A nearshore Hirnantian brachiopod fauna from South China and its ecological significance

Bing Huang[1*], Jiayu Rong[1], David A.T. Harper[2] and Hanghang Zhou[3]

[1] State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Center for Excellence in Life and Paleoenvironment, Chinese Academy of Sciences, 39 East Beijing Road, Nanjing 210008, China <bhuang@nigpas.ac.cn>, <jyrong@nigpas.ac.cn>

[2] Palaeoecosystems Group, Department of Earth Sciences, Durham University, Durham DH1 3LE, UK <david.harper@durham.ac.uk>

[3] University of Science and Technology of China, Hefei 230026, China <zhouhanghang@live.com>

* corresponding author.

Running Header: A nearshore Hirnantian brachiopod fauna from S China

Abstract.—The brachiopods collected from the Kuanyinchiao Beds (Hirnantian, uppermost Ordovician) in Meitan and Zunyi counties, northern Guizhou include 13 species and one undetermined taxon, dominated by *Hirnantia sagittifera* (M’Coy) accounting for over one-third of the specimens, together with common *Eostropheodonta hirnantensis* (M’Coy). They are assigned to the *Hirnantia-Eostropheodonta* Community which probably inhabited a shallow-water, near-shore BA2 to upper BA3 environment. Population analysis shows that the community was well adapted to this environment after the first phase of the end Ordovician mass extinction. Representative specimens of all the species are illustrated, and a new species, *Minutomena missa* n. sp. is described herein. The variation in *Hirnantia sagittifera* (M’Coy) was noted in many of previous studies but was not statistically evidenced. Here we have measured representative specimens of that famous species from the major paleoplates and terranes in the world, along with other species assigned to the genus from South China. Having used Principal Component Analysis (PCA), significant variations in the species are documented statistically and revised, and three nominal species, one subspecies and two morphotypes are now reassigned to *Hirnantia sagittifera* (M’Coy) *sensu stricto*.

UUID: http://zoobank.org/references/3f83fb1e-a6dd-4585-9f9f-9586dad28244

Introduction

The end-Ordovician marked the first major extinction event of the Phanerozoic. There were significant changes in the brachiopod faunas during the extinction and subsequent recovery. The biotic event heralded the arrival of new groups of brachiopod communities assigned to the *Hirnantia* Fauna (Temple, 1965). The *Hirnantia* Fauna is a worldwide, cool-water brachiopod fauna that originated and flourished in shallow-water marine environments at intermediate to low latitudes (e.g., Rong and Harper, 1988, 1999; Rong et al., 2002). The uniqueness of the *Hirnantia* Fauna throughout geological time, its near global distribution, distinctive and limited stratigraphical range (Hirnantian, uppermost Ordovician), have made it a focus for evolutionary paleobiologists and biostratigraphers.

After almost half century of intense investigation, the *Hirnantia* Fauna is now well known for its importance in the study of end-Ordovician macroevolutionary processes (e.g., Temple, 1965; Wright, 1968; Amsden, 1974; Lespérance and Sheehan, 1976; Rong 1979; Nikitin et al., 1980; Cocks, 1982; Benedetto, 1986; Rong and Harper, 1988, 1999; Owen et al., 1991; Harper and Rong, 1995, 2001; Rong et al., 2002; Jin and Zhan, 2008; Zhan et al., 2010; Hints et al., 2012; Benedetto et al., 2013; Harper and Hints, 2016). Detailed investigation of the *Hirnantia* Fauna on a global scale has already made a significant contribution to the recognition of the essence of the end-Ordovician mass extinction. There are more than 100 localities in nearly 30 countries and regions where the *Hirnantia* Fauna has been documented (Rong, 1979; Rong et al., 2002). In South China, *Hirnantia* faunas from 24 localities were summarized and discussed, most of which are in Guizhou, Sichuan, and Hubei provinces on the Upper Yangtze Platform (Rong et al., 2002; Zhan et al., 2010). Among them, the collections from Yichang, Hubei Province where the Hirnantian GSSP is situated, were systematically described in detail (Rong, 1984; Zeng et al., 2016). The brachiopod fauna is highly diverse (over 20 genera) and was assigned to Benthic Assemblage (BA) 3, the bathymetric zone of the deeper parts of the shallow-water platform (Rong, 1984).

Fieldwork by the author group during past several decades has dramatically increased collections of the *Hirnantia* Fauna in South China. Recently, we discovered two new associations of *Hirnantia* Fauna in Meitan County and on the east border of the Zunyi area

(Figure 1). The two associations dominated by *Hirnantia sagittifera* (M'Coy) with moderate diversity (14 species) are assigned to BA 2-3, a typical shallower-water environment. The sufficiency of specimens of *Hirnantia sagittifera* in the study has permitted analysis of its population dynamics following the previous study (Li, 1996) and detection of intraspecific variation. In this paper, the *Hirnantia* Fauna in Meitan County is reported for the first time and its ecology discussed. One new species, *Minutomena missa* n. sp. is systematically described. For *Hirnantia sagittifera* (M'Coy), Temple (1965) noted that significant variation exists in populations of the species, however, this fact and its significance has largely been ignored. Here, based on measurements of global representative specimens of species, together with related specimens from Yichang and this study, we quantatively analyze this variation.

Geological setting

The Kuanyinchiao Beds were also named as Kuanyinchaio Formation (e.g., Wang et al., 2018). However, due to its limited thickness which is mostly less than 2 meters, we retain the term Kuanyinchiao Beds in this study. Graptolites from shales underlying and overlying the Kuanyinchiao Beds in many nearshore areas indicate that the unit mostly lies between the *Metabolograptus extraordinarius* Biozone and the *M. persculptus* Biozone. The Kuanyinchiao Beds in South China is commonly composed of dark gray argillaceous limestone, containing abundant brachiopods, trilobites, corals, and a few other fossil groups (Rong, 1979). However, lithological and faunal variations in the Kuanyinchiao Beds have been reported at different localities (e.g., Rong et al., 2002). In many localities in the nearshore facies belt, the beds are split into two parts on lithological differences, such as those in Bijie, Renhuai, Tongzi, Fenggang, and Yinjiang, northern Guizhou, South China. The lower Bed is commonly a gray-black mudstone whereas the upper Bed argillaceous limestone (Wang et al., 2018).

The majority of the specimens in this study were collected from the Hetaoba section, Meitan, northern Guizhou Province (Figure 2). The shelly bed consists of calcareous mudstone with a thickness of only 20 cm, whereas the collection from the Baixiangyan section is confined to 15 cm of strata in calcareous mudstone.

Paleoecological significance

Community ecology. —The term “*Hirnantia* Fauna” was replaced by “*Hirnantia* Community” (Lespérance and Sheehan, 1976), and assigned to Benthic Assemblage 4, or even 5 (Sheehan, 1979), which belonged to relatively deeper-water environment settings; this was based on principally their understanding of the depth ranges of the *Hirnantia* Fauna from Pérce, Quebec. However, the *Hirnantia* Fauna may comprise more than one ecological community (Rong, 1979; Harper, 1979, 1981). Wang et al. (1987) recognized 6 communities, with four of them occupying BA3, the other two occupied BA2 and upper BA4, respectively. Detailed studies of the paleogeographic framework for the region indicate that *Hirnantia* bearing faunas may occupy a position equivalent to BA3 (Rong, 1984, 1986) or lower BA2 to BA3 (Rong and Harper, 1999), although the relative frequencies of the genera vary. Based on the data from South China, it is suggested that, the commonly, highly diverse *Hirnantia* Fauna

(>15 genera) may have lived in a deeper-water environment than that of the more strictly defined *Hirnantia* Fauna (commonly less than 10 genera) and may occupy a position in low Benthic Assemblage 3.

The brachiopod specimens collected from two sections in this study are all identified (Table 1). Although the relative abundance of common taxa such as *Hirnantia sagittifera* (M'Coy) and *Eostropheodonta hirnantensis* (M'Coy) differ between the two assemblages, the similarities in composition indicate that they may have belonged to a single paleoecologic community. Two communities dominated by *Hirnantia* and *Aphanomena* are assigned to upper BA3 (Rong, 1986; Wang et al., 1987). Rong (1986) recognized *Aphanomena-Hirnantia* Community based on the materials from Donggongsi section, Zunyi City, that is very close to the Baixiangyan section in this study. Since *Aphanomena* has been reassigned to *Eostropheodonta* (Cocks and Rong, 2000), the two assemblages are recognized as the *Hirnantia-Eostropheodonta* community, probably inhabiting a normal shallow-water environment and occupying an upper BA 3 position (Rong, 1986; Wang et al., 1987). With the assumption that a community dominated by *Paracraniops* lived in a lower BA3 environment (Wang et al, 1987), lower diversity, the absence of the two craniid genera *Petrocrania* and *Xenocrania*, together with the fact that there is a great deal of biological debris in shell beds in the Baxiangyan section, implying deposition above normal wave base, it may be inferred that the environmental setting for the *Hirnantia* Fauna in the Hetaoba section is relatively deeper than that of Baixiangyan.

Population ecology and its significance. —Since *Hirnantia* faunas immediately followed the first phase of the end Ordovician mass extinction, the ecological effect of the event was a major driver of the adaption of the *Hirnantia* Fauna to their environment. The environmental effects of the extinction can be monitored by population analysis of the main components of the *Hirnantia* Fauna.

Although fossil populations cannot be defined in the terms as those in modern biology because of the nature of the fossil record, and some attributes of fossil populations are difficult to study, paleoecologists have successfully applied their own approaches to population ecology, particularly the study of population structure or dynamics in analyzing fossil populations through time (see Dodd and Stanton, 1991; Brenchley and Harper, 1998). Many studies revealed that survivorship patterns of time-averaged normal populations without selective destruction can also represent an accurate census of their former living populations (e.g., Cate and Evans, 1992; Li, 1996). During the identification of the specimens from the Hetaoba section (GHH-02), we found that many delicate structures and even the juveniles are well preserved, which suggest that population dynamics in these fossil assemblages can be described and evaluated.

The brachiopods from Hetaoba are relatively abundant and assigned to a *Hirnantia*-*Eostropheodonta* community since specimens of two genera account for nearly 60% of the total. We measured complete specimens of the two taxa, and followed the method of Levinton and Bambach (1970), recommended by previous studies (e.g., Li, 1996), and calculated and plotted size frequency and survivorship curves for the two dominant components (Fig. 3). The size-frequency distributions of the two populations with abundant juveniles are all left-skewed, especially the population of *Hirnantia sagittifera*, indicating that there were many young individuals and fewer older ones. These two populations, featured by a high juvenile mortality and a lower mortality later in life, are characterized by survivorship curves that are concave upwards. Most of the brachiopods died young with few individuals living to maturity. The clear high juvenile mortality of *Hirnantia sagittifera* indicates that an ecological threshold may exist during the early life of the population. Compared with the curve of *Hirnantia sagittifera,* there is a lag in the peak for the population of *Eostropheodonta hirnantensis* (M’Coy), suggesting better adaptation to the same environment. The adaptation of both populations indicates that they are eurytopic, or their habitat was not as severe to affect the major components of the fauna even in the shallow-water environment after the end Ordovician mass extinction.

Materials and locations

The shelly beds of the Hirnantian Stage are widely distributed on the Yangtze Platform of South China. The brachiopod fauna in this study was collected from the lower part of the Kuanyinchiao Beds (for the division of the Kuanyinchiao Beds, see Wang et al., 2018 for details) at two sections in Meitan County, and on the east border of Zunyi (Figure 1) by the authors and their colleagues in 2011, 2017 and 2018. All specimens are preserved as internal and external molds.

