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Silicified Mississippian brachiopods from Muhua, southern China: Rhynchonellides, athyridides, spiriferides, spiriferinides, and terebratulides

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The second part of the monograph of the silicified brachiopod fauna from the Muhua Formation concludes with the descriptions of 36 species belonging to 32 genera and 22 families. Eighteen species are reported in open nomenclature. Two new rhynchonellide species are described: *Coledium bruntoni* sp. nov. and *Pleuropugnoides calcaris* sp. nov. The described brachiopod fauna is dominated by spiriferides (16 species), rhynchonellides (9 species), and athyridides (7 species), while spiriferinides and terebratulides are represented by 1 and 3 species, respectively. The brachiopod fauna from the Muhua Formation is characterised by remarkably high species diversity. Together with those species described in the first part of the monograph the fauna includes 69 species. The study of the brachiopod faunal dynamics during the late Famennian–late Tournaisian in southern China reveals that after a decline in the generic diversity at the Devonian–Carboniferous boundary (D–C boundary event), the Early Tournaisian brachiopod fauna shows slight impoverishment. In the middle Tournaisian the brachiopod fauna from South China shows an explosive increase in diversity on generic level which is well exemplified by the material from Muhua. The brachiopod fauna from the Muhua Formation represents a fully recovered high diversity fauna consisting of forms representing a wide spectrum of attachment strategies as well as highly specialised forms (e.g., micromorphs) adapted to special kinds of ecological niches. Numerous evidence of the biotic interaction between brachiopods and other co-occurring fauna have been revealed in the material from Muhua. These are drill holes of predatory origin, borings made on dead shells as post-mortem infestation, shell damages and malformations, and parasitic infestations.

Key words: Brachiopoda, biotic interaction, faunal dynamics, silicification, Carboniferous, Mississippian, Tournaisian, China.

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Introduction

The present paper constitutes the second part of the monograph of the silicified brachiopod fauna from the Muhua Formation which outcrops are scattered around villages of Muhua and Gedongguan in the Guizhou Province, South China (Fig. 1). In the first part of the monograph (Sun and Baliński 2008) we gave remarks on the geological setting, sampling, stratigraphy, material, and methods, as well as taxonomic descriptions of inarticulate (lingulides, craniides) and part of articulate (strophomenides, productides, orthotetides, and orthides) brachiopods. Here, we describe remaining taxa of the brachiopod fauna from the Muhua Formation along with evidence of biotic interactions observed in the studied material. We discuss also the brachiopod faunal dynamics in a broader spatial and temporal range, i.e., during the late Famennian through Tournaisian in the southern China.

The brachiopod fauna comes from limestone lenses (olistoliths) formed by sliding of sediment with skeletal debris down the slope (Olempska 1999; Sun and Baliński 2008). It is composed of species which almost certainly come from slightly different neighbouring areas and are thus adapted to diverse habitats. It can then be expected that several brachiopod samples collected from the Muhua Formation represent more or less space-averaged associations which dwelt in slightly different locations on the sea floor (Sun and Baliński 2008).

The brachiopod fauna from the Muhua Formation is characterised by remarkably high species diversity, probably the highest known from such limited time interval. As for now 69 species have been revealed from the formation spanning the middle and probably the lowest part of the upper Tournaisian. It appears that the most diversified in the studied fauna are productides and spiriferides being represented by

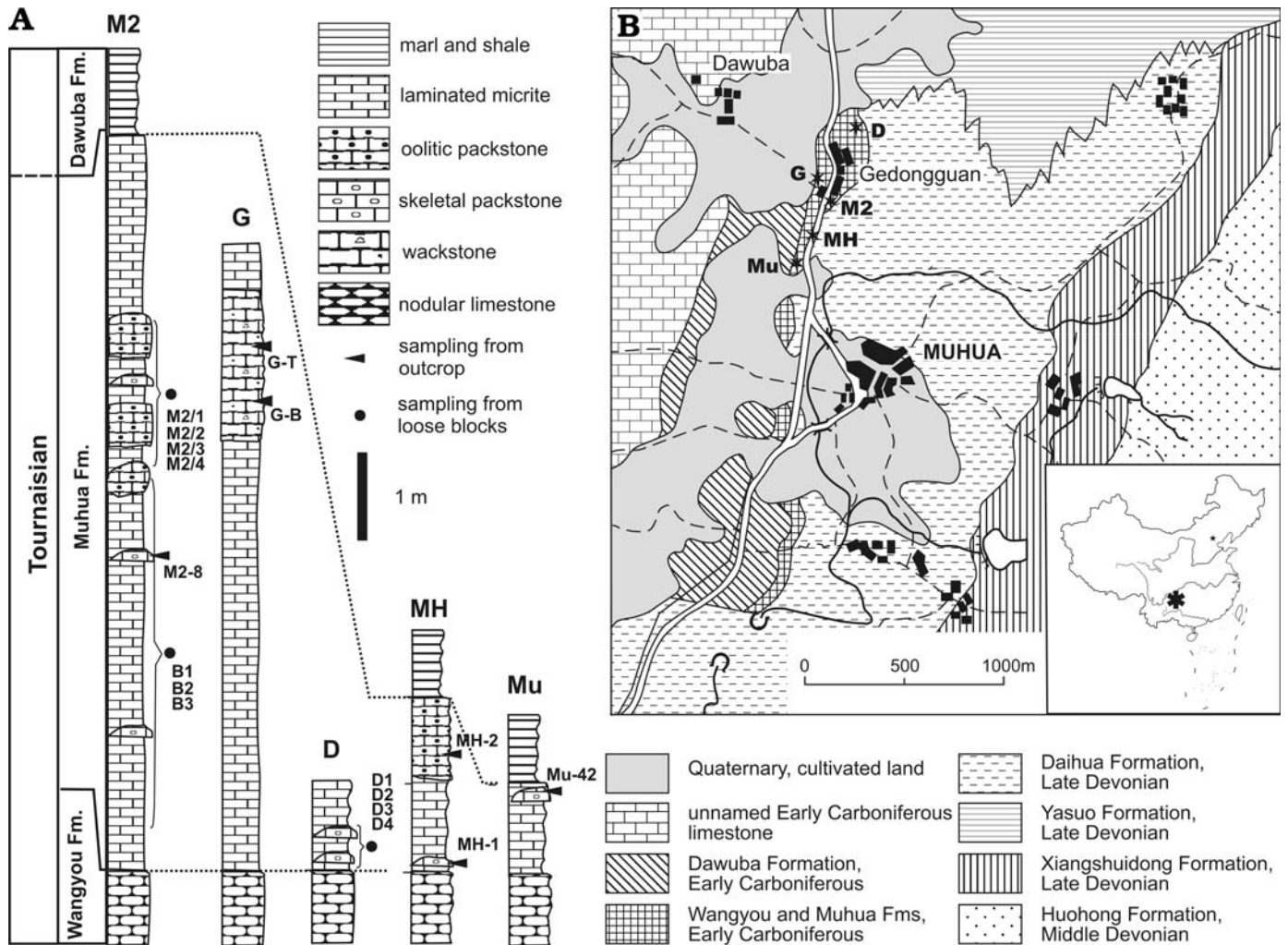


Fig. 1. Stratigraphic columns (A) and map (B) of the sampling sites around Muhua and Gedongguan villages in Guizhou Province, southern China (after Sun and Baliński 2008).

17 and 15 species, respectively. Rhynchonellides (9 species) and athyridides (7 species) are less numerous although some of them, e.g., *Cleiothyridina deroissyi* (Léveillé, 1835), are represented by great number of specimens. Other brachiopod orders achieve less species representation (1–5 species) although some of the species are represented by numerous specimens in some samples, as, e.g., the orthotetide *Lamellispirina spinosa* Sun and Baliński, 2008 and the orthide *Rhipidomella michelini* (Léveillé, 1835) and *Schizophoria* (*Schizophoria*) *resupinata* (Martin, 1809).

Among the brachiopod fauna from the Muhua Formation 5 genera are known only from this locality and can be regarded, for the time being, as endemic. These are: *Muhuarina* Baliński and Sun, 2005; *Lamellispirina* Sun and Baliński, 2008; *Dacryrina* Baliński and Sun, 2008; *Muhuathyris* Sun, Ma, Baliński, and Zhang, 2004; and *Changshunella* Sun, Baliński, Ma, and Zhang, 2004. Similarly, 15 species occurring in the Muhua Formation have been described either previously or in this report as new. These are: *Nematocrania pilea* Sun and Baliński, 2008; *Subglobosochonetes gedongguanensis* Sun and Baliński, 2008; *Globosochonetes gracilis* Sun and Baliński, 2008;

Muhuarina haeretica Baliński and Sun, 2005; *Lamellispirina spinosa* Sun and Baliński, 2008; *Pleuropugnoides calcaris* sp. nov.; *Coledium bruntoni* sp. nov.; *Lamdarina sinensis* Baliński and Sun, 2008; *Dacryrina dziki* Baliński and Sun, 2008; *Muhuathyris circularis* Sun, Ma, Baliński, and Zhang, 2004; *Changshunella yangi* Sun, Baliński, Ma, and Zhang, 2004; *Voiseyella bruntoni* Baliński and Sun, 2010a; and *Celsiformix carteri* Baliński and Sun, 2010a.

Late Famennian–Tournaisian brachiopod faunal dynamics in South China

The latest Famennian (Strunian) brachiopod fauna is known from several places all over the world, e.g., from many localities in Europe, Asia, North America, Australia, North Africa, and Western Australia (see detailed list and descriptions in Nicollin and Brice 2004; see also Halamski and Baliński

