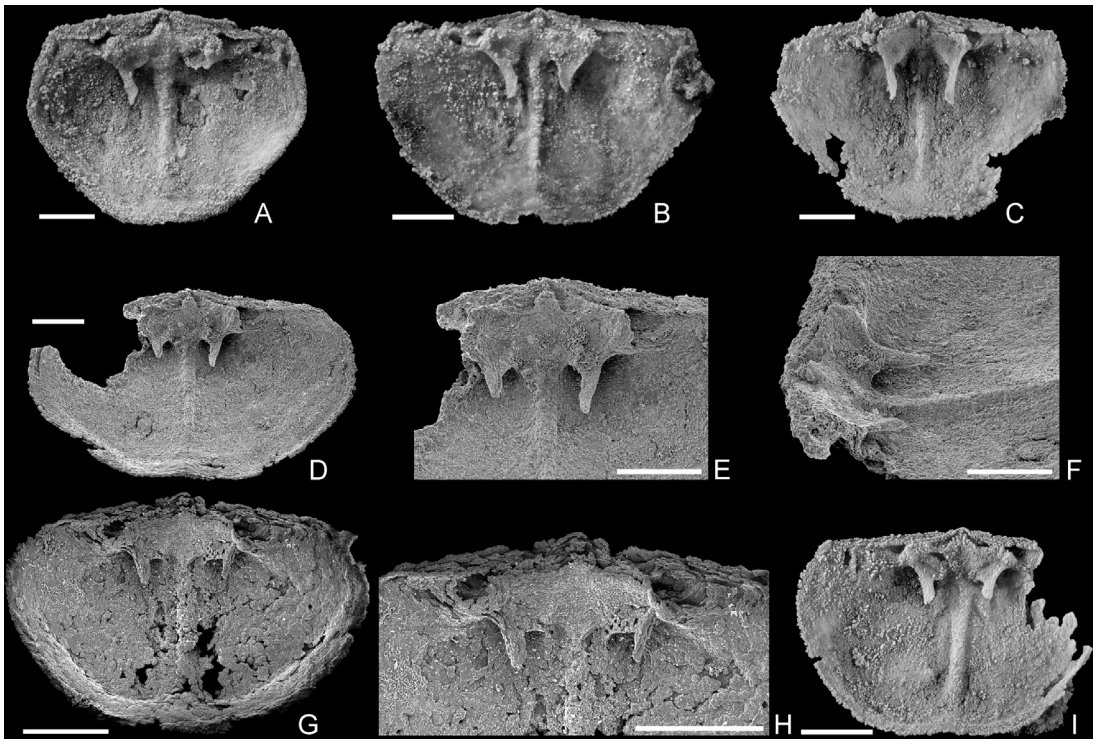

Fig. 4. *Cyrtinoides guangsiensis* (Sun, 1992) from the Mintang Formation, Liujing area, Guangxi Autonomous Region. (A–C, I) Interior of four dorsal valves. (D–F) SEM micrographs of dorsal interior in three views. (G–H) SEM micrographs of dorsal interior. Scale bar = 1 mm.

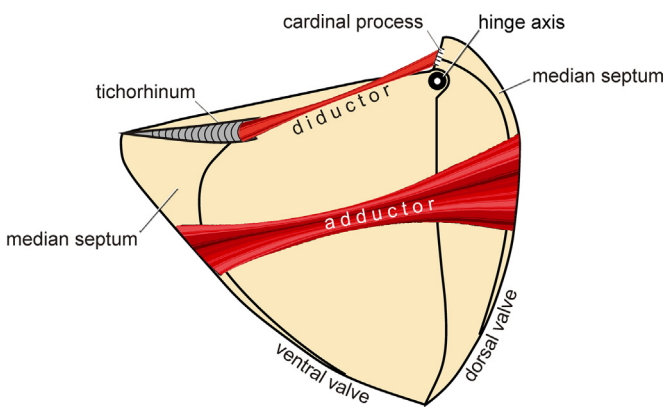

Fig. 5. Reconstruction of possible arrangement of adductor and diductor muscles and function of the tichorhinum in *Cyrtinoides guangsiensis* (Sun, 1992) (modified after Brunton, 1984).

to nearly straight, anterior margin narrow, weakly rounded, truncated to narrowly indented, anterior commissure nearly straight to weakly unisulcate.

Ventral valve strongly convex, hemipyramidal, without perceptible sulcus or fold, rarely with delicate median flattening; interarea triangular, high, flat to nearly flat, procline to catacline; delthyrium high, encompassing about 25–46°, apical two-fifth closed by conical, anteriorly open tube (tichorhinum) supported by narrow lateral plates; external surface of tichorhinum rounded or with longitudinal median ridge (Fig. 3E, R, S).

Dorsal valve gently convex, cap-like; interarea flat, anacline to nearly orthocline; median sulcus weak and narrow, developed in anterior three-quarter of the valve length.

Ventral valve interior with high posteriormost median septum where it supports tichorhinum, rapidly lowering anteriorly, reaching about midvalve, wide at the base and narrowing at the top (Fig. 3E, O, Q, T, U, X, AA, AB); muscle scars deeply incised on thick-shelled specimens, slightly converging anteriorly. Interior of dorsal valve with knob-like, triangular cardinal process; inner hinge plates wide, reaching valve floor posteriorly or more anteriorly, thus forming short crural plates (Fig. 4A–I; see remarks below); crura anteriorly directed and slightly converging; median myophragm low, rather wide, long, reaching about four-fifth of the valve length.