The section previously investigated is located at Hetaoba, 6 km northwest of Tiancheng village, east of Meitan County Town (GPS: 27°48'07.5"N, 107°34'22.9"E). Common fossils include abundant brachiopods, some trilobites, a few bryozoans and rare gastropods which are preserved in gray-yellow calcareous mudstone. There are 603 specimens and 13 species of brachiopods identified in our collections from the Kuanyinchiao Beds (GHH-02) in the section. More than 90 specimens (33.8%) of *Hirnantia sagittifera* (M’Coy) were collected together with many *Eostropheodonta hirnantensis* (M’Coy) (15.4%), *Paromalomena macmahoni* (Reed) (10.3%), *Dalmanella testudinaria* (Dalman) (8.0%), *Palaeoleptostrophia* sp.(6.5%), *Hindella crassa* (Williams) (6.5%), *Leptaena rugosa* (Dalman) (5.8%), *Minutomena missa* n. sp. (4.1%), *Pseudopholidops partibilis* (Rong) (4.8%), and *Cliftonia* cf. *psittacina* (Wahlenberg) (2.5%); and rare *Fardenia* (*Coolinia*) sp. (0.8%), *Xenocrania haimei* (Reed) (0.5%) *Petrocrania* sp. (0.2%) and Discinidae gen. et sp. indet. (0.2%).

During recent fieldwork, a relatively low abundance shallow-water shelly brachiopod association was collected from the Baixiangyan section (GMB-01), 7 km east of Yongle village, the east border of Zunyi area (GPS: 27°51'51.8"N, 107°24'36.15" E). The fauna is dominated by brachiopods together with a few trilobites and much crinoidal debris. In Total 79 specimens were gathered, including *Hirnantia sagittifera* (M’Coy)(35.4%), *Eostropheodonta hirnantensis* (M’Coy)(31.6%), *Leptaena rugosa* (Dalman)(15.2%), *Hindella crassa* (Williams)(7.1%), *Cliftonia* cf. *psittacina* (Wahlenberg)(5.1%), *Dalmanella testudinaria* (Dalman)(4.3%) and *Paromalomena macmahoni* (Reed)(2.9%) are identified in the sample.

Repository and institutional abbreviation.—Types, figures, and other specimens examined in this study are deposited in the following institution: Nanjing Institute of Geology and Paleontology, Chinese Academy of Sciences (the catalog numbers prefixed by NIGP).

Systematic paleontology

There are 13 species belonging to 13 genera together with an undeterminate species in the two collections under study. The list of species reported is as follows, with some representative specimens being illustrated of each: Discinidae gen. et sp. indet. (Fig. 4.7), *Pseudopholidops partibilis* (Rong) (Fig. 4.1–4.3), *Xenocrania haimei* (Reed) (Fig. 4.4–4.5), *Petrocrania* sp. (Fig. 4.6), *Leptaena rugosa* (Dalman) (Fig. 4.8–4.19), *Minutomena missa* n. sp. (Fig. 5), *Paromalomena macmahoni* (Reed) (Fig. 6), *Eostropheodonta hirnantensis* (M’Coy) (Fig. 7.10–7.15), *Palaeoleptostrophia* sp. (Fig. 7.1–7.9), *Cliftonia* cf. *psittacina (Wahlenberg)* (Fig. 10.9–10.12), *Fardenia (Coolinia)* sp. (Fig. 7.16–7.18), *Dalmanella testudinaria* (Dalman) (Fig. 10.1–10.4), *Hirnantia sagittifera* (M’Coy) (Fig. 8, Fig. 9), and *Hindella crassa* (Williams) (Fig. 10.5–10.8). The one new species and two most dominant species are discussed in detail. Data and some statistical information are also provided.

Class Strophomenata Williams, Carlson, Brunton, Holmer and Popov, 1996

Order Strophomenida Öpik, 1934

Superfamily Strophomenoidea King, 1846

Family Glyptomenidae Williams, 1965

Genus *Minutomena* Zeng et al., 2016

2016 *Minutomena* Zeng *et al.*, p. 21.

Type species.—*Minutomena yichangensis* Zeng et al., 2016, p. 21, pl. 2, figs. 1–5; Kuanyinchaio Beds (Hirnantian), Yichang, western Hubei, Central China.

Minutomena missa new species

Figure 5

Type specimens.—Holotype: NIGP 170742 (Fig. 10.5). Paratypes: NIGP 170738-170741, NIGP 170743-170746. All from Kuanyinchiao Beds (Hirnantian, uppermost Ordovician) of Hetaoba section, Meitan County, northern Guizhou, South China.

Diagnosis.—Larger *Minutomena* with coarser ornamentation and relatively small cardinalia.

Occurrence.—The new species is only known from Kuanyinchiao Beds (Hirnantian, uppermost Ordovician) of Meitan County, Guizhou Province, South China.

Description.—Shells small to medium sized, 3.5 to 11.8 mm long, 4.3 to 13.6 mm wide, transversely semi-circular; ventral valve slightly convex with maximum convexity near umbo, dorsal valve nearly flat to weakly concave, lateral profile rarely resupinate. Ornamentation of multicostellae, unequally round ribs increasing mostly by branching, about 3-4 per 2 mm at 10 mm from the umbo (Fig. 5.13); fine and prominent concentric growth lines well developed. Substance of shell coarsely pseudopunctate.

Ventral interior with thin and short dental plates, divergent at an angle of about 70º–110º; muscle scars small, broad, faintly visible, rarely extending beyond ends of dental plates anteriorly; diductor scars subtriangular. Pedicle callist broad and well developed (Fig. 5.2, 5.4).

Dorsal interior with small bilobed cardinal process situated in the depressed posterior end of notothyrial platform; socket ridges short, straight or slightly concave posteriorly, widely divergent about 110º–135º; paired low and conspicuous ridges well developed in front of socket plates (Fig. 5.5–5.10), divergent about 60º–100º; muscle field not seen.

Etymology.—Latin, *missus*, with regards to having overlooked this species during the previous study.

Materials.—Eight ventral internal molds, 14 dorsal internal molds and three external molds.

Remarks.—The genus was published for the first time in a Chinese book, based on the specimens collected from the GSSP area of the Hirnantian Stage (Zeng et al., 2016). Its close relationship with *Paromalomena* was not noticed in the original study. However, the specimens in this study were mistakenly assigned to species of *Paromalomena* by the first author during the earlier study because of a lack of sufficiently informative materials. On the basis of detailed systematic study, the differences between the two genera can be summarized as: 1). Ornamentation of *Paromalomena* is of fine costellae, and increasing by intercalation; concentric wrinkles or rugae commonly irregularly developed; weak and wavy (Fig. 6.2, 6.9).

Whereas costae of *Minutomena* are coarser and increasing mostly by branching, the wrinkles or rugae rarely found on the genus (Fig. 5.13). 2). More importantly, side septa or paired low ridges are absent or are inconspicuous in *Paromalomena* (Fig. 6.10), but are essentially developed in front of socket plates in *Minutomena* (Fig. 5.11).

The new species is different from the type species mainly in two aspects: 1). The size of *Minutomena yichangensis* Zeng et al., 2016 is commonly less than 8 mm in width; whereas the specimens of *M. missa* n. sp. are mostly larger than 10 mm in width. 2). For the type species, a pair of lateral ridges are often very prominent, with its anterior end even reaching half of the valve length (Zeng et al., 2016, pl. 2 fig. 4a); however, the lateral ridges of *M. missa* n. sp. are always weaker, with their anterior ends at 1/4 to 1/5 of valve length.

Order Strophomenida Öpik, 1934

Superfamily Strophomenoidea King, 1846

Family Leptostrophiidae Caster, 1939

Genus *Eostropheodonta* Bancroft, 1949

Type species.—*Orthis hirnantensis* M’Coy, 1851; Hirnant Formation (Hirnantian), Upper Ordovician, Aber Hirnant, near Bala, Wales, UK.

Eostropheodonta hirnantensis (M’Coy, 1851)

Figure 7.10–7.15

Type specimens.—Lectotype: Internal mould of pedicle valve, A 28831, from Aber Hirnant, North Wales(M'Coy, 1852, pl. 1H, fig. 11c; Temple, 1965, pl. 19, fig. 1).

Remarks.—The ornamentation of species assigned to *Eostropheodonta* has been considered to be of taxonomic significance. However, it is highly variable even in specimens from the same population (see discussion in Rong et al., 2019). Furthermore, the development of dental plates is also variable. During the early study of the fauna, all related specimens were assigned to *Eostropheodonta*. After detailed analysis of the variation, we consider that specimens with vestigial or absent dental plates, together with the triangular and weakly impressed muscle field, are better assigned to *Palaeoleptostrophia*, rather than *Eostropheodonta*. Based on the dorsal internal molds of the species of the two genera, it is difficult to differentiate the two (Rong and Cocks, 1994). Since species of *Palaeoleptostrophia* have numerous coarse pseudopunctae in the posterolateral parts of its both ventral and dorsal internal molds, we assign the dorsal internal molds with the developed coarse pseudopunctae to *Palaeoleptostrophia*. The genus *Palaeoleptostrophia* was thought to originate in the Rhuddanian, and the oldest Leptostrophiidae lacked dental plates (Rong and Cocks 1994). There are some specimens of that family recorded as leptostrohiids in the Hirnantian rocks of Latvia and Estonia (Hints and Harper, 2015). Thus, it could be regarded as a progenitor taxon evolved during the crisis interval (Rong et al., 2019). The evolutionary relationship between *Eostropheodonta* and *Palaeoleptostrophia* will be discussed together with other genera of Leptostrophiidae in detail elsewhere.

Order Orthida Schuchert & Cooper, 1932

Suborder Dalmanellidina Moore, 1952

Superfamily Enteletoidea Waagen, 1884

Family Draboviidae Havlíček, 1950

Subfamily Draboviinae Havlíček, 1950

Genus *Hirnantia* Lamont, 1935

Type species.—Orthis sagittifera M' Coy, 1851; Hirnant Formation (Hirnantian), Upper Ordovician, Aber Hirnant, near Bala, Wales, UK.

Hirnantia sagittifera (M'Coy, 1851)

Figure 8–9

Here only the data used in the analysis are listed, see Appendix of Rong et al., 2019 for detail list.

1851 *Orthis sagittifera* M'Coy, p. 398.

1935 *Hirnantia sagittifera* (M'Coy); Lamont, p. 313, pl.7, figs. 20–22.

1965 *Hirnantia sagittifera*; Temple, p. 349–401, pl.11, fig. 8; pl. 12, figs. 1–10; pl.13, figs. 1–10; pl. 14, figs.1–8.

1968 *Hirnantia sagittifera*; Bergström, p. 10, pl. 3, fig. 13; pl. 4, figs. 1, 2.

1974 *Hirnantia magna* Rong, Xu and Yang, p. 196, pl. 92, fig. 25, 26.

1976 *Hirnantia sagittifera*; Lespérance and Sheehan, p. 723, pl. 109, figs. 3–11.

1977 *Hirnantia sagittifera*; Havlíček, p. 266, pl. 29, figs. 15–23.

1979 *Hirnantia sagittifera fecunda* Rong, pl. 1, figs. 10, 14, 15.

1980 *Hirnantia sagittifera*; Nikitin, p. 43, pl. 11, figs. 1–4.

1982 *Hirnantia sagittifera*; Cocks, p. 763–764, pl. 78, figs. 6–10; pl. 79, figs, 1–3; pl. 80, fig. 8.

1983 *Hirnantia sagittifera*; Mergl, p. 343–344, pl. 4, figs. 14–16.