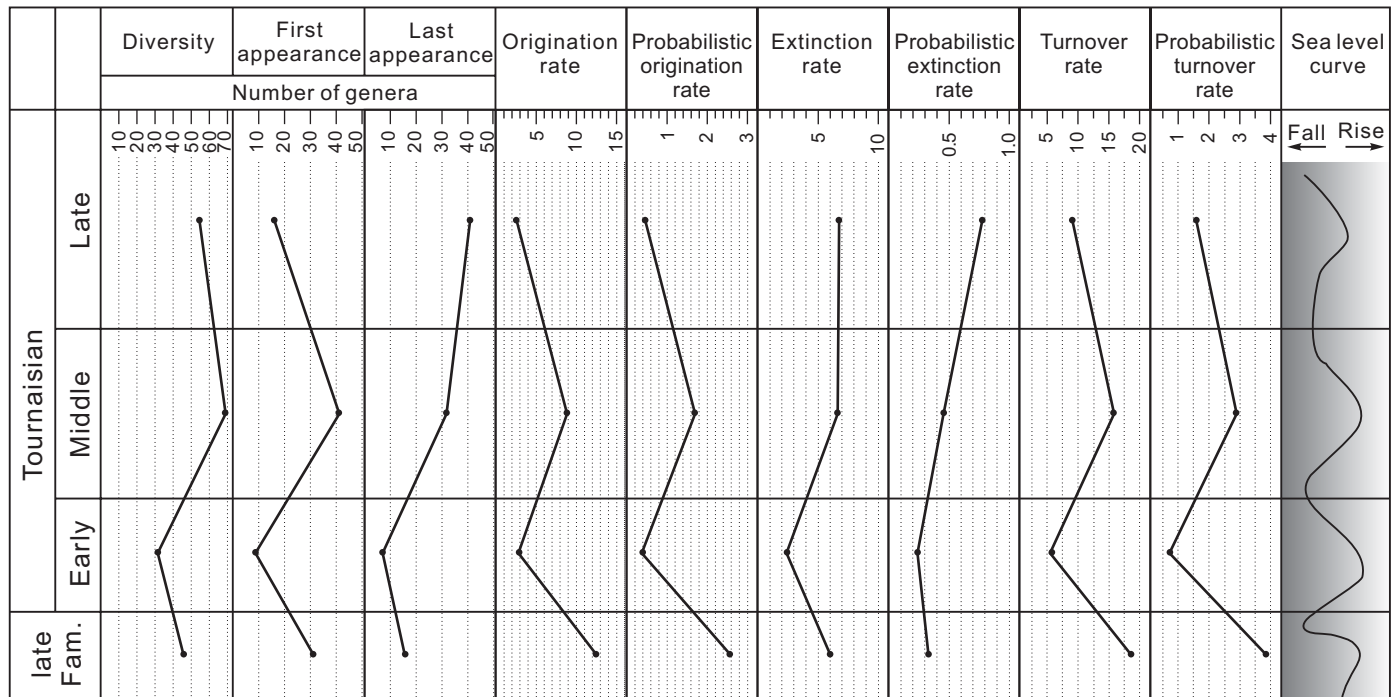


Fig. 2. Diversity, origination, extinction and turnover data for brachiopod genera during late Famennian–late Tournaisian in the Southern China. Duration of intervals assumed approximately as 2.5 Ma for the late Famennian, 3 Ma for the early Tournaisian, 4.6 Ma for the middle Tournaisian, and 6.3 Ma for the late Tournaisian. The informal late Famennian interval corresponds approximately to the “Strunian”, i.e., to the late *Palmatolepis expansa* and *Siphonodella praesulcata* conodont zones. Origination rate equals to the number of newly appeared genera divided by the duration of the interval in million of years; probabilistic origination rate equals to the number of newly appeared genera divided by the number of genera crossing bottom boundary; extinction rate equals to the number of last occurrences of genera divided by the duration of the interval in million of years; probabilistic extinction rate equals to the number of last occurrences of genera divided by the total number of genera in the interval; turnover rates equals the number of originated and extinct genera divided by the duration of the interval in million of years; probabilistic turnover rate equals the number of originated and extinct genera divided by the number of genera crossing bottom boundary. Sea level curve adopted from Zhang et al. (2000).

2009). The Strunian brachiopods have a characteristic aspect of a transitional fauna consisting of Devonian (in minority) and Carboniferous (prevailing) forms (Conil et al. 1986). According to Simakov (1993) the most important consequence of the D–C event was not a mass extinction of Devonian taxa but the appearance of new forms of a Carboniferous aspect. Some researchers, however, regard the end Devonian biotic event (Hangenberg Event) as one of the most severe (although not as intense as the late Frasnian) bio-events in the Phanerozoic history (e.g., Johnson and Sandberg 1989; Sandberg et al. 1989; 2002; Walliser 1996; Streel et al. 2000; Kaiser et al. 2006). Shallow and deep-marine organisms, benthos (e.g., corals, bivalves, and stromatoporoids), nekton (ammonoids, placoderms, conodonts), plankton (acritarchs, ostracods) as well as terrestrial ecosystems were severely affected (Blumenstengel 1993; Becker 1993; Walliser 1996; Olempska 1997; Głuchowski 2002; Schwark and Empt 2006; Kaiser et al. 2006). Nicollin and Brice (2004) summarised that the Strunian brachiopods were represented by 13 genera of Productidina, 7 genera of Rhynchonellida, 13 genera of Spiriferida, and one genus of Spiriferinida.

The temporal patterns of brachiopod generic diversity, first and last appearances (originations and extinctions), as well as origination, extinction, and turnover rates during late Famennian–late Tournaisian in southern China are shown on

figures 2 and 3. The data (Sun et al. 2006; present study) reveal that the early Tournaisian brachiopod fauna declined in diversity by around 13 genera in comparison to that of the late Famennian. However, 28 genera (61%) of the late Famennian brachiopods successfully survived into the Early Carboniferous. Among them, 23 genera were recorded as early as in the early Tournaisian fauna, including about 14 long-ranging cosmopolitan forms and 6 progenitor or Devonian–Carboniferous transitional forms. Six genera, namely *Palaeochoristites*, *Unispirifer*, *Celsifornix*, *Brachythyrina*?, *Neospirifer*?, and *Guilinospirifer* are newly originated, whereas 3 others, i.e., *Rhipidomella*, *Pugnax*, and *Cyrtina*? may be regarded as immigrants. These 9 newly appeared genera in the early Tournaisian make up 28% of the fauna at generic level from that interval. Interestingly, the late Famennian brachiopods are characterised by quite high values of origination and turnover rates (Fig. 2). Also extinction rate in the late Famennian is much higher than in the succeeding interval but is lower in comparison with that of the middle and late Tournaisian. The high origination rate recorded for the late Famennian is evidently caused in large extent by the data from the Nanbiancun section where several genera, including those characteristic for the Carboniferous, have been recorded just below the Devonian–Carboniferous boundary (Xu and Yao 1988; Fig. 3).

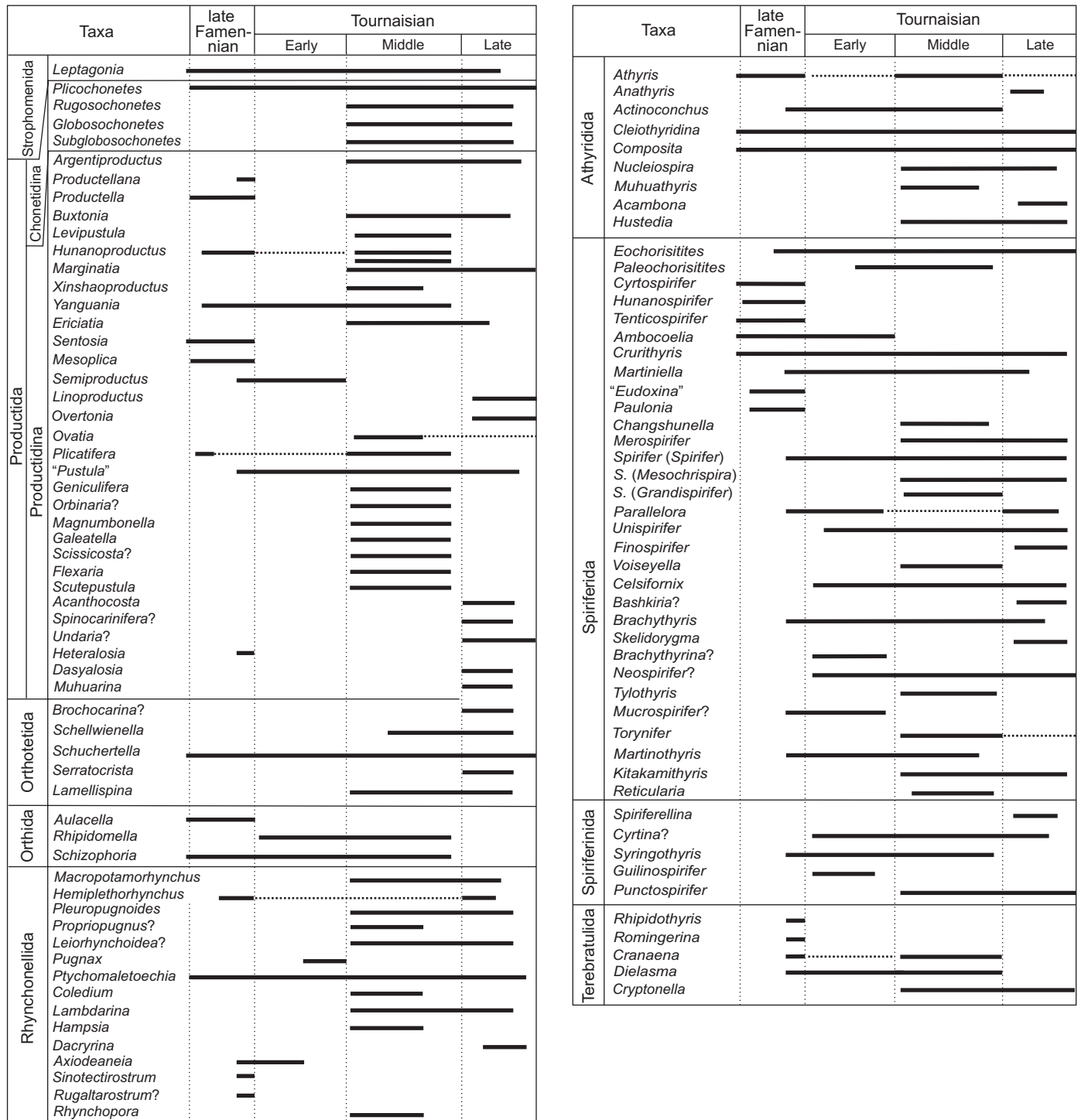


Fig. 3. Distribution of the brachiopod genera during late Famennian–late Tournaisian in southern China. The informal late Famennian interval corresponds approximately to the “Strunian”, i.e. to the Late *Palmatolepis expansa* and *Siphonodella praesulcata* conodont zones. Distributional data based on Chu (1933), Jin (1961), Yang (1964, 1978, 1984), Hou (1965), Yang et al. (1977), Tan (1986, 1987, 2010), Xu and Yao (1988), Wang (2006), Wang et al. (2006), Li (2010), Li et al. (2011), and the present study. Some genera cited in the literature and shown in the diagram (e.g., “*Pustula*”, *Neospirifer?*, *Mucrospirifer*, and *Rhipidothyris*) most certainly represent other forms.

The brachiopod fauna from the early Tournaisian shows low origination rate and, noteworthy, the lowest diversity, extinction and turnover rates (Fig. 2) in comparison to faunas from other intervals included in our evaluation.

During the middle Tournaisian, the brachiopod fauna

shows an explosive increase in diversity on generic level, encompassing 69 genera. Among them, 28 genera (ca. 41%) are derived from the early Tournaisian or late Famennian faunas and the rest are newly originated or immigrated forms from areas outside of South China. Not surprisingly, the total

Table 1. Occurrence of brachiopod species in samples from the Muhua Formation.