Micro-ornament poorly preserved due to a coarse silicification, so the presence of micro-spines cannot be ascertained; concentric growth lamellae present, those near anterior margin more crowded.

Ontogeny: The size range of the specimens from the Mingtang Formation is from 1.9 to 6.6 mm in width. The smallest ventral valves of this range show a well developed interarea (Fig. 3A–D) and tichorhinum, but median septum is proportionally much shorter in comparison with large specimens. The median septum of immature specimens supports the tichorhinum in its most umbonal part whereas in large specimens the septum reaches near the anterior end of tichorhinum.

Crural plates: There is a controversy concerning a presence of crural plates in the type species of the genus, *Cyrtinoides ajica* Yudina and Rzhonsnitskaya, 1985. Yudina and Rzhonsnitskaya (1985) revealed the presence of crural plates in the original description of the type species coming from the Givetian of the western slope of the Southern Urals, whereas Johnson and Blodgett (1993, p. 952), with the aid of the material from

New York and Nevada, re-interpreted the structure as recumbent crural bases. Goldman and Mitchell (1990) noted the absence of crural plates in the latest Eifelian to early Frasnian species of the genus *Mucroclipeus*, a junior synonym of the genus *Cyrtinoides*. On the other hand, Sun (1992) noted the presence of crural plates in *Echinocoelia guangsiensis* (= *Cyrtinoides guangsiensis*) from the latest Eifelian Mingtang Formation of Liujing section in Guangxi Autonomous Region. Indeed, the present re-examination of the type material of *C. guangsiensis* clearly shows that the crural bases in this Chinese form hang quite high above the valve floor and are supported by thin and variable in extent plates. These plates are fused to the valve floor and therefore should be regarded as short crural plates (Fig. 4A–I). It appears that the support of the crura is variously developed not only within *C. guangsiensis*, but also between different species of *Cyrtinoides*. Moreover, this difference might be due to palaeogeographic variation as the species from the easternmost Laurussia and South China (*C. guangsiensis* and, reportedly, *C. ajica*) possess crural plates whereas species occurring more to the west, i.e., from North America (*C. eliei* and *C. septata*), have apparently recumbent crural bases (see Fig. 1). However, detailed relationship between species of *Cytinoides* is not possible to assess owing to inadequate knowledge on the internal shell structure and its variability in the type species of the genus and *C. eliei*.

Function of tichorhinum: It is generally assumed that the anterior part of tichorhinum in *Cyrtina* supported some of the muscle attachments as indicated by the presence of myotest tissue located on this structure (MacKinnon, 1974, pp. 230–232, figs. 15, 16a, c; Williams et al., 1997, p. 392, fig. 354). A similar tube known as a syrinx in some Upper Devonian–Carboniferous spiriferinidine Syringothyrididae possibly performed a similar function (Williams et al., 1997). Williams and Rowell (1965, p. 115, fig. 120) supposed that the tichorhinum in *Cyrtina* accommodated the base of the pedicle (unpaired median pedicle muscle). On the other hand, MacKinnon (1974, pp. 230–231, figs. 15, 16), extending the muscle arrangement of recent articulate brachiopods to *Cyrtina*, concluded that the tichorhinum provided areas of attachment for the adductor muscles (see also Williams et al., 1997, p. 392, fig. 354). Brunton (1984, pp. 76–77) remarked that such an arrangement of the adductor and diductor muscles raise a functional problem because they must have crossed close together. Thus, he interpreted that the tichorhinum accommodated the diductor muscle bases (Brunton, 1984, p. 77, fig. 94). Despite some controversy in the interpretation of the function of the tichorhinum, it is highly probable that this structure in the ambocoeliid *Cyrtinoides* performed the same function as analogical tubes in the spiriferinide *Cyrtina* and Syringothyrididae. We are more inclined to the Brunton's interpretation of the muscle arrangement in *Cyrtina* species, and consequently it seems probable that the anterior part of the tichorhinum in *Cyrtinoides* accommodated the diductor attachments (Fig. 5).

Remarks: Comparison of the described species with the type species of the genus *Cyrtinoides ajica* appears to be difficult as no satisfactory illustrations are available of the latter form. It seems, however, that in comparison with the Chinese specimens the Russian form is slightly less expanded in width and has more concave and narrower ventral interarea.

C. guangsiensis resembles *Echinocoelia septata* Johnson (in Johnson et al., 1980) (= *Cyrtinoides septata*) from the Eifelian–Givetian of the northern Antelope Range (central Nevada) in some respects, but the latter is more rounded in outline and has a less developed crural support. *Cyrtinoides eliei* (Goldman and Mitchell, 1990) from the Skaneateles Formation (lower Givetian) of western New York differs from the Chinese species in having proportionally more elongated shell, less distinctive ventral interarea and longer ventral and dorsal median septa, reaching the anterior margin of valves. The crural plates are absent in *C. eliei* (Goldman and Mitchell, 1990), but well developed in *C. guangxiensis*.

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