1984 *Hirnantia sagittifera*; Rong, 139. 141, pl. 6, figs 1–17; pl. 7, figs 1–8; pl. 12, fig. 15; text-figs 10, 11.

1986 *Hirnantia sagittigera*; Benedetto, p. 444, pl. 1, figs 11–15; pl. 2, figs 1–3.

1987 *Hirnantia sagittifera*; Rong and Xu, p. 5–6, pl. 1, figs 9, 12, 13, 16, 17, 20–22, 24, 26.

1999 *Hirnantia sagittifera*; Villas, Lorenzo and Gutierrez-Marco, p. 193, fig. 4 (a–i).

2012 *Hirnantia sagittifera*; Hints, Parnaste and Gailite, p. 67–70, fig. 2. A–J.

2016 *Hirnantia sagittifera* morph. Bohemia Havlíček (1977), Zeng et al., p. 69–70, pl. 35, figs. 1–12; pl. 36, figs. 1–2.

2016 *Hirnantia sagittifera* morph. Poland Temple (1965), Zeng et al., p. 70–71, pl. 37, figs.1–11.

2016 *Hirnantia magna*; Zeng et al., p. 71–72, pl. 36, figs. 3–12.

2016 *Hirnantia septumis* Zeng et al, p. 72–73, pl. 38, figs. 1–12.

2016 *Hirnantia fecunda* (Rong), Zeng et al., p. 74, pl. 34, figs. 6–12.

Type specimens.—Lectotype: Internal mold of brachial valve, A 41217, from Aber Hirnant, North Wales (M’Coy, 1852, pl. 1H, fig. 17; Temple, 1965, pl. 11, fig. 8).

Remarks.—*H. sagittifera* has been described in detail by many different authors (e.g., Temple, 1965; Havlíček, 1977; Cocks, 1982; Villas et al., 1999; Hints et al., 2012 and therein). The population variation in the species was noted mainly in size and outline (Temple 1965; Cocks 1982; Cocks and Torsvik, 2002). Its adult shell width can reach 50 mm (Bergström, 1968; Hints et al., 2012) or less than 15 mm in different populations. The variation of its internal characters is also significant. Rong (1984) initially discussed the morphology variation of the cardinal process and considered it can be both simple and bilobate with peculiar crenulations on its top and sides. The variation in *H. sagittifera* is so considerable that some specimens in the same population could be easily identified as separate species.

Recently Zeng et al. (2016) monographed a *Hirnantia* Fauna from Yichang, where the GSSP of Hirnantian Stage is situated. With abundant and well-preserved specimens of *Hirnantia* from the same beds, they identified 5 species (or morphotypes), *H. sagittifera* (M'Coy) morph. Bohemia, *H. sagittifera* (M'Coy) morph. Poland, *H. magna* (Rong et al.), *H. septumis* (Zeng) and *H. fecunda* (Rong). The main criteria for discrimination were shell size and the development of muscle fields. However, these key differences are not clear with reference to their specimens.

In order to assess the value of the differences between the "5 species", we measured most of the taxa from published figures. We also compared several specimens from other collections from South China: 1) Donggongsi section (AAE-080) of Zunyi city, Guizhou province; 2) Tianbatou section of Gongxian, Sichuan province; 3) Wangjiawan section of

Yichang area, Hubei Province (the GSSP of the Hirnantian). Seven parameters are selected for dorsal internal molds, such as length, width, length of cardinalia (from anterior margin of brachiophore bases to the apex of shell), width of cardinalia (the maximum distance between two brachiophore bases), muscle field position (distance from anterior margin of muscle fields to the apex of shell), width of muscle fields, and angle of brachiophore supporting plates; six parameters are available for the ventral internal molds, as length, width, length of muscle field, width of muscle field, width of adductor muscle scar, and angle of dental plates (Appendix 1 and 2). Using PCA (principal components analysis) to interrogate the measurements above, most of the variation in these specimens can be analyzed and evaluated. Since related specimens from a previous study (Rong, 1979, 1984) were collected from the same locality, we also included them in the analysis. The results (Fig. 10.1) displayed a clear pattern of variation. No single morphological group can be clearly recognized from the scatters, indicating that the variation of each “species” is significant but continuous for both outline and internal structures.

As Zeng (2016) considered that ‘*H. sagittifera* (M’Coy) morph.’ Bohemia is different from ‘*H. sagittifera* (M’Coy) morph.’ Poland mainly on its larger size. However, as the specimens were collected from the same beds, we consider that many of ‘*H. sagittifera* (M’Coy) morph. Poland’ are immature specimens lacking the development of the dorsal muscle field. Since the material from Bohemia and Poland are both assigned to *H. sagittifera*, this morphotype is not necessarily present. Similarly, *H. magna* (Rong et al.) was erected mainly by virtue of its larger size (It can reach 40 mm) and the development of cardinalia and muscle fields based on specimens from very shallow-water (BA2) populations and is represented only by large adult shells rather than different species. Most of the shells were significantly larger than those collected from other localities at that time (Rong et al., 1974). However, large and even larger specimens *H. sagittifera* have been reported from Sweden (Bergström, 1968), Oslo (Cocks, 1982), Argentina (Benedetto, 1986) and Estonia (Hints et al., 2012), which undermine the validity of the species *H. magna*. Here, we figure the holotype of this species (Fig. 9.11) and note the similarity between the holotype of *H. magna* and the large specimens from this study (Fig. 8.11), suggesting *H. magna* can be treated as a junior synonym of *H. sagittifera* (M'Coy).

H. fecunda Rong (Zeng et al., 2016) was firstly erected as *H. sagittifera fecunda* (Rong, 1979) mainly on the basis of its shorter and narrower cardinalia and ventral muscle fields. Both the measurements and the results of the PCA analysis indicates that the variation of *H. sagittifera* encompasses that of *H. fecunda*. In this study, specimens collected from Meitan with short brachiophore bases and muscle fields are also similar to "*H. sagittifera fecunda*". However, we consider that the subspecies should be suppressed and assigned to *H. sagittifera*. The typical character of *H. septumis* Zeng is a short and narrow medium septum developed in the ventral valves. We consider that this character is an indicator of adult or gerontic individuals; these specimens are quite large with a well-developed muscle field, and some of the ventral valves have even muscle bounding ridges. Similar but weaker muscle-bounding ridges are also identified on the specimens collected from Guizhou (Fig. 9.5, 9.6).

We suggest that the "five species" of Zeng et al. (2016) together with *H. magna* (Rong et al., 1974) and *H. sagittifera fecunda* (Rong, 1979) should be reassigned to *H. sagittifera sensu stricto*. The "unique characters" described for each of the above taxa are part of wide ranging, continuous intra-specific variation rather than criteria for the establishment of different species. Besides the data from Yichang of China presented above, representative specimens of *H. sagittifera* from different regions and paleo-plates reveal further variation in these species. We measured the figured specimens from Wales (Temple, 1965; Walmsley et al., 1969; Brenchley et al., 2006), Sweden (Bergström, 1968), Quebec, Canada (Lespérance and Sheehan, 1976), Bohemia (Havlíček, 1977), Kazakhstan (Nikitin, 1980), Oslo (Cocks, 1982), Algeria (Mergl, 1983), Argentina (Benedetto, 1986), Tibet of China (Rong and Xu, 1987), Spain (Villas et al., 1999) and Estonia (Hints et al., 2012). Most of the specimens are preserved as internal molds, with the exception of those from Estonia with calcareous shells, mainly from drill cores. Using the specimens from Yichang as a template, based on their measurements (Appendix 1 and 2), the results from PCA clearly indicate that the variation of the global species can be captured in the data from Yichang, China (Fig. 10.2). Some outliers, such as the data from Estonia and Sweden, may be due to different modes of preservation, which introduce a bias into the measurements. The differences between specimens from other regions were emphasized (e.g., Zeng et al., 2016). However, we consider that given the wide variability of the Yichang material, these differences may be accommodated within the intra-specific variability of *H. sagittifera*.

Specimens of *Hirnantia sagittifera* collected from Guizhou, South China display a marked range of variation. Dorsal valves can be relatively flat or occasionally very convex (Fig. 8.13). The cardinal process can be simple (Fig. 8.15) or bilobed with crenulations (Fig. 9.10) in adult specimens. Dorsal muscle fields also vary from weak to well developed, with different outlines. The anterior pairs of dorsal muscle scars can be equal to (Fig. 8.10) or smaller (Fig. 9.11) than the posterior pairs. The angle between the brachiophore supporting plates or dental plates is clearly varied. The ventral adductor muscle field can be wide to very narrow. The anterior extremity of adductor field on a few specimens can form a short septum as described in the different species (Zeng et al., 2016). With sufficient sampling of populations, more variation will be discovered.

Acknowledgments

The authors would like to thank Wang G.X., Wang Y., Zhan R.B.,Tang P., Luan X.C., Gong F.Y. (NIGPAS) and Zhou Z.Q. (Xi'an Center of China Geological Survey) for help during fieldwork. The comments of Dr. Ian Percival and Robin Cocks together with those of the editor greatly improved the clarity of the manuscript. Financial support for this study was provided by the Strategic Priority Research Program of Chinese Academy of Sciences, Grant No. XDB26000000; the National Natural Science Foundation of China (NSFC) 41530103. Harper acknowledges support from the Leverhulme Trust (UK) and IGCP Project 653 ‘The Onset of the Great Ordovician Biodiversification Event’.

References

Amsden, T.W., 1974, Late Ordovician and Early Silurian articulate brachiopods from Oklahoma, southwestern Illinois, and eastern Missouri: Oklahoma Geological Survey Bulletin, v. 119, p. 1–154.

Bancroft, B.B., 1949, Welsh Valentian brachiopods and the *Strophomena antiquata* group of fossil brachiopods, *in* Lamont, A., ed., Welsh Valentian Brachiopods and the *Strophomena antiquata* Group of Fossil Brachiopods: Preprint from Quarry Managers' Journal. Yorkshire, Times Printing Co., Inc., Mexborough, p. 2–16.

Benedetto, J.L., 1986, The First Typical Hirnantia Fauna from South America (San Juan Province, Argentine Precordillera), *in* Racheboeuf, P.R., and Emig, C., eds., Les Brachiopodes Fossiles et Actuels: Biostratigraphie du Paleozoique (Lyon), v. 4, p. 439–447.

Benedetto, J.L., Halpern, K., and Galeano Inchausti, J.C., 2013, High-latitude Hirnantian (latest Ordovician) brachiopods from the Eusebio Ayala Formation of Paraguay, Paraná Basin: Palaeontology, v. 56, p. 61–78.

Bergström, J., 1968, Upper Ordovician brachiopods from Västergötland, Sweden: Geologica et Palaeontologica, v. 2, p. 1–37.

Brenchley, P.J., and Harper, D.A.T., 1998, Palaeoecology: Ecosystems, environments and evolution: London, Stanley Thornes, 402 p.

Brenchley, P.J., Marshall, J.D., Harper, D.A.T., Buttler, C.J., and Underwood, C.J., 2006, A late Ordovician (Hirnantian) karstic surface in a submarine channel, recording glacio-eustatic sea–level changes, Meifod, central Wales: Geological Journal, v. 41, p. 1–22.

Caster, K.E., 1939, A Devonian Fauna from Colombia: Bulletins of American Paleontology (Ithaca), v. 24, p. 1–218.

Cate, A.S., and Evans, I., 1992. Life Histories and Population–Structure of Pennsylvanian Brachiopods from North-Central Texas as Determined from Size-Frequency Analysis:

Journal of Paleontology, v. 66, p. 868–880.