Species	Sample													
	MH1	D1	D2	D3	D4	MH2	M2-8	M2/1	M2/2	M2/3	M2/4	Mu42	GB	GT
<i>Langella</i> sp.														
<i>Orbiculoidea</i> sp.														
<i>Nematocrania pilea</i>														
<i>Nematocrania</i> sp.														
<i>Acanthocrania</i> sp.														
<i>Petrocrania?</i> sp.														
Craniidae gen. et sp. indet.														
<i>Leptagonia</i> cf. <i>analoga</i>														
<i>Subglobosochonetes gedongguanensis</i>														
<i>Subglobosochonetes</i> cf. <i>malevkensis</i>														
<i>Globosochonetes gracilis</i>														
<i>Globosochonetes</i> sp.														
<i>Rugosochonetes</i> cf. <i>celticus</i>														
<i>Rugosochonetes</i> sp.														
<i>Plicochonetes</i> sp.														
<i>Argentiproductus margaritaceus</i>														
<i>Dasyalosia</i> cf. <i>panicula</i>														
<i>Muhuarina haeretica</i>														
Semicostellini gen. et sp. indet.														
Strophalosiidina gen. et sp. indet.														
Productininae gen. et sp. indet.														
<i>Orbinaria?</i> sp.														
<i>Spinocarinifera?</i> sp.														
<i>Acanthocosta</i> sp.														
Echinoconchoidea gen. et sp. indet.														
Auriculispininae gen. et sp. indet.														
Juresaniinae gen. et sp. indet.														
<i>Brochocarina?</i> sp.														
<i>Schellwienella</i> sp.														
<i>Schuchertella</i> sp.														
<i>Serratocrista</i> sp.														
<i>Lamellispirina spinosa</i>														
<i>Rhipidomella michelini</i>														
<i>Schizophoria</i> (S.) <i>resupinata</i>														
<i>Schizophoria</i> sp.														
<i>Macropotamorhynchus</i> cf. <i>insolitus</i>														
<i>Hemiplethorhynchus?</i> sp.														
<i>Pleuropugnoides calcaris</i> sp. nov.														

Species	Sample													
	MH1	D1	D2	D3	D4	MH2	M2-8	M2/1	M2/2	M2/3	M2/4	Mu42	GB	GT
<i>Leiorhynchoidea?</i> sp.														
<i>Propriopugnus?</i> sp.														
<i>Coledium bruntoni</i> sp. nov.														
<i>Lambdarina sinensis</i>														
<i>Hampsia cooperi</i>														
<i>Dacryrina dziki</i>														
<i>Actinoconchus</i> sp.														
<i>Cleiothyridina deroissyi</i>														
<i>Cleiothyridina tenuilineata</i>														
<i>Muhuathyris circularis</i>														
<i>Nucleospira</i> sp.														
<i>Acambona</i> sp.														
<i>Hustedia</i> sp.														
<i>Palaeochoristites cinctus</i>														
<i>Eochoristites neipentaiensis</i>														
<i>Crurithyris</i> cf. <i>nastus</i>														
<i>Changshunella yangi</i>														
<i>Merospirifer</i> sp.														
<i>Spirifer</i> (<i>Mesochorospira</i>) sp.														
<i>Parallelora</i> sp.														
<i>Finospirifer</i> sp.														
<i>Voiseyella bruntoni</i>														
<i>Voiseyella</i> cf. <i>texana</i>														
<i>Celsifornix carteri</i>														
<i>Bashkiria?</i> sp.														
<i>Brachythyris</i> sp.														
<i>Skelidorygma</i> sp.														
<i>Tylothyris laminosa</i>														
<i>Kitakamithyris</i> sp.														
<i>Spiriferellina</i> cf. <i>insculpta</i>														
<i>Cryptonella</i> sp. 1														
<i>Cryptonella</i> sp. 2														
<i>Cryptonelloid</i> gen. et sp. indet.														

Number of specimens						
absent	1–5	6–10	11–25	26–50	51–100	>100

diversity and originations in this interval attain the highest values. Noteworthy, in comparison to the late Famennian and early Tournaisian, the extinction rates increases rapidly to the value almost as high as that recorded for the late Tournaisian (Fig. 2).

In the late Tournaisian the brachiopod fauna displays decline in diversity at generic level. Of 54 late Tournaisian brachiopod genera, 37 (69%) were also present in the middle Tournaisian and only 16 (30%) genera appeared in the late Tournaisian for the first time.

In general, the brachiopod faunal dynamics in the late Famennian–Tournaisian observed in South China reveals a characteristic pattern. After a certain decline in the generic diversity at the Devonian–Carboniferous boundary, markedly alleviated by data from the Nanbiancun section, the early Tournaisian brachiopod fauna shows some slight im-

poverishment. In the early–middle Tournaisian there is evidence of recovery of taxonomic diversity which attains its maximum at the end of the interval. The high-diversity middle–upper Tournaisian brachiopod fauna is well documented from the Muhua Formation (Sun and Baliński 2008; this paper: Table 1). It can be assumed then, that the process of recovery of the brachiopod fauna in South China might have taken about 3–4 Ma.

It should be noted, however, that evaluation of the brachiopod faunal dynamics in South China is somewhat hampered by the taphonomic bias. The middle–upper Tournaisian silicified brachiopod fauna from Muhua allowed acid digestion of the limestone samples, which revealed an extremely interesting fauna, unique in regard to its diversity. This “taphonomic window” reveals a much more reliable faunal diversity than the fossil data collected by traditional mechan-

ical processing. The middle Tournaisian “radiation” or explosion in taxonomic diversity observed among brachiopod faunas in the South China is caused, at least partially, by these taphonomic peculiarities. However, there is no doubt that brachiopods from the Muhua Formation represent a fully recovered high diversity fauna. It consists of forms representing a wide spectrum of attachment strategies, e.g., species attached by pedicle, free lying, soft bottom dwellers, infaunal and quasi-infaunal, and cementing to hard substrate. Of special interest are five species of articulate micromorphic brachiopods (see Baliński and Sun 2008) representing Productida (1 species: *Muhuarina haeretica* Baliński and Sun, 2004), Rhynchonellida (3 species: *Lambdarina sinensis* Baliński and Sun, 2008; *Dacryrina dziki* Baliński and Sun, 2008; *Hampsia cooperi* Morris, 1994), and Spiriferida (1 species: *Changshunella yangi* Sun, Baliński, Ma, and Zhang, 2004). These are probably highly specialised forms adapted to special kinds of ecological niches. Lambdarinids might have been anchored epifaunally to many kinds of skeletal debris or lived in cryptic niches. Their very small shell dimensions permitted them also to live in interstitial microenvironments. The appearance of these micromorphic specialised forms with narrow environmental tolerances is very characteristic for recovered, normally functioning biocenosis (Erwin 1998; Kauffman and Harries 1996; Harries et al. 1996).

As noted above, the post-extinction survival interval in South China spans probably the entire early Tournaisian, i.e., about 3–4 Ma. This is in accordance with observations of Kirchner and Weil (2000: 177) who demonstrated that extinctions do not trigger immediate evolutionary rebounds and that significant originations of new taxa following mass extinction took as long as 10 Ma. According to Erwin (1998, 2000) survival intervals have highly variable durations. Similarly, McGhee (1996) noticed that the timing of brachiopod recoveries after the Frasnian–Famennian extinction varied from region to region. Jablonski (1998) documented similar geographic variation in patterns of biotic recovery of molluscs following the end-Cretaceous extinction. The delayed rebound and re-diversification of echinoderms in the early Famennian of northwest China and Europe was discussed by Lane et al. (1997) and Erwin (1998). On the other hand, the post-extinction recovery of the brachiopod fauna following the F–F extinction was quite rapid in the Dębnik area of southern Poland, spanning some 1.5–2.0 Ma (Baliński 1996, 2002). Thus, the presumed duration of the post Devonian recovery of brachiopod fauna in South China seems quite comparable. Our brachiopod fauna from Muhua is one of the most diversified taxonomically known from the Tournaisian stage globally.

Evidence of biotic interactions

Brachiopods of the Muhua Formation lived in a complex relationship with other diverse co-occurring fauna and some of this evidence is distinct and can be traced on their shells. Drill holes of predatory origin are the most common evidence of

this category in the studied brachiopod fauna. These borings, however, should be distinguished from those made on dead brachiopod shells as post-mortem infestation. Damages and repair scars probably of predatory origin are also recorded on shells from Muhua. Of special importance are those records on brachiopod shells which document the presence and life activity of soft-bodied organisms. Such evidence as predatory and post-mortem borings, shell damages and malformations bear significant information about complexity and relations of studied fauna. The unusual finding of tubular outgrowth named recently as *Haplorygma dorsalis* Baliński and Sun, 2010b on the inner surface of the dorsal valve of *Tylothyrus laminosa* (M’Coy, 1841) and *Spiriferellina* cf. *insculpta* Phillips, 1836 is the fifth case of presumably parasitic (kleptoparasitic) interaction of this kind recorded in fossil brachiopods.

Boreholes in shells

Borings in the brachiopod shells is the most common evidence of biotic interactions which can be easily revealed in the fossil material. There are numerous records of drillings in brachiopod shells from the Phanerozoic and quantity of this kind of reports is growing even more rapidly in recent years (e.g., Kowalewski 2002; Hoffmeister et al. 2003; Taddei Ruggiero and Bitner 2008; Mottequin and Sevastopulo 2009). Generally, the drilling activities can be ascribed either to predator–parasite activities, when the attacked brachiopod was alive, or to non-predatory in nature riddling left by organisms (including other brachiopods) looking for substrate. In brachiopod material from the Muhua Formation both types of the drillings could be recognised.

Borings to living shells.—There are a few drill holes observed in the studied material which could be attributed to the carnivorous predators. These borings are generally circular, cylindrical (parallel-sided), penetrating perpendicularly through the whole thickness of the valve. They range from 0.60 to 0.65 mm in diameter (see Fig. 4A–H). This kind of boreholes were recorded in *Subglobosochonetes gedongguensis* Sun and Baliński, 2008; *Rugosochonetes* cf. *celticus* Muir-Wood, 1962; *Schellwienella* sp.; *Cleiothyridina de-roissy* (Léveillé, 1835); *Crurithyrus* cf. *nastus* Brunton and Champion, 1974; and *Changshunella yangi* Sun, Baliński, Ma, and Zhang, 2004. Among 150 complete shells and about 300 isolated valves of *C. de-roissy* only 14 dorsal and 10 ventral valves have been bored which represents about 5.3% of all specimens. In *C. cf. nastus* only 11 specimens (2.75%) out of more than 400 have been bored. Thus, the frequency of bored valves in the studied material is generally rather low especially in comparison to corresponding records in other Carboniferous and Permian brachiopod faunas (e.g., Brunton 1966; Hoffmeister et al. 2003; Mottequin and Sevastopulo 2009). Among Cainozoic brachiopods the predatory drilling frequencies may also be locally high (e.g., Delance and Emig 2004; Baumiller and Bitner 2004; Baumiller et al. 2006).

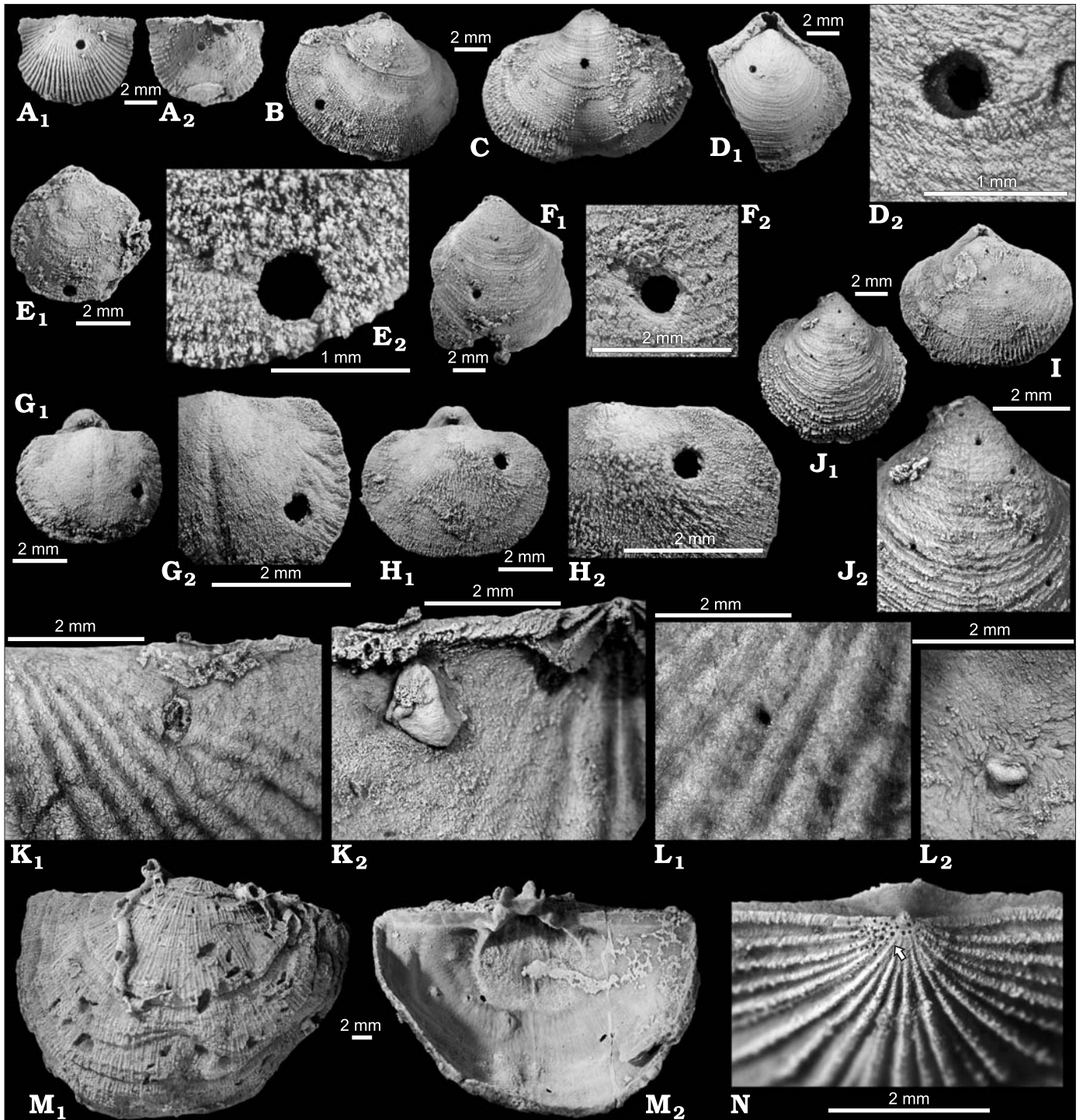


Fig. 4. Shell damage in silicified brachiopods from the Tournaisian Muhua Formation, southern China. **A**. Drilled ventral valve of *Subglobochoonetes gedongguensis* Sun and Baliński, 2008, PKUM02-0390, in exterior (A₁) and interior (A₂) views. **B**, **C**. Two shells of *Cleiothyridina deroissyi* (Léveillé, 1835) with boreholes, PKUM02-0391 (**B**) and PKUM02-0392 (**C**), in dorso-lateral (**B**) and ventral (**C**) views, respectively. **D**, **E**. Two damaged shells of *Cleiothyridina tenuilineata* (Rowley, 1900) with boreholes, PKUM02-0393 (**D**) and PKUM02-0394 (**E**), in dorsal (D₁, E₁) and enlarged (D₂, E₂) views. **F**. Damaged ventral valve of *Cleiothyridina tenuilineata* (Rowley, 1900), PKUM02-0395, in general exterior (F₁) and more detailed (F₂) views. **G**, **H**. Two shells of *Crurithyris* cf. *nastus* Brunton and Champion, 1974 with boreholes, PKUM02-0396 (**G**) and PKUM02-0397 (**H**), in general dorsal (G₁, H₁) and detailed (G₂, H₂) views. **I**. Shell of *Cleiothyridina deroissyi* (Léveillé, 1835), PKUM02-0398, with a few small-sized boreholes in dorsal valve. **J**. Shell of *Cleiothyridina tenuilineata* (Rowley, 1900) with a series of small-sized boreholes, PKUM02-0399, in ventral (J₁) and enlarged (J₂) views. **K**, **L**. Two dorsal valves of *Cesiformix carteri* Baliński and Sun, 2010a, PKUM02-0400 (**K**) and PKUM02-0401 (**L**), bored from the exterior (K₁, L₁) and showing “blister” deposits in the interior (K₂, L₂) as a response to borings. **M**. Dorsal valve of *Schellwienella* sp., PKUM02-0317, showing numerous external borings of a barnacle (M₁) and internal “blisters” sealing the damages (M₂) (illustrated by Baliński and Sun 2008: fig. 21D; M₂ new photograph). **N**. Koskinoid perforations in posterior region of ventral valve of *Serratocrista* sp., PKUM02-0402. Samples GB/GT (A, N), MH1 (B–G, I–L), and MH2 (H, M).

This may be explained at least in part by the taphonomic features of the Muhua's material which is characterised by mostly incomplete, strongly crushed specimens, especially when larger, more susceptible for this kind of predatory borings individuals are concerned. There are numerous suggestions that the borings like those here described and recorded in the Palaeozoic were possibly made by archeogastropods (e.g., Brunton 1966; Carricker and Yochelson 1968; Smith et al. 1985; Mottequin and Sevastopulo 2009; but see also discussion in Rohr 1976) which evolved a boring habit independently from the Mesozoic and Cainozoic neogastropods (Ausich and Gurrola 1979). Baumiller (1990), Baumiller et al. (1999), and Baumiller and Gahn (2002) suggested that certain drill holes in the Devonian and Carboniferous echinoderms and brachiopods might be tentatively attributed to platyceratid gastropods. It is noteworthy, that platyceratid gastropods are quite common in some samples of the Muhua Formation.

Noteworthy is also the distribution of boreholes in *Subglobosochonetes gedongguensis* Sun and Baliński, 2008, recorded in the material from Muhua. Although this evidence is quite rare, being found in four specimens out of total 25 (16%), all drill holes are restricted to ventral valves. This suggests that in these concavo-convex brachiopods the ventral valve was more exposed to drilling behaviour of predators and thus these brachiopods lived with the convex (ventral) valve in the uppermost position. Similar phenomenon was observed by Lescinsky (1995) who presented epibiotic and taphonomic evidence that some concavo-convex brachiopods lived with the convex (ventral) valve on top. Recently Baliński (2010) noted that colour pattern in the Early Devonian concavo-convex *Plectodonta* sp. from Podolia (Ukraine) was developed exclusively on the ventral valves performing probably a protective function through disruptive camouflage against visual systems of potential predators. This suggests that these brachiopods lived with the patterned (convex) ventral valve uppermost and the patternless (concave) dorsal valve lying next to the underlying substrate. These observations challenge the paradigm that concavo-convex brachiopods lived with their convex valves on the sediment (see also Lescinsky 1995).

Among the bored specimens two representing spiriferide *Celsiformix carteri* Baliński and Sun, 2010a are especially interesting, because they show a clearly defensive reaction of the attacked brachiopod. Both specimens are dorsal valves and both were bored from the exterior. One of the drill holes

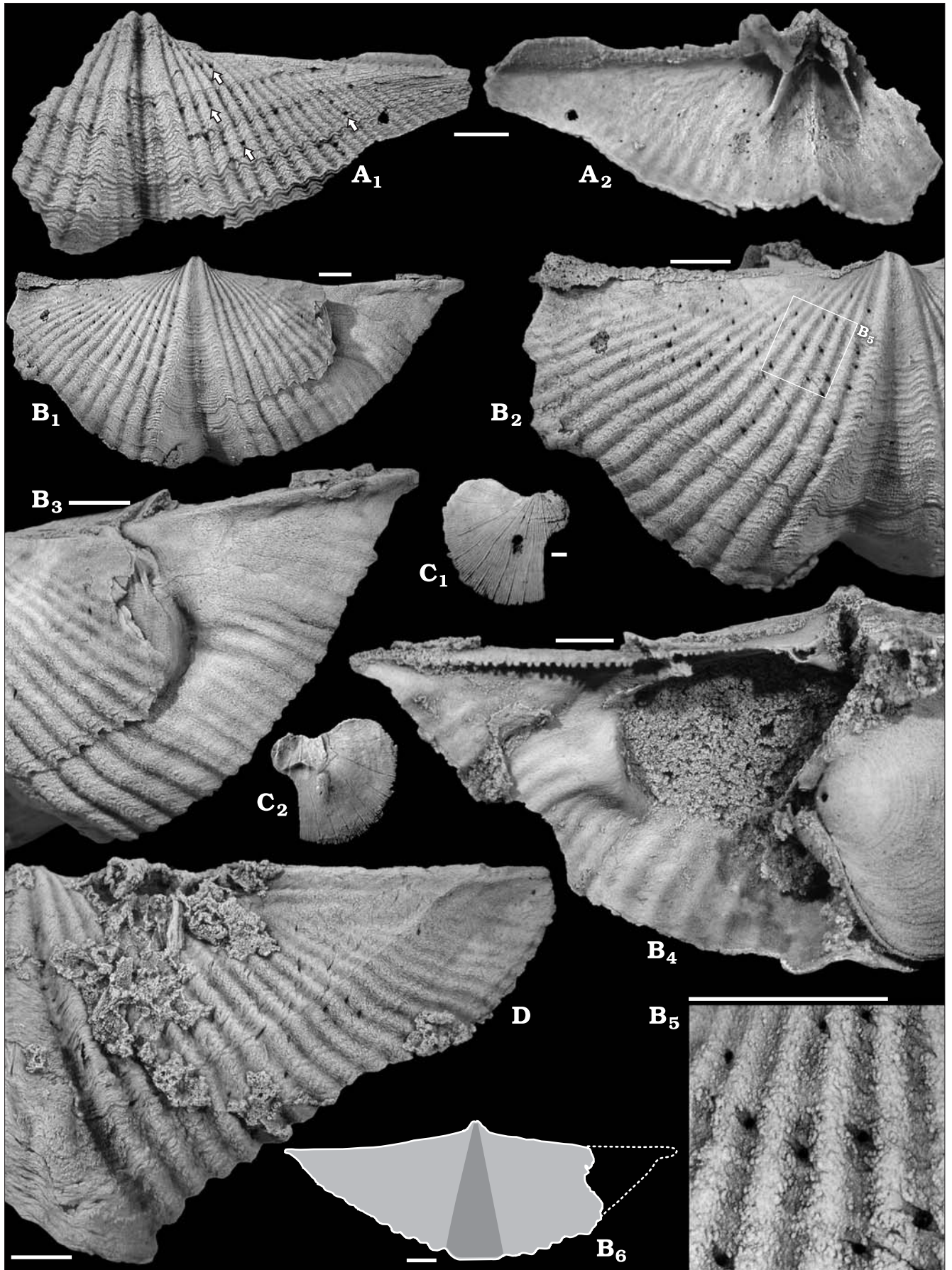
is slightly elliptical in outline and attains 0.26 mm of greater diameter (Fig. 4L) whereas the boring in other specimen is larger attaining 0.65 mm of greater diameter (Fig. 4K). Interior of both dorsal valves reveals a presence of "blister" deposits exuded by the brachiopod mantle clearly in response to borings (Fig. 4K₂, L₂).