Cocks, L.R.M., 1982, The commoner brachiopods of the latest Ordovician of the Oslo-Asker District, Norway: Palaeontology, v. 25, p. 755–781.

Cocks, L.R.M., and Torsvik, T.H., 2002, Earth geography from 500 to 400 million years ago: a faunal and palaeomagnetic review: Journal of the Geological Society, v. 159, p. 631–644.

Dodd J.R., and Stanton R.J.J., 1990, Paleoecology, Concepts and Applications, 2nd Edition: New York, John Wiley and Sons, 528 p.

Harper, D.A.T., 1979, The environmental significance of some faunal changes in the upper Ardmillan succession (Upper Ordovician), Girvan, Scotland: Geological Society of London, Special Publication, v. 8, p. 439–445.

Harper, D.A.T., 1981, The stratigraphy and faunas of the Upper Ordovician High Mains Formation of the Girvan district: Scottish Journal of Geology, v. 17, p. 247–255.

Harper, D.A.T., and Hints, L., 2016, Hirnantian (Late Ordovician) brachiopod faunas across Baltoscandia: A global and regional context: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 444, p. 71–83.

Harper, D.A.T., and Rong, J.Y., 1995, Patterns of change in the brachiopod faunas through the Ordovician-Silurian interface: Modern Geology, v. 20, p. 83–100.

Harper, D.A.T., and Rong, J.Y., 2001, Palaeozoic brachiopod extinctions, survival and recovery: patterns within the rhynchonelliformeans: Geological Journal, v. 36, p. 317–328.

Havlíček, V., 1950, Ramenonozci Ceskeho Ordoviku. (The Ordovician Brachiopoda from

Bohemia.): Ustredni Ustav Geologicky, Rozpravy (Praha), v. 13, p. 1–135.

Havlíček, V., 1977, Brachiopods of the order Orthida in Czechoslovakia: Rozpravy Ústředního ústava geologichého, v. 44, p. 1–327.

Hints, L., and Harper, D.A.T., 2015, The Hirnantian (Late Ordovician) brachiopod fauna of the East Baltic: Taxonomy of the key species: Acta Palaeontologica Polonica, v. 60, p. 395–421.

Hints, L., Parnaste, H., and Gailite, L.I., 2012, *Hirnantia sagittifera* (Brachiopoda) and *Mucronaspis mucronata* s.l. (Trilobita) in the Upper Ordovician of the East Baltic: taxonomy and distribution: Estonian Journal of Earth Sciences, v. 61, p. 65–81.

Jin, J.S., and Zhan, R.B., 2008, Late Ordovician Orthide and Billingsellide Brachiopods from Anticosti Island, Eastern Canada: Ottawa, NRC Research Press, 151 p.

King, W., 1846, Remarks on certain genera belonging to the Class Palliobranchiata: Annals and Magazine of Natural History (Series 1), v. 18, p. 26–42, 83–94.

Lamont, A., 1935, The Drummuck Group, Girvan: A Stratigraphical Revision, with Descriptions of New Fossils from the Lower Part of the Group: Geological Society of Glasgow, Transactions, v. 19, p. 288–334.

Lespérance, P.J., and Sheehan, P.M., 1976, Brachiopods from the Hirnantian Stage (Ordovician–Silurian) at Perce, Quebec: Palaeontology, v. 19, p. 719–731.

Levinton, J.S., and Bambach, R.K., 1970, Some ecological aspects of bivalve mortality patterns: American Journal of Science, v. 268, p. 97–112.

Li R.Y., 1996, Population dynamics of *Dalmanella testudinaria* and *Dorytreta longicrura* (brachiopods) of late Ordovician *Hirnantia* fauna from Northwestern Guizhou, SW China:

Acta Palaeontologica Sinica, v. 35, p.752—765. [in Chinese with English abstract]

M’Coy, F., 1851, On some new Cambro–Silurian Fossils: Annals and Magazine of Natural History (London), v. Ser.2, p. 387–409.

M’Coy, F., 1852, Systematic Description of the British Paleozoic Fossils in the Geological Museum of the University of Cambridge. Fasc. v. 2 , p. 185–660.

Mergl, M., 1983, New Brachiopods (Cambrian-Ordovician) from Algeria and Morocco (Mediterranean Provinces): Casopis pro Mineralogii a Geologii (Prague), v. 28, p. 337–348.

Moore, R.C., 1952, Brachiopods, *in* Moore, R.C., Lalicker, C.G., and Fischer, A.G., eds., Invertebrate fossils: New York, McGraw–Hill, p. 197–267.

Nikitin, I.F., Popov, L.E., and Rukavishnikova, T.B., 1980, Articulate brachiopods, *in* Apollonov, M.K., Bandaletov, S.M. and Nikitin, I.F., eds., The Ordovician-Silurian boundary in Kazakhstan: Alma-Ata, Nauka, p. 37–74.

Öpik, A., 1934, Ueber Klitamboniten: Tartu Universitatis (Dorpatensis): Acta and Commentationes, Ser.A, v. 26, p.1–239.

Owen, A.W., Harper, D.A.T., and Rong, J.Y., 1991, Hirnantian trilobites and brachiopods in space and time, *in* Barnes, C.R., and Williams, S.H., eds., Advances in Ordovician Geology: Geological Survey of Canada Paper, p. 179–190.

Rong, J.Y., 1979, The *Hirnantia* fauna of China with comments on the Ordovician-Silurian boundary: Journal of Stratigraphy (formerly Acta Stratigraphica Sinica), v. 3, p. 1–29. [in Chinese]

Rong, J.Y., 1984, Brachiopods of Latest Ordovician in the Yichang District, Western Hubei, Central China, *in* Mu, E.Z., ed., Proceedings of a Symposium on the Stratigraphy and Palaeontology of Systemic Boundaries in China, 1, Ordovician–Silurian Boundary: Hefei, Anhui Science and Technology Publishing House, p. 111–176.

Rong, J.Y., 1986, Ecostratigraphy and community analysis of the Late Ordovician and Silurian in Southern China, *in* Palaeontological Society of China, ed., Selected Paper Collections of the Annual Symposium of the thirteenth and fourteenth committee of the Palaeontological Society of China: Hefei, Anhui Science and Technology Press, p. 1–24. [in Chinese with English summary]

Rong, J.Y., Aung, K. P., Zhan, R.B., Huang, B., Harper, D.A.T., Chen, D., Zhou, H.H., and Zhang, X.L., 2019, The latest Ordovician *Hirnantia* brachiopod Fauna of Myanmar: Significance of new data from the Mandalay Region: Palaeoworld, published online: https://doi.org/10.1016/j.palwor.2019.07.002.

Rong, J.Y., Chen , X., and Harper, D.A.T., 2002, The latest Ordovician *Hirnantia* fauna (Brachiopoda) in time and space: Lethaia, v. 35, p. 231–249.

Rong, J.Y., and Cocks, L.R.M., 1994, True *Strophomena* and a Revision of the Classification and Evolution of Strophomenoid and Strophodontoid Brachiopods: Palaeontology, v. 37, p. 651–694.

Rong, J.Y., and Harper, D.A.T., 1988, The Ordovician-Silurian boundary and the *Hirnantia* fauna: Lethaia, v. 21, p. 168.

Rong, J.Y., and Harper, D.A.T., 1999, Brachiopod survival and recovery from the latest Ordovician mass extinctions in South China: Geological Journal, v. 34, p. 321–348.

Rong, J.Y., and Xu, H.K., 1987, Terminal Ordovician *Hirnantia* fauna of the Xainza District, northern Xizang: Bulletin of Nanjing Institute of Geology and Palaeontology, Academia Sinica, v. 11, p. 1–19. [in Chinese, with English abstract]

Rong, J.Y., Xu, H.K., and Yang, X.C., 1974, Silurian brachiopods, *in* Nanjing Institute of Geology and Palaeontology, Academia Sinica, ed., A Handbook of Stratigraphy and Palaeontology of Southwest China: Beijing, Science Press, p. 195–208. [in Chinese]

Schuchert, C., and Cooper, G.A., 1932, Brachiopod genera of the Suborders Orthoidea and Pentameroidea: Peabody Museum Natural History Memoir, v. 4, p. 1–270.

Sheehan, P.M., 1979, Swedish Late Ordovician Marine Benthic Assemblages and their bearing on Brachiopod Zoogeography, *in* Gray, J. and Boucot, A.J., eds., Historical Biogeography, Plate Tectonics, and the Changing Environment, Proceedings of the Annual Biology Colloquium and Selected Papers, Corvallis: Oregon State University Press, v. 37, p. 61–73.

Temple, J.T., 1965, Upper Ordovician brachiopods from Poland and Britain: Acta Palaeontologica Polonica, v. 10, p. 379–427.

Villas, E., Lorenzo, S., and Gutierrez-Marco, J.C., 1999, First record of a *Hirnantia* Fauna from Spain, and its contribution to the Late Ordovician palaeogeography of northern Gondwana: Earth and Environmental Science Transactions of The Royal Society of Edinburgh, v. 89, p. 187–197.

Waagen, W., 1884, Salt Range fossils, vol. I, part 4. Productus Limestone fossils, Brachiopoda: Memoirs of the Geological Survey of India, Palaeontologia Indica (series 13), v. fasc. 3–4, p. 547–728.

Walmsley, V.G., Boucot, A.J., and Harper, C.W., 1969, Silurian and Lower Devonian salopinid brachiopods: Journal of Paleontology, v. 43, p. 492–516.

Wang, G.X., Zhan, R.B., Rong, J.Y., Huang, B., Percival, I.G., Luan, X.C., and Wei, X., 2018, Exploring the end-Ordovician extinctions in Hirnantian near-shore carbonate rocks of northern Guizhou, SW China: A refined stratigraphy and regional correlation: Geological Journal, v. 53, p. 3019–3029.

Wang, Y., Boucot, A.J., Rong, J.Y., and Yang, X.C., 1987, Community Paleoecology as a Geologic Tool: The Chinese Ashgillian-Eifelian (Latest Ordovician Through Early Middle Devonian) as an Example: Geological Society of America, Special Papers (Boulder), v. 211, p. 100.

Williams, A., 1965, Suborder Strophomenidina, *in* Moore, R.C. ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda: The Geological Society of America and The University of Kansas Press, p. 362–412.

Williams, A., Carlson, S.J., Brunton, C.H.C., Holmer, L.E., and Popov, L., 1996, A supra-ordinal classification of the Brachiopoda: Philosophical Transactions of the Royal Society of London Series B–Biological Sciences, v. 351, p. 1171–1193.

Wright, A.D., 1968, A Westward Extension of the Upper Ashgillian *Hirnantia* Fauna: Lethaia, v. 1, p. 352–367.

Zhan, R.B., Liu J.B., Ian G.P., Jin J.S., and Li G.P., 2010, Biodiversification of Late Ordovician *Hirnantia* Fauna on the Upper Yangtze Platform, South China: Science China, Earth Sciences, v. 53, p. 1800–1810.

Zeng, Q.L., Chen, X.H., Wang, C.S., Zhang, M., and Han, H.Q., 2016, *Hirnantia* Fauna of Yichang District, its Paleoecology and Extinction, and the Biotic Evolution in Llandovery:

Wuhan, China University of Geosciences Press, 112 p. [in Chinese, with English abstract]

Figure and table Captions

Figure 1. Map showing the locations of the two sections, from where the near-shore *Hirnantia* brachiopod Fauna was discovered.

Figure 2. The Hirnantia Fauna occurring in the Kuanyinchiao Beds at two sections from northern Guizhou, South China.

Figure 3. Size frequency histograms and survivorship curves for the two populations of the dominant components (*Hirnantia* and *Eostropheodonta*) in the Hetaoba section (GHH-02).