Yet another kind of borings occurs on a single dorsal valve of *Schellwienella* sp. (Fig. 4M; see also Sun and Baliński 2008: fig. 21D). These numerous borings are of diverse irregular outline and size and scattered almost over the whole exterior of the valve. The largest boring attains 1.2 by 2.6 mm in diameters. It must be noted that borings do not penetrate the whole thickness of the valve; instead a bottom of the hole is well seen in some large borings. Interior of the valve shows the stumpy callus "blisters" of shell repair formed over areas of the largest borehole intrusion (Fig. 4M₂). The borings were made by acrothoracican barnacles and are very similar to those described, e.g., by Cooper and Grant (1974) and Rodriguez and Gutschick (1977). The presence of blisters is a conclusive evidence that the biotic interaction between brachiopod and barnacle took place while the brachiopod host was alive. According to Seilacher (1969) boring barnacles strongly prefer shells of live hosts to inorganic or dead-shell substrates.

Microscopic holes known as koskinoid perforations have been found in *Serratocrista* sp. These perforations range from about 20 to 70 µm in diameter and occur in the umbonal region of the ventral valve (Fig. 4N). Koskinoid perforations have been interpreted as related to an attachment organ (byssus-like pedicle) characteristic for athyridid *Uncites* Defrance, 1825 and orthotetidines (e.g., Jux and Strauch 1966; Schumann 1969; Martínez Chacón and Garcia-Alcalde 1978; Grant 1980) but Thomas (1958) and Williams and Brunton (1993) suggest that more probably the perforations have been made by drilling parasites living by digesting the soft tissue of brachiopod host.

Borings in dead shells.—In our material there are several specimens showing a characteristic arrangement of small-sized borings. The most illustrative is a ventral valve of *Celsiformix carteri* Baliński and Sun, 2010a shown in Fig. 5A, B, and D. The borings are circular or more frequently elongated and countersunk, with larger diameter ranging usually from 0.09 to 0.18 mm. They are scattered irregularly over the valve exterior but are crowded on the left flank where 43 holes

Fig. 5. Shell damage in silicified spiriferide *Celsiformix carteri* Baliński and Sun, 2010a (A, B, D) and orthide *Schizophoria* sp. (C), from the Tornaisian Muhua Formation, southern China. A. Incomplete ventral valve of *C. carteri*, PKUM02-0403, in exterior (A₁) and interior (A₂) views showing several small-sized, sub-circular, probably ctenostomate borings (a few of them arrowed) located almost exclusively in intercostal troughs and terminating as small openings in the interior of the valve. B. Almost complete ventral valve of *C. carteri*, PKUM02-0404; B₁, general external view showing numerous (46) small-sized, probably ctenostomate borings grouped mainly on the left flank and seriously damaged and repaired the right flank; B₂, enlarged left flank of the valve showing sub-circular to elongated apertures of the boreholes; B₃, enlarged right flank of the valve showing details of damage; B₄, interior of the valve showing repaired part; attached shell of athyridide *Cleiothyridina deroisseyi* (Léveillé, 1835) and silica obscure rest of the valve interior; B₅, enlargement of B₂ showing details of the bored shell surface; B₆, explanatory drawing showing the valve at a growth stage of the predatory attack and extent of damage to the right flank of the valve. C. Ventral valve of *Schizophoria* sp., PKUM02-0346, showing external indentation or puncture (C₁), completely sealed by the shell material from the interior (C₂) (illustrated by Sun and Baliński 2008: fig. 27B). D. Exterior of a right flank of the dorsal valve of *C. carteri*, PKUM02-0405 with probably ctenostomate borings. Sample MH1. Scale bars 2 mm.



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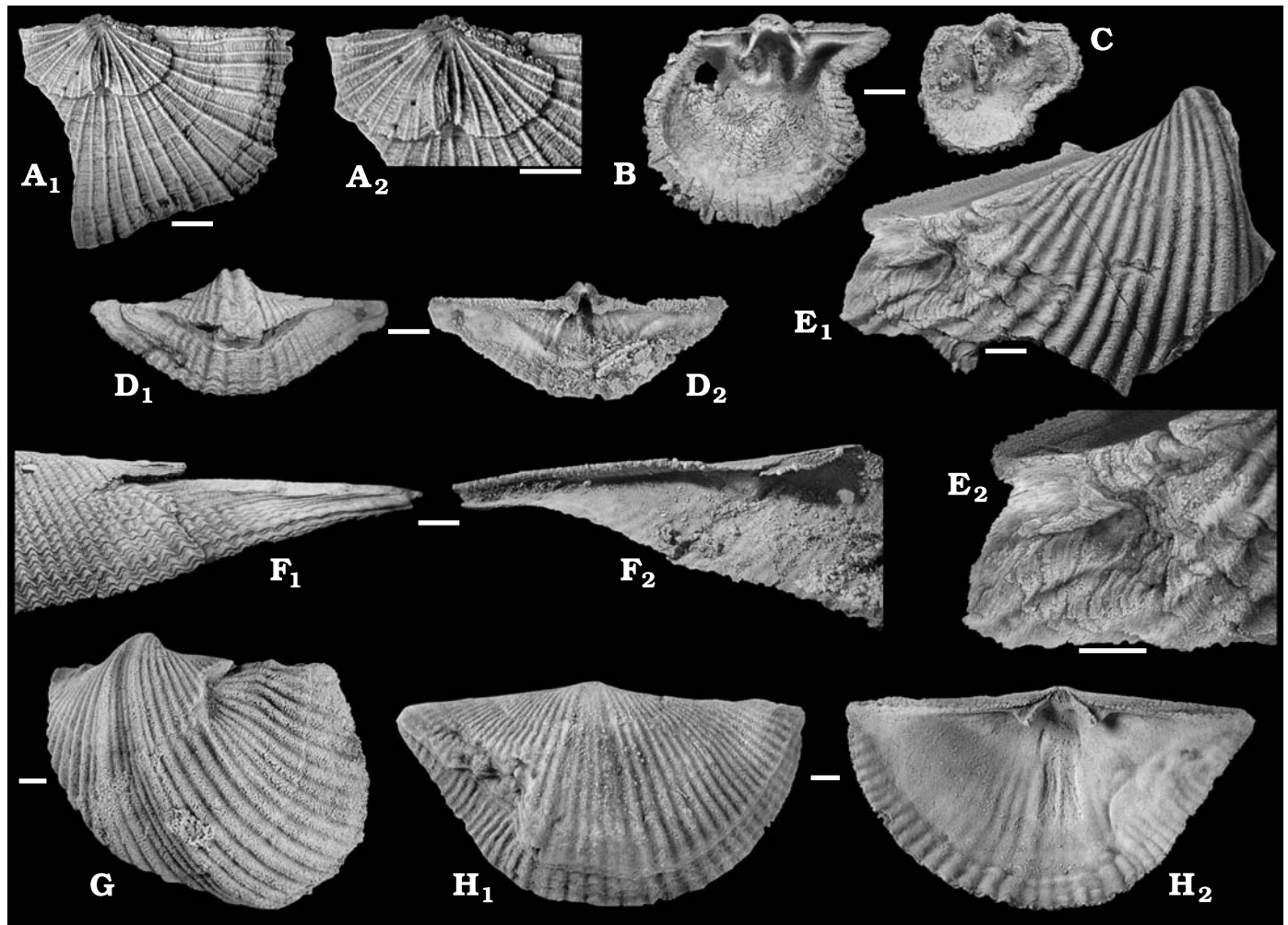


Fig. 6. Shell damage and malformation in silicified brachiopods from the Tornaisian Muhua Formation, southern China. **A.** Incomplete dorsal valve of orthotetide *Schuchertella* sp., PKUM02-0320, in general external (A_1) and more detailed (A_2) views showing damage to the middle anterior margin at the earlier stage of growth resulting in bilobate outline of the valve; note also disturbance of median costellae and a later recovery after some arrest of growth (specimen illustrated also by Sun and Baliński 2008: fig. 22C). **B, C.** Two dorsal valves of orthotetide *Lamellispina spinosa* Sun and Baliński, 2008, PKUM02-0406 and PKUM02-0407, viewed from the interior showing distortion/malformation of growth due to crowding. **D.** Seriously damaged ventral valve of spiriferide *Celsifornix carteri* Baliński and Sun, 2010a, PKUM02-0408, in external (D_1) and internal (D_2) views showing full recovery after some arrest of growth; note another (subsequent) repaired damage on the left flank of the specimen. **E.** Incomplete ventral valve of spiriferide *Parallelora* sp., PKUM02-0409, in external (E_1) and enlarged (E_2) views showing repaired damage. **F.** Incomplete ventral valve of spiriferide *Celsifornix carteri* Baliński and Sun, 2010a, PKUM02-0410, in external (F_1) and internal (F_2) views showing broken off and repaired the lateral part of the right flank. **G.** Ventral valve of spiriferide *Eochoristites neipentaiensis* Chu, 1933, PKUM02-0411, in oblique lateral view showing repaired damage of the right lateral extremity. **H.** Dorsal valve of spiriferide *Eochoristites neipentaiensis*, PKUM02-0412, in external (H_1) and internal (H_2) views with scalloped anterolateral margin of the left flank showing full repair of the damage. Samples MH1 (A–D, F), MH2 (G, H), and GB (E). Scale bars 2 mm.

can be recognised. On the right flank there are only two holes and one hole is in the sulcus. All borings are located in depressions of the valve making either intercostal grooves or, exceptionally, sulcus. Although the borings are circular at some depth, externally they are frequently fusiformly notched. Some borings show consistency in the orientation of their longer axis. Internal surface of the valve is obscured by sediment thus making the observation of the boring effect in the interior impossible. However, another similarly bored ventral valve of the same species shows that boreholes penetrate the whole thickness of valve resulting in preservation of small openings also from the valve interior (Fig. 5A). There is no clear evidence as to whether these borings were made while brachio-

pod was still alive or post-mortem, but the lack of any indication of brachiopod mantle reaction suggests that the latter is more likely. The appearance of the borings suggests that probably the dead brachiopod shells might have been inhabited by ctenostomate bryozoans which have the ability to penetrate the substrate by chemical means. The pattern of borings observed in material from Muhua, although not perfectly preserved, shows some similarity to the traces left by terebriporoideans on calcitic shells (see e.g., Pohowsky 1978; Bałuk and Radwański 1979). Besides *C. carteri* this kind of borings have been found on shells of other species recovered from the Muhua Formation, i.e., *Schuchertella* sp. (Fig. 6A), *Cleiothyridina deroissyi* (Léveillé, 1835) (Fig. 4I), *Cleiothyridina*

tenuilineata (Rowley, 1900) (Fig. 4J), and *Spirifer (Meso-chorispira)* sp. (Fig. 26L).