Figure 4. *Pseudopholidops partibilis* (Rong) (**1–3**), (**1**) a dorsal (?) internal mold (NIGP 170724); (**2, 3**) and two dorsal(?) external molds (NIGP 170724, 170726); *Xenocrania haimei* (Reed) (**4, 5**), dorsal external mold (**4**) and its local enlargement (**5**) showing detail of ornamentation (NIGP 170727); *Petrocrania* sp., (**6**) dorsal internal mold (NIGP 170728); Discinidae gen. et sp. indet. (**7**) dorsal valve exterior (NIGP 170729); *Leptaena rugosa* (Dalman) (**8–19**), (**8–11**) four ventral internal molds (NIGP 170730–170733); (**12**) dorsal internal mold (NIGP 170734); (**13–15**) dorsal internal mold (**13**), its latex cast (**15**) with local enlargement showing detail of cardinalia (**14**) (NIGP 170735); (**17, 18**) dorsal internal mold (**17**) and its latex cast (**18**) (NIGP 170736); (**16, 19**) dorsal external mold (**19**) and its local

enlargement (**16**) showing detail of ornamentation (NIGP 170737). All specimens from GHH-02 except (**17**) and (**18**) from GMB-01. Scale bar represent 2 mm except where noted.

Figure 5. *Minutomena missa* n. sp. (**1–4**) four ventral internal molds (NIGP 170738–170741); (**5, 6, 8**) dorsal internal mold (**5**), its latex cast (**8**) with local enlargement showing detail of cardinalia (**6**) (NIGP 170742); (**7, 11**) dorsal internal mold (**11**) and local enlargement of its latex (**7**) showing detail of cardinalia (NIGP 170743); (**9, 10**) two dorsal internal molds (NIGP 170744, 170745); (**12, 15, 16**) dorsal internal mold (**12**), its external mold (**16**) with local enlargement of its latex (**15**) showing detail of ornamentation (NIGP 170746); (**13, 14**) dorsal external mold (**13**) and its local enlargement (**14**) showing detail of ornamentation (NIGP 170747). All specimens from GHH-02. Scale bar represents 2 mm except where noted.

Figure 6. *Paromalomena macmahoni* (Reed). (**1, 2**) two ventral internal molds (NIGP 170748, 170749); (**3, 4, 10, 11**) four dorsal internal molds (NIGP 170750–170753); (**5–8**) dorsal internal mold (**5**) and its latex cast (**8**), with local enlargement of mold (**6**) and cast (**7**) showing detail of cardinalia (NIGP 170754); (**9, 12**) dorsal external mold (**12**) and its local enlargement (**9**) showing detail of ornamentation (NIGP 170755). All specimens from GHH-02. Scale bars represent 2 mm except where noted.

Figure 7. (**1–9**) *Palaeoleptostrophia* sp. (**1, 4**) two ventral internal molds (NIGP 170756, 170757); (**2, 3**) ventral internal mold and its local enlargement showing absence of dental

plates (NIGP 170758); (**5, 8, 9**) dorsal internal mold (**5**), its external mold (**8**) with local enlargement (**9**) showing detail of ornamentation (NIGP 170759); (**6, 7**) two dorsal internal molds (NIGP 170760, 170761); *Eostropheodonta hirnantensis* (M'Coy) (**10–15**), (**10–12**) three ventral internal molds (NIGP 170762–170764); (**13, 14**) two dorsal internal molds (NIGP 170765, 170766); (**15**) local enlargement of a dorsal internal mold (NIGP 170767); *Fardenia (Coolinia)* sp. (**16–18**), (**16, 18**) ventral internal mold and its external mold (NIGP 170768); (**17**) dorsal internal mold (NIGP 170769). All specimens from GHH-02. Scale bars represent 2 mm.

Figure 8. *Hirnantia sagittifera* (M'Coy). (**1–3, 6**) four ventral internal molds (from GHH-02, NIGP 170770–170773); (**4, 5, 7–9, 14**) seven dorsal internal molds (all from GHH-02 except 7 from GMB-01, NIGP 170774–170779); (**10, 16**) dorsal internal mold and its external mold (from GHH-02, NIGP 170780); (**11–13, 15**) dorsal internal mold (**11**) and its posterior view (**13**), its latex cast (**15**) with local enlargement (**12**) showing detail of cardinalia (from GMB-01, NIGP 170781). Scale bars represent 2 mm.

Figure 9. *Hirnantia sagittifera* (M'Coy). (**1–3**) ventral internal mold (**1**), dorsal internal mold (**2**) with its latex cast (**3**), from Huangtian section of Gongxian, Sichuan province (NIGP 170782, 170783); (**4, 7**) ventral internal mold and a dorsal internal mold, from Wangjiawan section of Yichang area (the GSSP of Hirnantian Stage) (NIGP 170784, 170785); (**5, 6**) ventral internal and its latex cast (from AAE-080, NIGP 170786); (**9, 10**) dorsal internal mold and its latex cast (from AAE-080, NIGP 170787); (**8, 11**) ventral internal mold and dorsal

internal mold (AAE-080), the two specimens were designated as paratype and holotype of *Hirnantia magna* Rong et al., 1974 separately (NIGP 22275, 22276). Scale bars represent 2 mm.

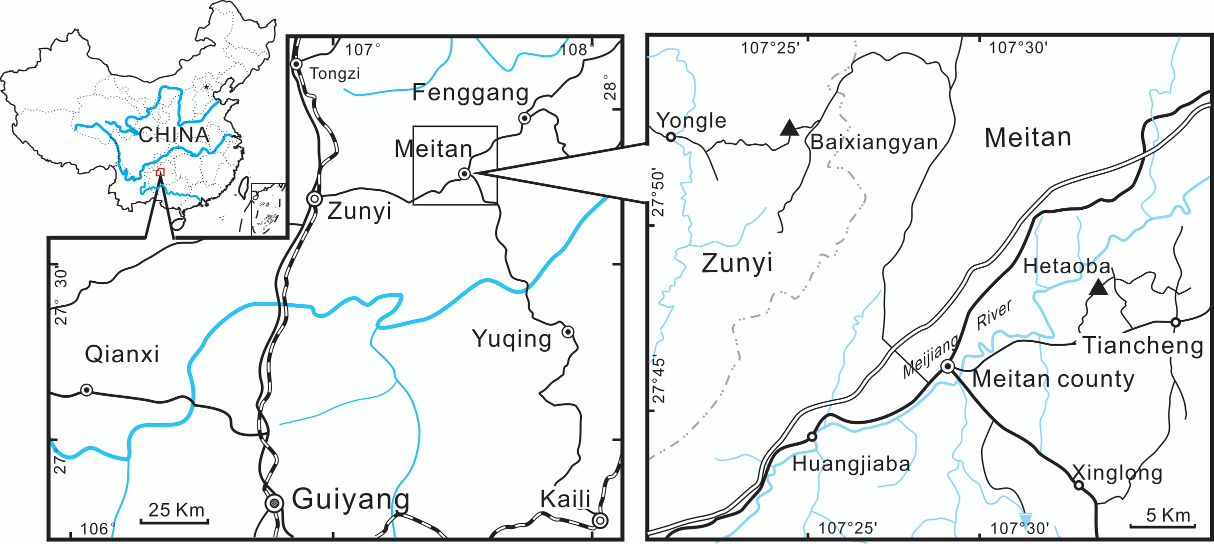
Figure 10. Principal components analysis of data for 6 parameters for seven “species” of *Hirnantia* (**1**), and globally-distributed *Hirnantia sagittifera* (**2**), to show the variation.

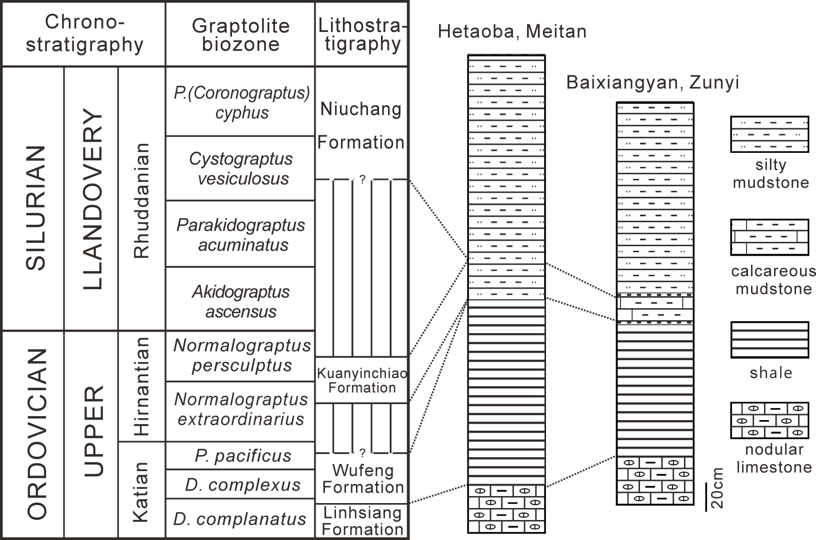
Figure 11. *Dalmanella testudinaria* (Dalman) (**1–4**), (**1**) ventral internal mold (NIGP 170788); (**2–4**) three dorsal internal molds (NIGP 170789–170791); *Hindella crassa* (Williams) (**5–8**), (**5, 6**) two ventral internal molds (NIGP 170792, 170793); (**7, 8**) two dorsal internal molds (NIGP 170794, 170795); *Cliftonia* cf. *psittacina* (Wahlenberg) (**9–12**), (**9**) ventral internal mold (NIGP 170796); (**10**) ventral external mold (NIGP 170797); (1**1, 12**) two dorsal internal molds (NIGP 170798, 170799). All from GHH-02 except **11** and **12** from GMB-01. Scale bars represent 2 mm.

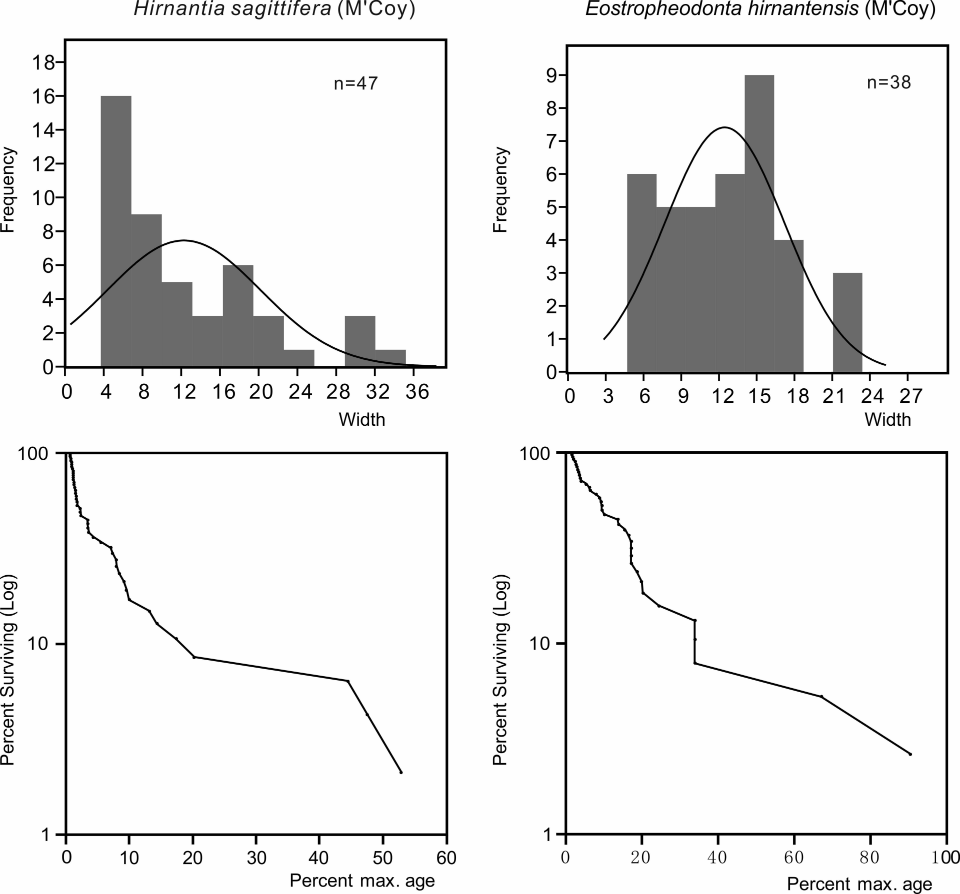
Table 1. Taxonomic list at species level for this study with numbers of specimens from the two collections.