Shell damage

Damages to the brachiopod shell (other than borings which are described above) of living individuals are possible to locate because they result in more or less evident distortion and irregularities in the shell growth. The nature of these damages, however, may be of various origins and sometime difficult to resolve. Generally, they resulted from interaction between brachiopod and its physical environment (abiotic conditions) or brachiopod and other co-occurring organisms, including other brachiopods (biotic conditions; frequently exemplified as parasite-host or predator-prey relations).

In the material from Muhua there are several valves that show evidence of severe malformations expressed in disturbance of growth symmetry caused by the close proximity of foreign objects including possibly other brachiopod shells. This disturbance resulted from arrested secretion along the lateral margin of a shell addressed against an obstacle. The malformations are particularly well seen in the orthotetoid *Lamellispirina spinosa* Sun and Baliński, 2008 (Fig. 6B, C) which cemented with umbonal region of the ventral valve to the substrate and probably lived in crowded concentrations. Thus, the individuals of the species, being firmly attached, had practically no chance to change their orientation while growing in size. In the case of *L. spinosa* crowding rather than disease seems more probable cause of the shell malformation (see, e.g., Bassett 1984; Fürsich 1984: 328; Hoel 2007: 595; Martínez Chacón and Winkler Prins 2010).

Another case of distortion of the normal shell growth was revealed in the central region of the ventral valve of *Schizophoria* sp. (Fig. 5C). This distortion is developed from an indentation or puncture which measures 1.2 by 2.6 mm in diameter and is of more or less elliptical outline but with irregular, slightly chipped edges. From the interior this damage is completely sealed by the shell material of the brachiopod host. The shape of the hole as well as the distorted host external ornamentation around it strongly suggest that the damage must have been done to the anterior margin of the valve resulting in ripping away of part of the shell. The injured brachiopod, however, survived and its mantle epithelium was capable of reformation and continued normal growth anterior to damage. The origin of the damage is difficult to explain but the shape of the indentation suggests suspects among co-occurring abundantly chondrichthyan fishes (see Ginter and Sun 2007). The damage and full recovery of the mantle margin can be observed also in *Schuchertella* sp. (Fig. 6A).

In the material from Muhua a number of serious damages or breakages to the brachiopod shells of living individuals was found. This evidence is very important as it may shed some light on evolutionary changes or stability in brachiopod physiology. The most illustrative is the ventral valve of *Celsiformix carteri* Baliński and Sun, 2010a which was de-

scribed above in the context of its infestation by ctenostomate bryozoan (Fig. 5B). The specimen shows trace of a very heavy mechanical damage to the right flank of the valve. The damage was done when brachiopod attained 9.7 mm of the shell length and about 26.3 mm in width. In the result of damage the brachiopod lost almost a half of its right flank what makes nearly one-quarter of the whole shell width. It is highly probable that not only the shell but also the soft tissue of the brachiopod, especially the mantle and right coil of the spiral lophophore suffered serious wounds. Although it is possible that this shell break as well as others of this kind observed on shells from Muhua might have been caused by abiotic agents, it seems more probable that it can be attributed to predatory activities. Lack of pebbles or other large objects in the sediment which might cause damage from impacts on one hand and presence of a single puncture on the described specimen of *C. carteri* on the other supports the latter suggestion. It should be emphasised that unusually rich and diverse chondrichthyan fauna occur with brachiopods in Muhua and most of them possessed crushing crown teeth well adapted to feed on shelly invertebrates, mainly on abundant brachiopods (Ginter and Sun 2007).

The extent of the shell damage described above indicates that the brachiopod suffered severe sublethal wounds. However, predatory attack, probably by durophagous shark, was not successful in killing the brachiopod although successfulness in partial eating it could not be excluded. Additionally, the probable subsequent loss of metabolites and haemolymph from injured soft tissues might have attracted other predators and scavengers. Nevertheless, for some reason the injured brachiopod was abandoned and it could continue its growth and begin a process of the soft tissue regeneration and shell repair. As it can be observed on the illustrated specimen the process of sealing the wound was successful, because the brachiopod could fully reconstruct the ripped away portion of the valve with new shell material, and it continued growth in undamaged sectors of mantle margin without any disturbance. The new shell material sealing the wound does bear costae, although the regenerated costae are markedly weaker and slightly sinuous. Also, the lost part of the cardinal margin was restored together with such important hinge structures as accessory denticles (Fig. 5B₄). Regeneration of the lost portion of the lophophore and returning to its normal anatomical and functional properties is also highly probable. The ability to regenerate damaged lophophore in some articulated brachiopods was reported by Hoverd (1986).

From a mechanical resistance point of view, the region of the shell of *C. carteri* damaged by the attacker was evidently confined to its weakest part. The other possible sectors of shell as thickened posterior or plicate anteromedian regions present obviously an enhanced resistance to shell breakage (e.g., Alexander 1986). Other evidence of predatory attacks on more or less expanded laterally or alate spiriferoid shells from Muhua bear the traces of damage on their flanks, suggesting clearly a preferential direction of attacks. These kind of damages, although not as severe as in the case described

above, are found on specimens of *Eochoristites neipentaiensis* Chu, 1933 (Fig. 6G, H), *Parallelora* sp. (Fig. 6E), and other specimens of *Celsifornix carteri* (Fig. 6D, F). This suggests that relations between brachiopods as a prey and durophagous predators were well established at that time and brachiopod shell architecture (and certainly physiology as well) might have responded to selection pressure from predators. Evidence of morphologic adaptations to minimise predator-induced shell breakage in the Mississippian and Ordovician brachiopods were described by Alexander (1981, 1986).

Baliński (1993) described an analogous example of severe sublethal damage to the shell of the Late Devonian spiriferoid *Cyrtiorina* sp. The shell bears a series of punctures caused by a jawed or clawed predator which are confined to one of the flanks. Besides the superficial injuries the brachiopod suffered severe damage of the hinge mechanism preventing tight shell closure and exposing a vast surface of fleshy parts to the external environment. Despite these severe injuries the brachiopod was eventually abandoned by the predator and was able to secrete a skeleton cover on exposed mantle and restore tight shell closure. As an explanation for abandoning of half-crushed shell of *Cyrtiorina* sp., Baliński (1993) suggested that the brachiopod developed a skill to emit a repellent. This kind of chemical defence is well known in extant articulate brachiopods (Thayer 1985; Thayer and Allmon 1991), pleurotomarioidean gastropods (Harasewych 2002), and phoronids (Larson and Stachowicz 2009). Recent experiments of Mahon et al. (2003) on palatability of soft tissue of terebratulid *Liothyrella uva* (Broderip, 1833) from Antarctica show that the brachiopod is unpalatable to the sympatric macropredators, such as omnivorous sea stars and epibenthic fish. Chemically defended brachiopods could be tasted and rejected by durophagous predators. According to Peck (1993) the low organic and high inorganic contents of brachiopod tissues dramatically affect their value and palatability to predators and may also explain the rejection of some brachiopod tissues by carnivores without invoking chemical defence mechanisms. Taste-rejection behaviour among foraging predators is a common phenomenon (e.g., Skelhorn and Rowe 2006). Potential prey possessing defence chemicals had greater chance to survive predatory attacks and recover than the undefended prey. Harper et al. (2009) found that some terebratulid brachiopods from the Antarctic Peninsula, Falkland Islands, and Chile frequently survive predatory attacks because predators do not complete attacks when tissues are found to be unpalatable or of very low nutritional value. The case of *Cyrtiorina* sp. suggests that unpalatability of brachiopod soft tissue may have appeared as early as the Late Devonian (Baliński 1993). This is supported to some extent by our specimen of *Celsifornix carteri* Baliński and Sun, 2010a. A chemical defence is also suggested for the Ordovician–Devonian orthides by Daley (2008). Recent discovery of chemical defense against epibenthic predators in phoronids (Larson and Stachowicz 2009) may shift the time of acquiring unpalatability by brachiopods (and phoronids) even further back in time, i.e.,

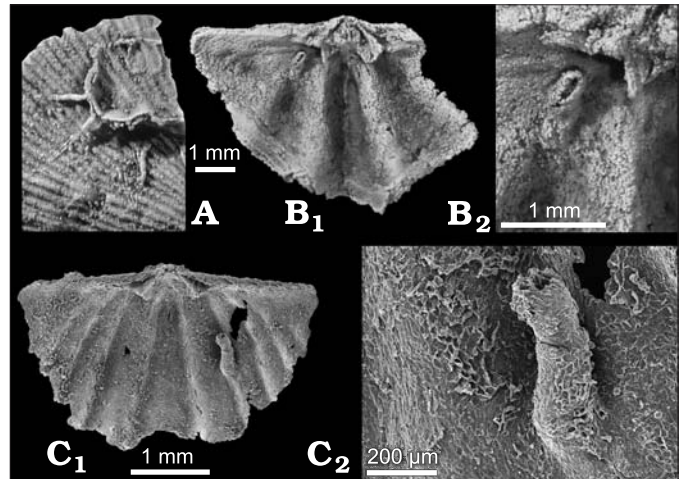


Fig. 7. Shell encrustation in silicified brachiopods from the Tomaisian Muhua Formation, southern China. **A.** Chonetoid shell encrusted by strophalosiidine *Muhuarina haeretica* Baliński and Sun, 2005, PKUM02-0080, (new photograph of specimens illustrated by Baliński and Sun 2008: fig. 1E and Sun and Baliński 2008: fig. 18C). **B.** Interior of dorsal valve of spiriferinide *Spiriferellina* cf. *insculpta* Phillips, 1836, PKUM02-0388, in general (**B**₁) and enlarged (**B**₂) views showing infestation by endobiont *Haplorygma dorsalis* Baliński and Sun, 2010b (see also Baliński and Sun 2010b: fig. 1A; new photographs). **C.** SEM micrographs of dorsal valve of spiriferide *Tylothyrus laminosa* (M'Coy, 1841), PKUM02-0389, showing infestation by *H. dorsalis* in general (**C**₁) and enlarged (**C**₂) views (see also Baliński and Sun 2010b: fig. 1B; new photographs). Samples GB (A, B) and MH1 (C).

to the earliest Cambrian, if we accept the hypothesis of inheriting of unpalatability from their common ancestor.