Table 1. Taxonomic list at species level for this study with numbers of specimens from the two collections.

Species	Hetaoba section (GHH-02)			Baixiangyan section (GMB-01)		
	Ventral internal molds	Dorsal internal molds	External molds	Ventral internal molds	Dorsal internal molds	External molds
Pseudopholidops partibilis (Rong)	12	8	9			
Petrocrania sp.		1	1			
Xenocrania haimei (Reed)		1	2			
Leptaena rugosa (Dalman)	15	11	9	5	4	3
Paromalomena macmahoni (Reed)	19	27	16		2	
Minutomena missa n.sp.	8	14	3			
Eostropheodonta hirnantensis (M'Coy)	43	21	30	12	2	11
Palaeoleptostrophia sp.	26	4	9			
Fardenia (*Coolinia*) sp.	1	1	3			
Hirnantia sagittifera (M'Coy)	87	78	41	11	14	3
Dalmanella testudinaria (Dalman)	9	31	8	1	2	
Cliftonia cf. *psittacina* (Wahlenberg)	6	2	7	1	2	1
Hindella crassa (Williams)	16	14	9	1	4	
Discinidae gen. et sp. indet.		1				


CHINA
107°
108°
Tongzi
Fenggang
28°
Meitan
Zunyi
27° 30'
Qianxi
Yuqing
27°
Guiyang
Kaili
25 Km
106°
107°25'
107°30'
Yongle
Baixiangyan
Meitan
27°50'
Zunyi
Hetaoba
River
Meijiang
Tiancheng
Meitan county
27°45'
Huangjiaba
Xinglong
107°25'
107°30'
5 Km

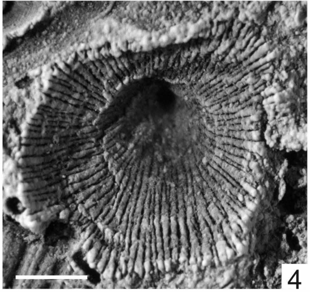

Chrono-stratigraphy
Graptolite biozone
Lithostratigraphy
SILURIAN
LLANDOVERY
Rhuddanian
ORDOVICIAN
UPPER
Hirnantian
Katian
P.(Coronograptus) cyphus
Cystograptus vesiculosus
Parakidograptus acuminatus
Akidograptus ascensus
Normalograptus persculptus
Normalograptus extraordinarius
P. pacificus
D. complexus
D. complanatus
Niuchang Formation
?
Kuanyinchiao Formation
?
Wufeng Formation
Linhsiang Formation
Hetaoba, Meitan
Baixiangyan, Zunyi
20cm
silty mudstone
calcareous mudstone
shale
nodular limestone


Hirnantia sagittifera (M'Coy)
Eostropheodonta hirnantensis (M'Coy)
n=47
n=38
Frequency
Width
0
2
4
6
8
10
12
14
16
18
20
24
28
32
36
0
1
2
3
4
5
6
7
8
9
3
6
9
12
15
18
21
24
27
Percent Surviving (Log)
Percent max. age
1
10
100
0
10
20
30
40
50
60
0
20
40
60
80
100

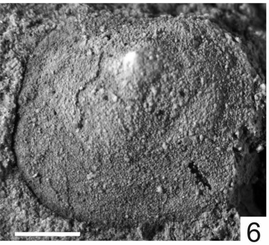
1

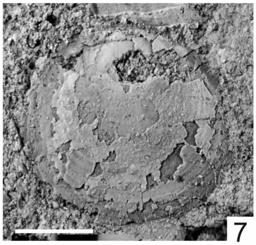
2

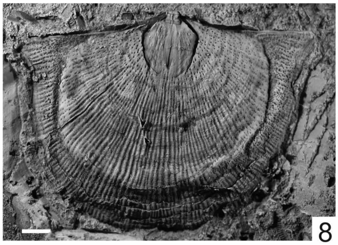
3


4

5

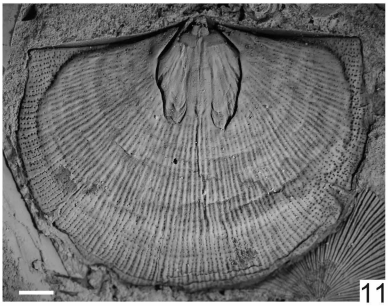

6


7

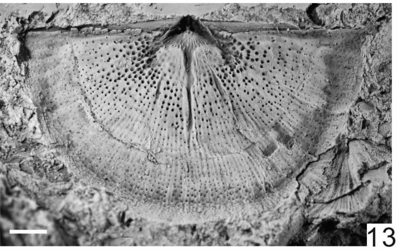

8

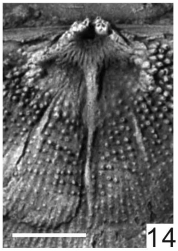

9

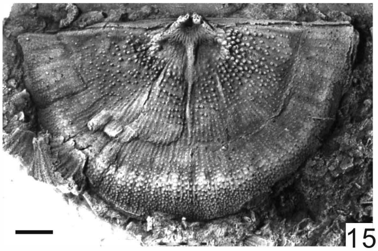

10

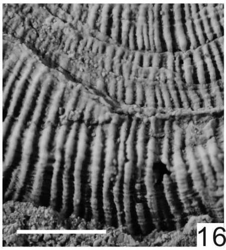

11

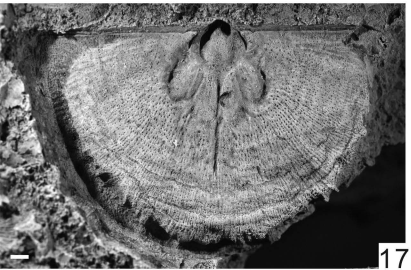

12

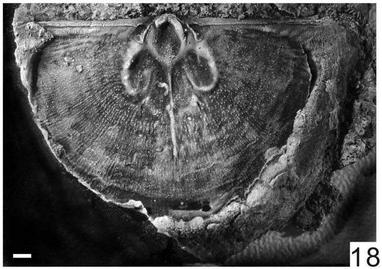

13

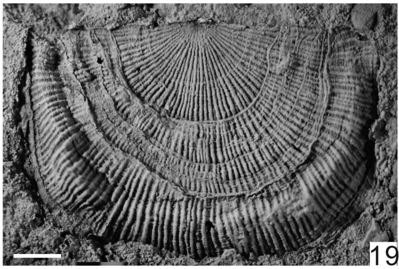

14

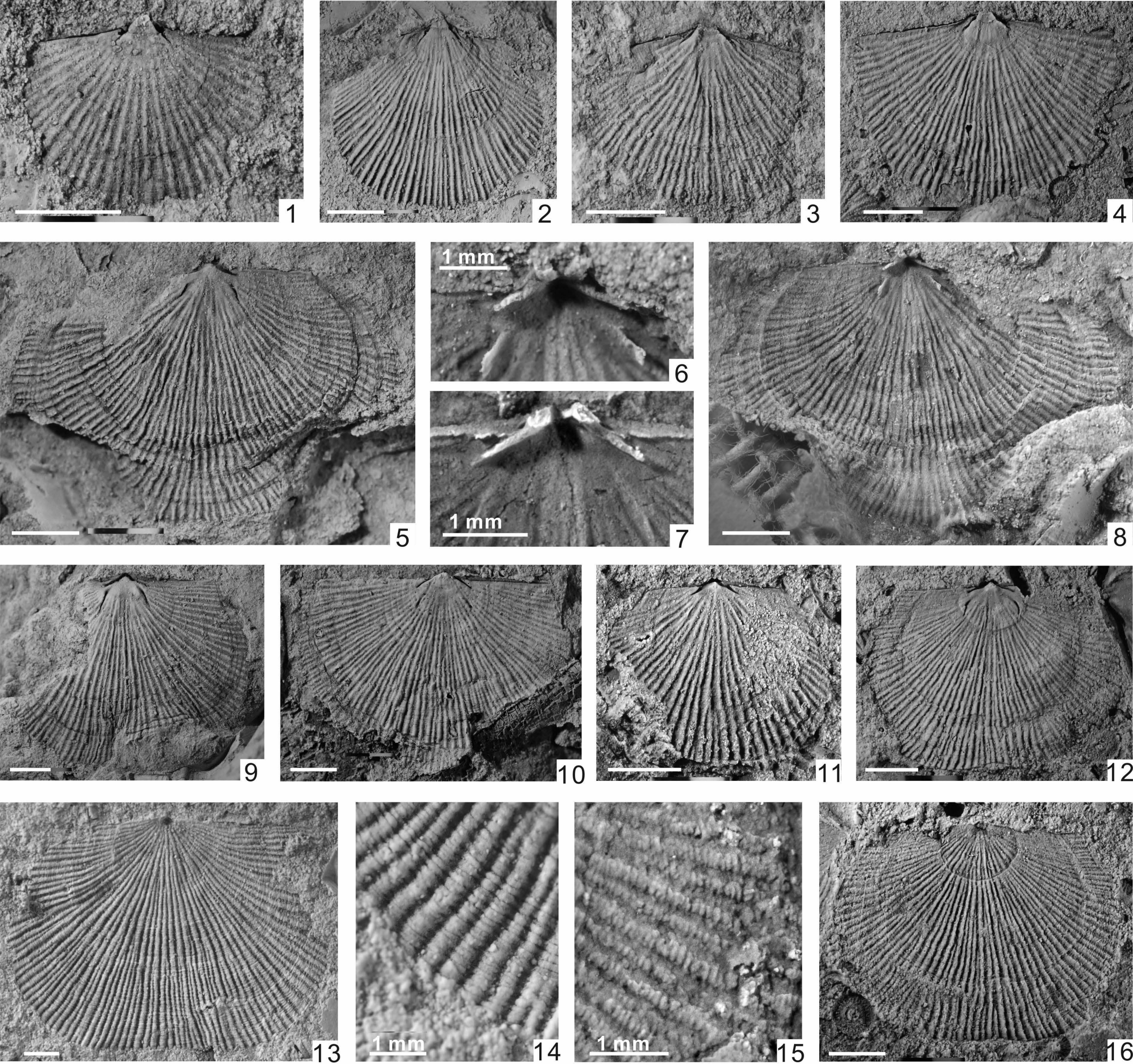

15

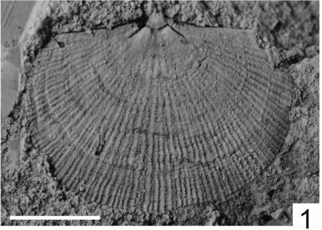

16

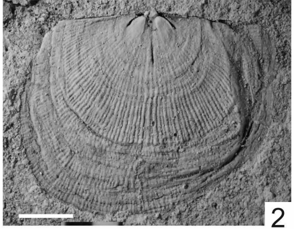

17

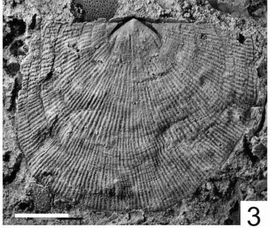

18

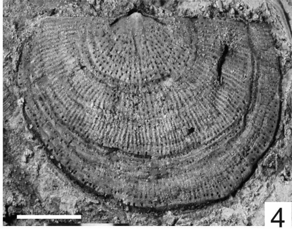

19

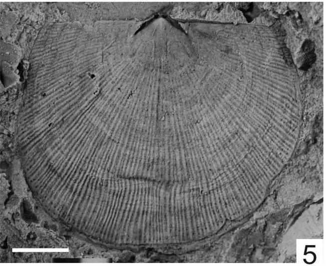

1
2
3
4
5
1 mm
6
1 mm
7
8
9
10
11
12
13
1 mm
14
1 mm
15
16

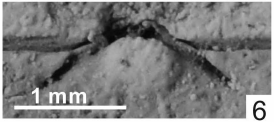

1


2

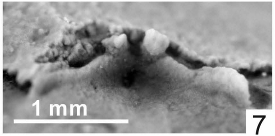

3


4

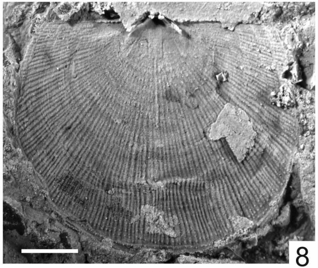

5

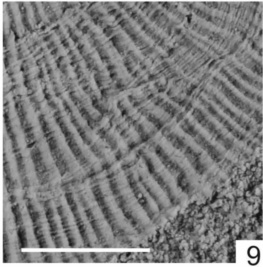


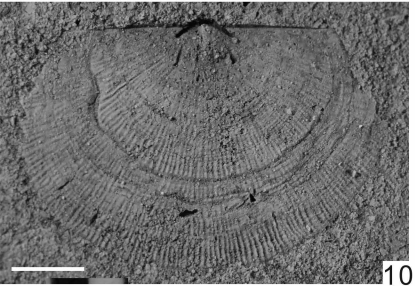
6

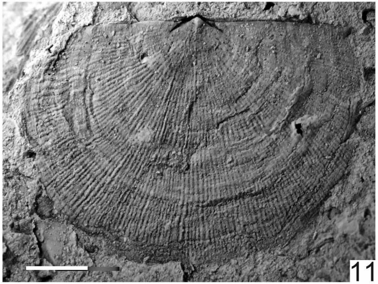


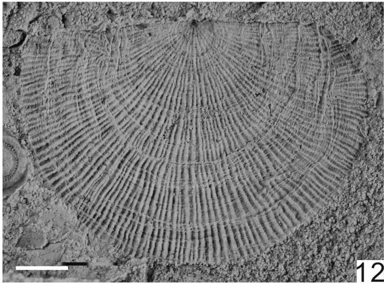
7

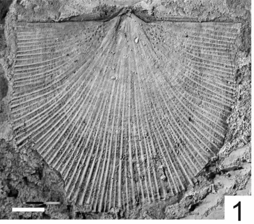

8

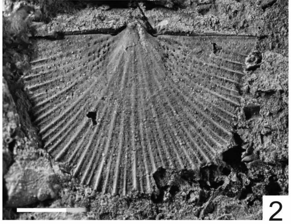

9


10

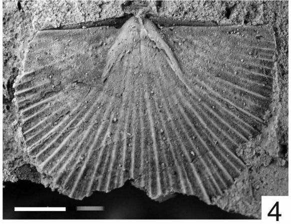

11

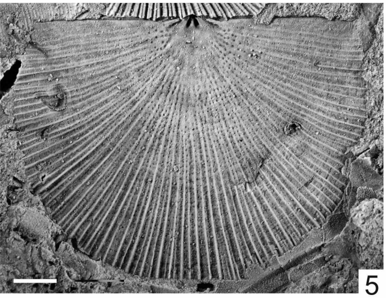

12

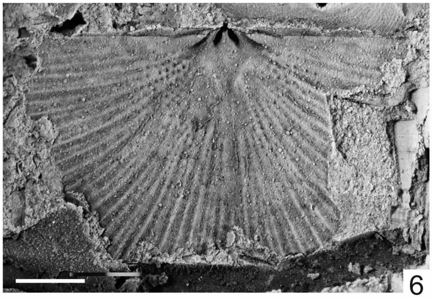

1

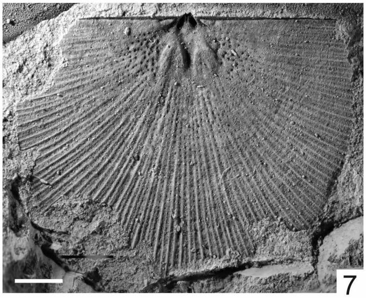

2

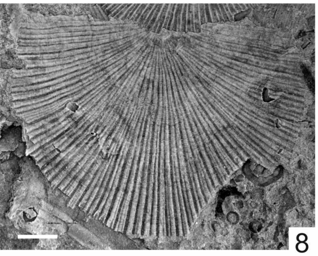

3

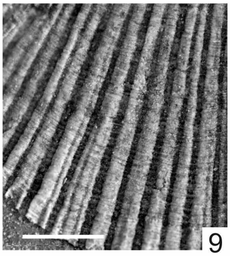

4

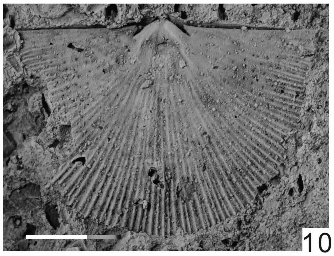

5

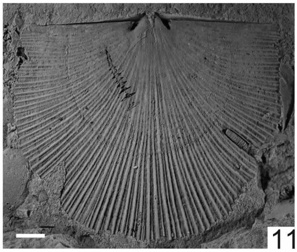

6

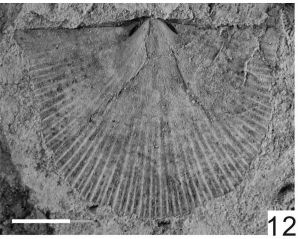

7


8

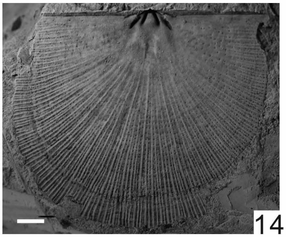

9

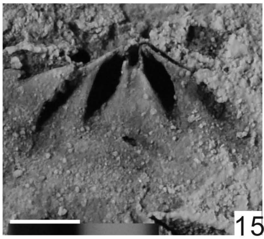

10

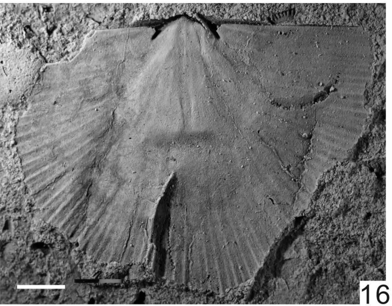

11

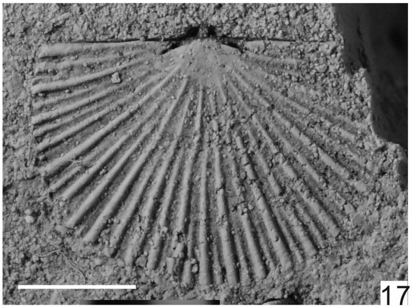

12

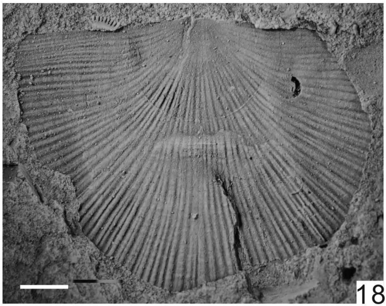

13

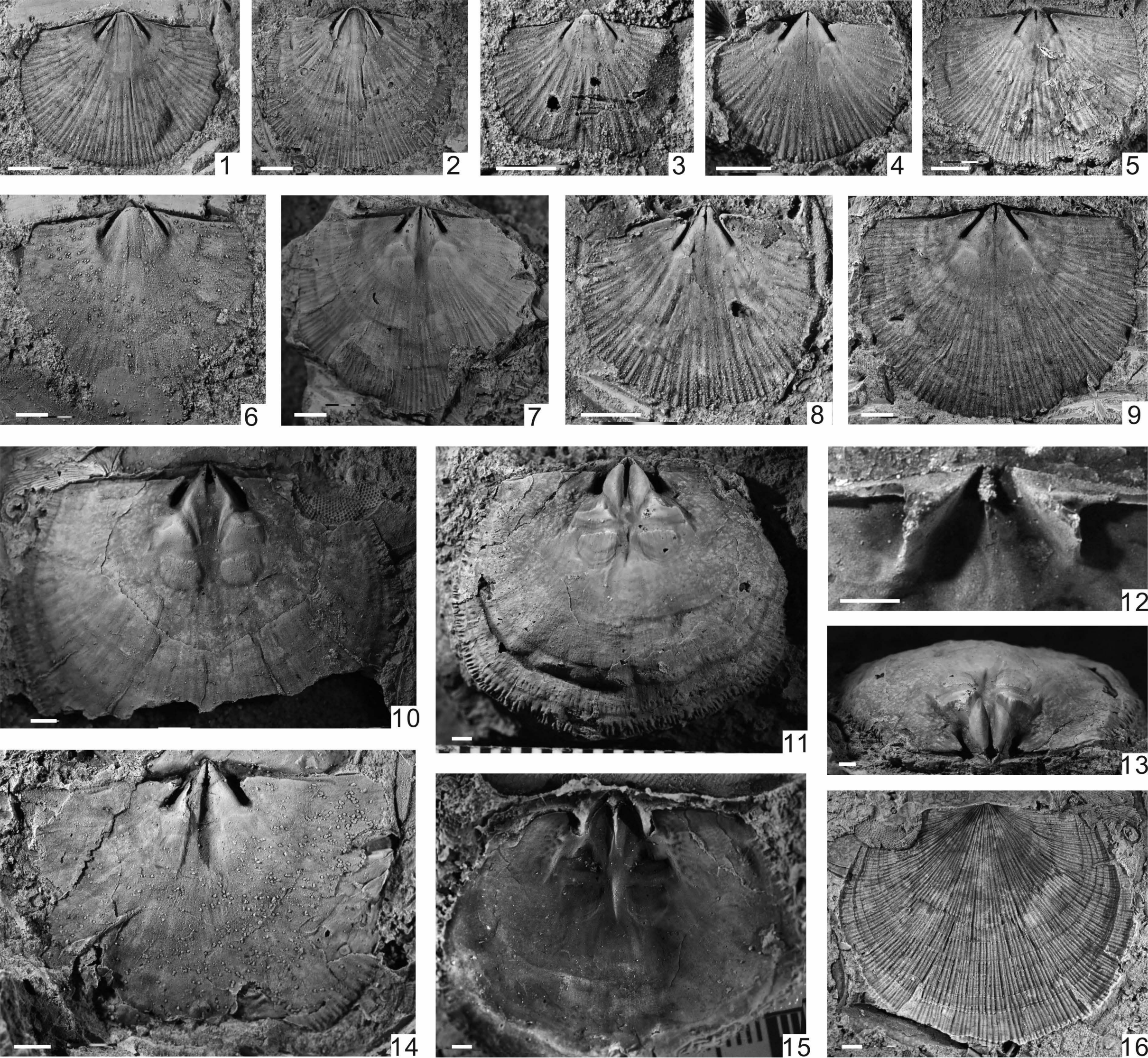

14

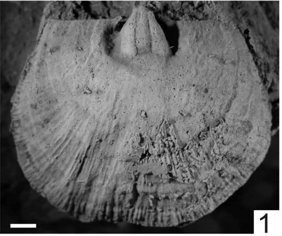

15

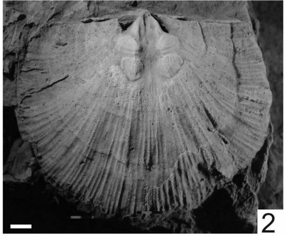

16

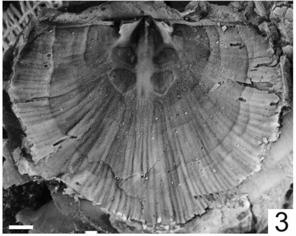

17