Experiments by Alexander et al. (1992) on damaged and repaired shells of *Terebratulina retusa* (Linnaeus, 1758) showed that Recent terebratulides do not have ability to survive and repair such severe injuries. On the other hand, the extinct strophomenides (Alexander 1986; Alexander et al. 1992; Ebbestad and Högström 2000) and spiriferides (Baliński 1993; present study) could survive such damage and return to normal shell growth. Baliński (1993) suggested that reparability of severe shell damage in Palaeozoic articulates could have been replaced later by improving a chemical ability to repel potential predators.

External shell encrustation

Although the evidences of shell encrustation by other invertebrates in our material are uncommon (see, e.g., Fig. 7) there are some findings of brachiopod shells encrusted by other brachiopods. A good example of this relationship is specimen illustrated in Fig. 7A, showing a fragment of a chonetoid shell encrusted by the strophalosiidine productide *Muhuarina haeretica* Baliński and Sun, 2005. This micromorphic brachiopod cemented to the hard substrate by quite large portion of the ventral valve (almost all visceral disk) and numerous rhizoid spines (see also Baliński and Sun 2008: fig. 1C–H). Due to the scarce material and its preservation it is not possible to conclude whether *M. haeretica* settled on living or dead shells.

Internal shell infestation

Infestations of brachiopod shell by tube dwelling parasitic or commensal organisms are very scarce in the fossil record. The oldest evidence of this kind of the biotic interaction was described as *Eodiorygma acrotretophilia* Bassett, Popov, and Holmer, 2004 from the Lower Cambrian phosphatic acrotretoid *Linnarsonia*. Earlier Biernat (1961) discovered and discussed origin (MacKinnon and Biernat 1970) of characteristic tube-like protuberances named as *Diorygma atrypophilia* Biernat, 1961, inside ventral valves of *Atrypa zonata* Schnur, 1851 from the Givetian of Poland. Chatterton (1975) found similar tubular structures on the inner surface of dorsal valves of three different Emsian spiriferide species from Australia and named them as *Burrinjuckia spiriferidophilia* Chatterton, 1975. Recently, Kiel (2008) documented the worm-infested specimens of the Early Cretaceous hydrocarbon seep-restricted brachiopod *Peregrinella multicastrata* Lamarck, 1819 from southeastern Crimea, Ukraine. Among our brachiopods from the Muhua Formation the tubular infestation structures were recently revealed and described in detail in two silicified dorsal valves of spirolophous brachiopods (Baliński and Sun 2010b). One of the tube, measuring about 600 µm in length and 160–190 µm in diameter, was found on the inner right flank of a juvenile dorsal valve of *Tylothyris laminosa* (M'Coy, 1841) (Fig. 7C). The second tubular structure was found in a dorsal valve of *Spiriferellina* cf. *insculpta* Phillips, 1836 on its left internal flank and attains about 800 µm in length and 250–360 µm in thickness (Fig. 7B). Baliński and Sun (2010b) named these protuberances as *Haplorygma dorsalis*. The authors discussed also a biotic inter-relationship between brachiopod hosts and invading their mantle cavity tube-dwelling filter-feeding organism suggesting that annelid affinity of the latter seemed probable. The tube dwelling organisms, while living in the mantle cavity of a brachiopod, nourished on stolen undigested nutrients from their hosts, and thus probably were kleptoparasitic (Baliński and Sun 2010b).

Systematic palaeontology

The suprageneric classification and terminology given in this report follows that of the Treatise on Invertebrate Paleontology Part H, Brachiopoda, Revised (Williams et al. 1997–2007).

Phylum Brachiopoda Duméril, 1806

Order Rhynchonellida Kuhn, 1949

Superfamily Rhynchotrematoidea Schuchert, 1913

Family Trigonirhynchiidae Schmidt, 1965

Subfamily Trigonirhynchiinae Schmidt, 1965

Genus *Macropotamorhynchus* Sartenaer, 1970

Type species: Camarotoechia mitchelleanensis Vaughan, 1905; Carboniferous Limestone (Tournaisian); Gloucestershire, England.

Macropotamorhynchus cf. *insolitus* Carter, 1987

Fig. 8.

Material.—Two almost complete shells and 49 fragments of conjunct and single valves from samples D2 and M2-8; the material is poorly preserved, consists of highly fragmented specimens which are additionally obscured by silica and frequently attached bioclasts.

Description.—Shell small in size (dimensions of a largest complete shell in mm: length 6.2, width 6.4, thickness 2.5; Fig. 8D), subequally biconvex, subovate to subrounded; immature shells elongate, adults usually as wide as long to slightly transverse; cardinal margin obtuse angled, passing gently into the arched lateral and anterior margins; anterior commissure weakly uniplicate and serrate. Ventral valve weakly convex; beak elongate, suberect; palintrope high, delthyrium narrow and high, deltidial plates not observed; sulcus very weak, marked in the anterior half of the valve. Dorsal valve regularly convex in lateral profile, posteriorly with shallow median depression, anteriorly with very low median fold; anterolateral margins in large specimens slightly deflected toward the ventral valve marking the reduction of the shell growth in length.

Shell ornament of strong, simple, rounded costae extending almost from beaks; sulcus with 2–3 and fold with 3–4 costae, flanks with up to 5 costae, those on ventral valve sometimes with their anterior ends reflected in ventral direction.

Interior of ventral valve with quite long, slightly divergent dental plates. Dorsal valve interior with long median septum reaching half of the valve length; septum supports V-shaped septalium; outer hinge plates triangular, slightly concave (Fig. 8E, G); crura wide, anteriorly divergent, slightly convex laterally, tips wide, curving ventrally (Fig. 8C).

Remarks.—The material is very fragmentary and obscured by siliceous deposits attached to specimens but reveals external morphology and internal structures which seem to be characteristic for the genus *Macropotamorhynchus*. Morphological characteristics of the species from Muhua, especially the small shell dimensions, elongate outline of the immature and more transverse in adult specimens, elongate ventral beak, and shell costation pattern suggest close similarity to *Macropotamorhynchus simplex* (Roberts, 1971) from the Tournaisian Burt Range Formation, Bonaparte Gulf Basin, north-western Australia (Roberts 1971) and to *M. insolitus* from the lower Carboniferous of western Alberta, Canada (Carter 1987) and south-eastern Idaho, USA (Christensen 1999). From the former species our specimens differ by having less uniplicate commissure, weaker shell costation which commences slightly more anteriorly to the beaks, and usually slightly greater number of the median costae. The material from Muhua seems to be very close to the highly variable externally *M. insolitus*. Both forms have similar shell shape and character of the surface costation. The former differs in having less pronounced sulcus and fewer median and flank costae, although the latter feature falls within limits

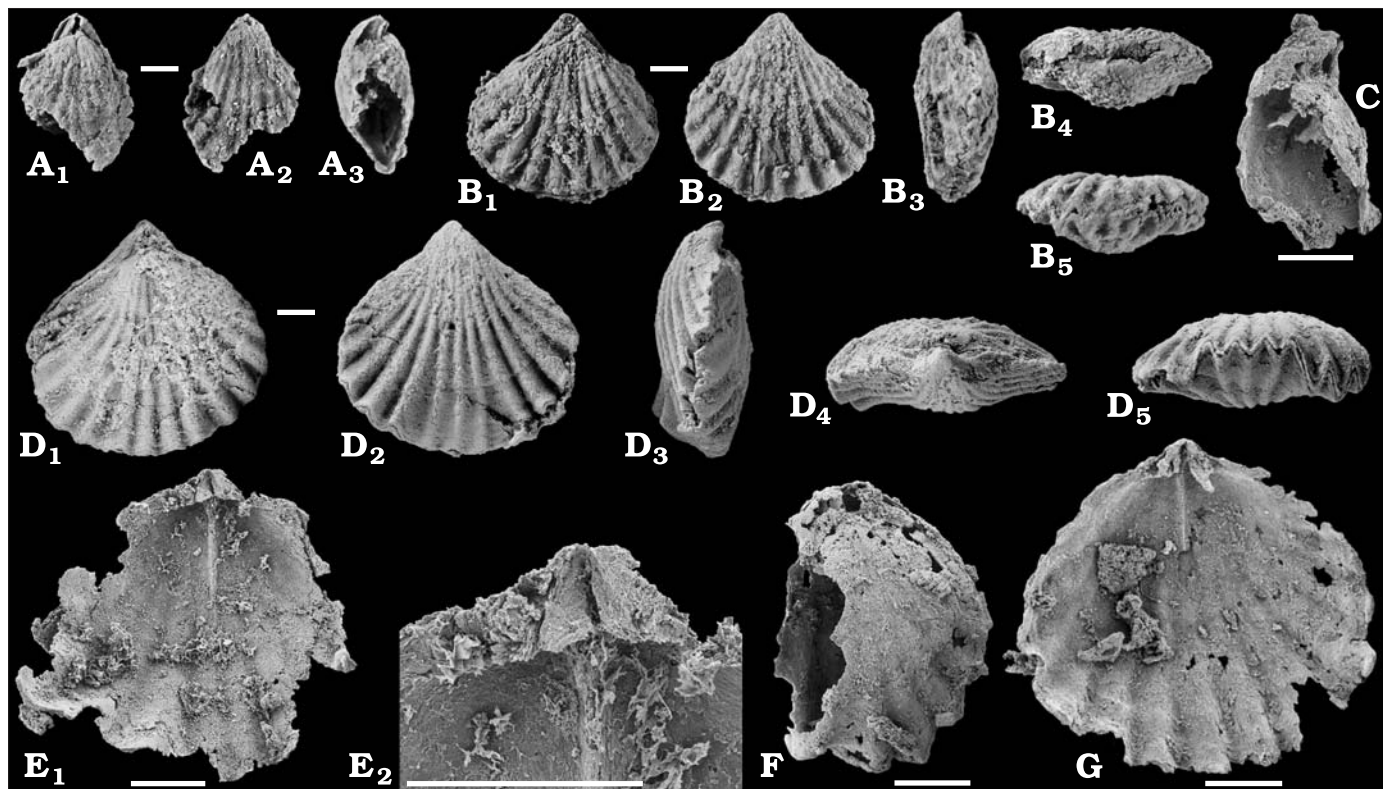


Fig. 8. Rhynchotrematoid brachiopod *Macropotamorhynchus* cf. *insolitus* Carter, 1987 from the Tournaisian Muhua Formation, southern China. **A.** Incomplete juvenile shell, ZPAL V.XXVI/60, in dorsal (A₁), ventral (A₂), and lateral (A₃) views. **B.** Shell, ZPAL V.XXVI/61, in dorsal (B₁), ventral (B₂), lateral (B₃), posterior (B₄), and anterior (B₅) views. **C.** Incomplete juvenile shell, ZPAL V.XXVI/62, in oblique lateral view showing distal parts of crura. **D.** Almost complete shell, PKUM02-0413, in dorsal (D₁), ventral (D₂), lateral (D₃), posterior (D₄), and anterior (D₅) views. **E.** Incomplete and slightly deformed dorsal valve, ZPAL V.XXVI/63, in interior view (E₁), and enlargement showing cardinalia (E₂). **F.** Incomplete shell, ZPAL V.XXVI/64, in dorsal view. **G.** Interior of dorsal valve, ZPAL V.XXVI/65. Sample D2 (A–C, F, G) and M2-8 (D). C, E–G, SEM micrographs. Scale bars 1 mm.

of variability of the Canadian species. Besides these differences the species from Muhua and western Australia seem to be quite close morphologically.