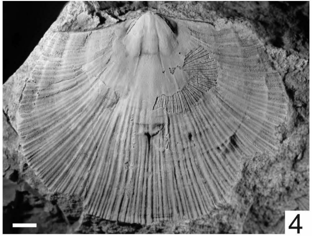

18


1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16

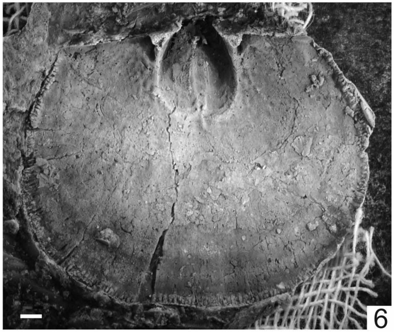

1

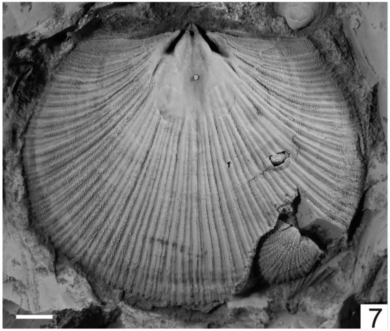

2

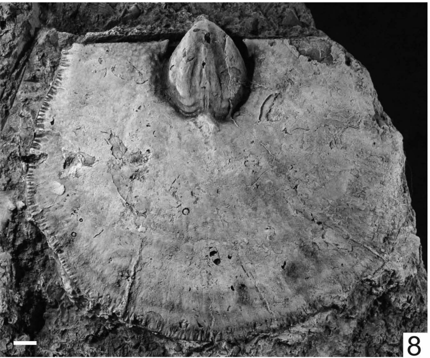

3


4


5


6

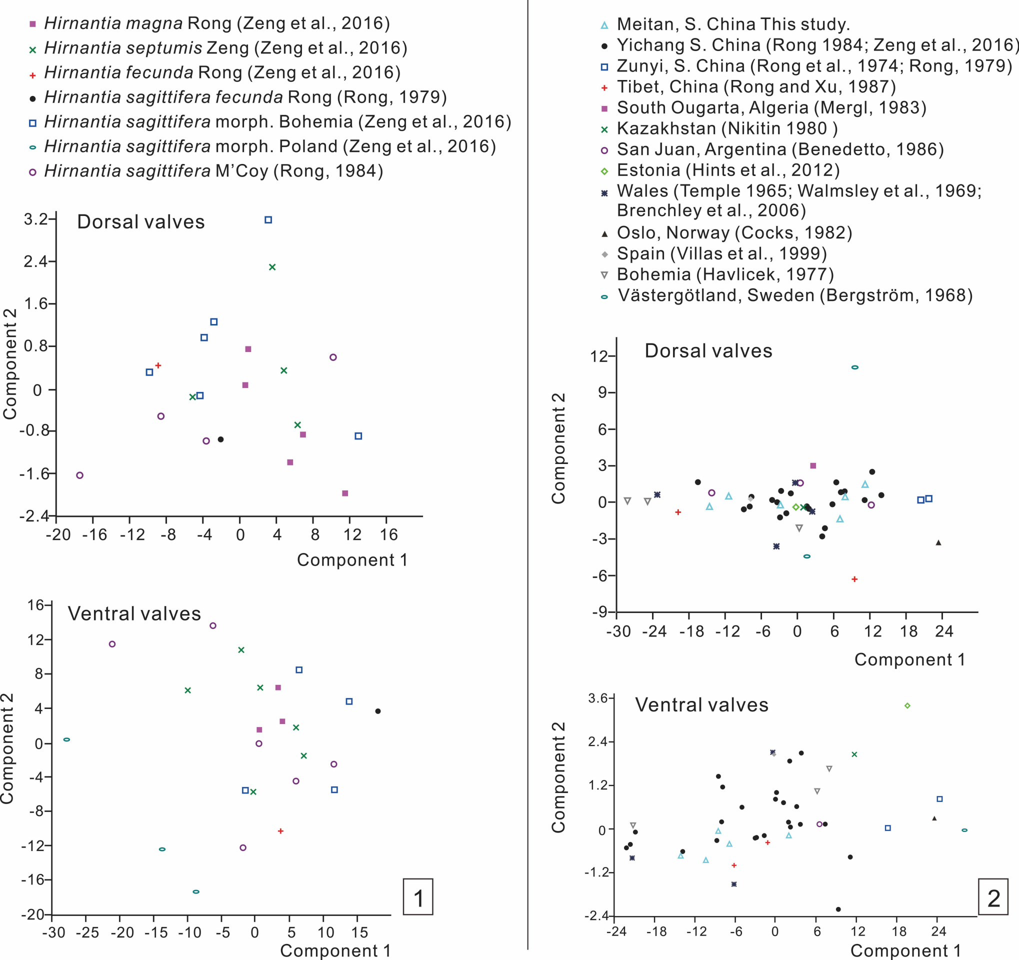

7

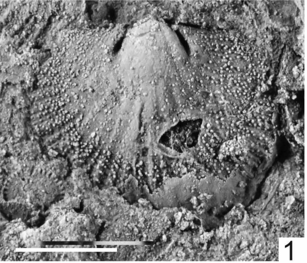

8

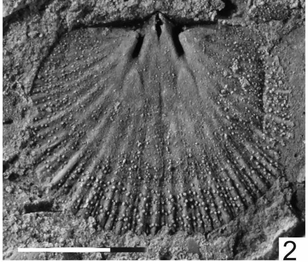

9

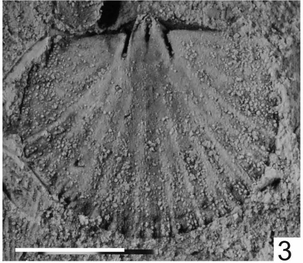

10

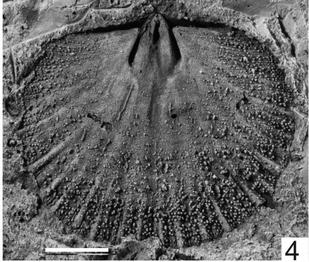

11

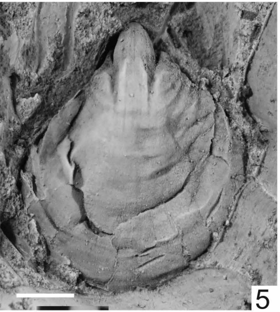

■ Hirnantia magna Rong (Zeng et al., 2016)
× Hirnantia septumis Zeng (Zeng et al., 2016)
+ Hirnantia fecunda Rong (Zeng et al., 2016)
● Hirnantia sagittifera fecunda Rong (Rong, 1979)
□ Hirnantia sagittifera morph. Bohemia (Zeng et al., 2016)
⊖ Hirnantia sagittifera morph. Poland (Zeng et al., 2016)
○ Hirnantia sagittifera M'Coy (Rong, 1984)
Dorsal valves
3.2
2.4
1.6
0.8
0
-0.8
-1.6
-2.4
Component 2
-20
-16
-12
-8
-4
0
4
8
12
16
Component 1
Ventral valves
16
12
8
4
0
-4
-8
-12
-16
-20
Component 2
-30
-25
-20
-15
-10
-5
0
5
10
15
Component 1
1
△ Meitan, S. China This study.
● Yichang S. China (Rong 1984; Zeng et al., 2016)
□ Zunyi, S. China (Rong et al., 1974; Rong, 1979)
+ Tibet, China (Rong and Xu, 1987)
■ South Ougarta, Algeria (Mergl, 1983)
× Kazakhstan (Nikitin 1980)
○ San Juan, Argentina (Benedetto, 1986)
◇ Estonia (Hints et al., 2012)
✱ Wales (Temple 1965; Walmsley et al., 1969; Brenchley et al., 2006)
▲ Oslo, Norway (Cocks, 1982)
◆ Spain (Villas et al., 1999)
▽ Bohemia (Havlicek, 1977)
⊖ Västergötland, Sweden (Bergström, 1968)
Dorsal valves
12
9
6
3
0
-3
-6
-9
Component 2
-30
-24
-18
-12
-6
0
6
12
18
24
Component 1
Ventral valves
3.6
2.4
1.2
0
-1.2
-2.4
Component 2
-24
-18
-12
-6
0
6
12
18
24
Component 1
2

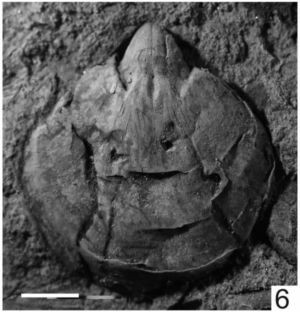

1

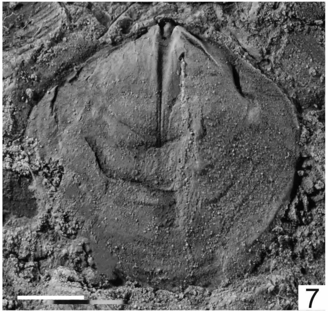

2

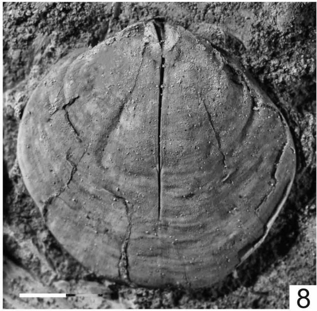

3

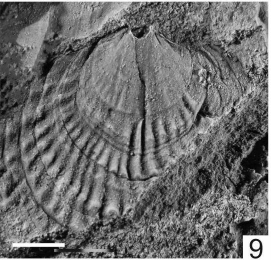

4

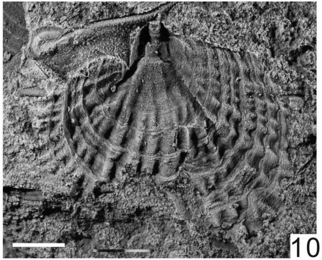

5

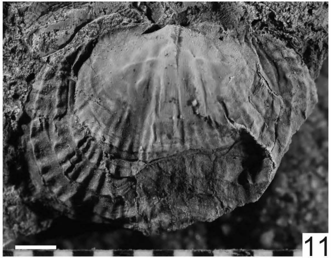

6

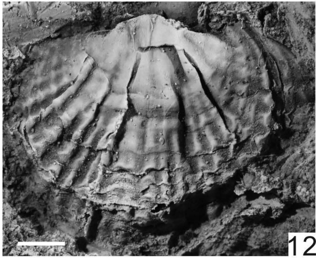

7


8


9


10


11


12