The specimens from the Muhua Formation are similar externally to *Camarotoechia tuta* (Miller, 1881) described by Weller (1914: 179–180) from the Mississippian of the Mississippi Valley Basin, USA. The former differ in having less inflated shell, less developed sulcus, fold, tongue, and less numerous costae in the sulcus and on the flanks. From the type species of the genus, i.e., *Camarotoechia mitchelleanensis* Vaughan, 1905 described from Carboniferous Limestone (Tournaisian) of England and *Macropotamorhynchus* sp. aff. *M. insolitus* Carter, 1987 described from the Strunian–Tournaisian of southern Morocco and the Tournaisian of Algeria (Brice et al. 2005), our specimens differ in having smaller shell with more elongate outline and less developed sulcation.

Stratigraphic and geographic range.—*Macropotamorhynchus insolitus* Carter, 1987, to which the species from Muhua is very similar, is known from the Banff Formation (Tournaisian) of western Alberta, Canada (Carter 1987) and the Lower Mississippian of south-eastern Idaho, USA (Christensen 1999). *M. cf. insolitus* is a rare species in samples D2 and M2-8.

Genus *Hemiplethorhynchus* von Peetz, 1898

Type species: Hemiplethorhynchus fallax von Peetz, 1898; upper Tournaisian, Kuznetsk Basin, Altai, Russia.

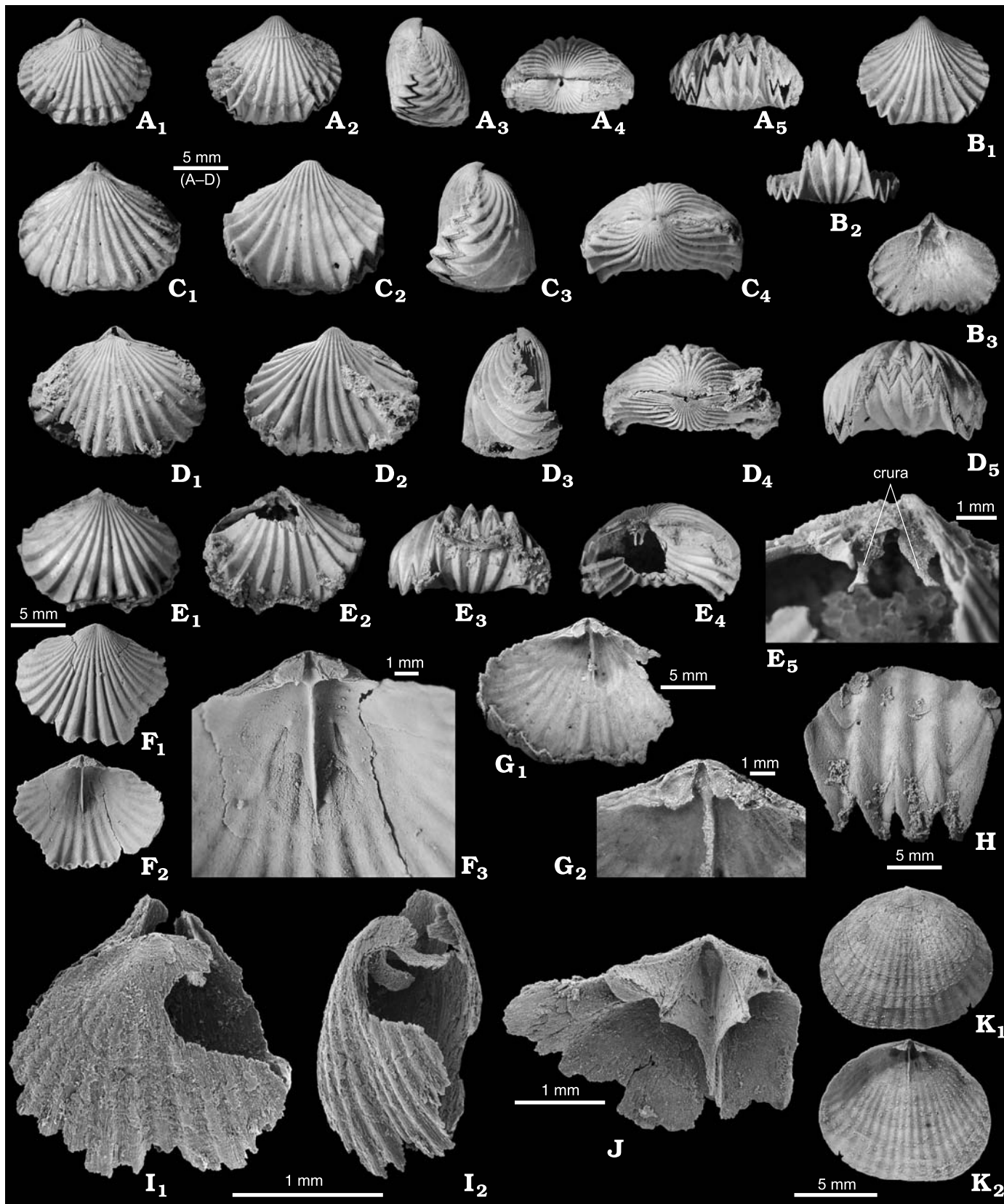
Hemiplethorhynchus? sp.

Fig. 9K.

Material.—Single complete dorsal valve from sample MH2.

Remarks.—The complete dorsal valve is 8.6 mm long and 10.3 mm wide. It is subcircular in outline and has longitudinal, posteriorly deeper, median excavation (sulcus) characteristic to many juvenile rhychonellides. The valve is ornamented with about 25 very weak, rather rounded ribs which arise near the umbonal region. Internally the specimen shows short septalium and thin median septum reaching about one-

Fig. 9. Rhynchotrematoid and pugnacoid brachiopods from the Tournaisian Muhua Formation, southern China. **A–G, I, J.** Pugnacoid *Pleuropugnoides calcaris* sp. nov. **A, C, D.** Three shells, PKUM02-0414 (A), PKUM02-0415 (C, holotype), and PKUM02-0416 (D), in dorsal (A₁, C₁, D₁), ventral (A₂, C₂, D₂), lateral (A₃, C₃, D₃), posterior (A₄, C₄, D₄), and anterior (A₅, D₅) views. **B.** Ventral valve, PKUM02-0417, in exterior (B₁), anterior (B₂), and interior (B₃) views. **E.** Slightly damaged shell, PKUM02-0418, in dorsal (E₁), ventral (E₂), anterior (E₃), posterior (E₄) views and enlargement of the posterior region showing crura (E₅). **F.** Dorsal valve, ZPAL V.XXVI/66, in exterior (F₁), interior (F₂), and enlarged interior (F₃) views. **G.** Dorsal valve, →



PKUM02-0419, general interior (G_1) and enlarged view of cardinalia (G_2). **I.** SEM micrograph of an incomplete juvenile shell, ZPAL V.XXVI/67, in dorsal (I_1) and oblique lateral views showing crura (I_2). **J.** SEM micrograph of a fragment of dorsal valve, ZPAL V.XXVI/68, viewed internally, showing cardinalia. **H.** Pugnacoid *Propriopugnus?* sp., PKUM02-0420, fragment of ventral valve. **K.** Rhynchotrematoid *Hemipletrhynchus?* sp., PKUM02-0421, complete dorsal valve in exterior (K_1) and interior (K_2) views. Sample MH1 (A–E, G), MH2 (K), and D1 (F, I, J).

third of the valve length. It seems that this dorsal valve represents a juvenile costate rhynchonelloid and can be compared with, e.g., *Hemipletorhynchus* which is known from the Tournaisian of North America, Asia, and Europe (Savage 2002: 1077). The specimen cannot be, however, attributed to this genus convincingly, because the connectivum, which is characteristic structure for *Hemipletorhynchus*, is not visible in the valve here described, probably due to the preservation.

Superfamily Pugnacoidea Rzhnosnitskaya, 1956

Family Pugnacidae Rzhnosnitskaya, 1956

Genus *Pleuropugnoides* Ferguson, 1966

Type species: Terebratula pleurodon Phillips, 1836; Carboniferous Limestone, lower Viséan; Boland, England.

Pleuropugnoides calcaris sp. nov.

Fig. 9A–G, I, J.

Etymology: From Latin *calcar*, spur, refers to spurs formed by lateral ventral costae.

Holotype: Complete shell PKUM02-0416 illustrated in Fig. 9C.

Type locality: Muhua section, between villages of Muhua and Gedongguan (Guizhou province, South China).

Type horizon: Muhua Formation, correlated with the middle Tournaisian Lower *Siphonodella crenulata* Conodont Zone.

Diagnosis.—*Pleuropugnoides* with subelliptical shell outline and coarse, anteriorly angular radial costae; usually 4 costae in sulcus and 7–11 costae on each flank; lateral costae form distinct spurs on ventral valve; median septum attains nearly a half of the length of dorsal valve.

Material.—Four complete to almost complete shells and 20 nearly complete or fragmentary single valves, mostly with well preserved internal structures from samples MH1, M2-8, and D1.

Description.—Shell medium sized for genus, attaining about 18 mm in width, dorsibiconvex in profile, subelliptical in outline, wider than long, length attains 73–80% of width; commissure serrate, strongly uniplicate. Adult ventral valve weakly convex in posterior region but concave at flanks; umbo protruding, beak suberect; sulcus strong, anteriorly forms subtrapezoidal tongue. Dorsal valve regularly convex in posterior view, sometimes with flattened to weakly concave anterior in lateral profile and steep ventrally curving flanks resulting in slight geniculation at anterolateral margins; fold clearly separate at anterior half, becoming broader and much higher anteriorly. Shell ornament of strong, simple costae extending from beaks; costae rounded posteriorly, becoming angular and high anteriorly, those on ventral flanks reflected at their ends in ventral direction forming short but distinct spurs which protrude ventrally at valve margin (Fig. 9C–E); sulcus with 4 and fold with 5 costae, flanks with commonly 7–8 costae, but may reach 11.

Interior of ventral valve with long divergent dental plates. In dorsal valve long median septum attains slightly less than half of the valve length and supports V-shaped septalium (Fig. 9F₃, G₂); outer hinge plates triangular, flat, up to 2 mm

long, flanked laterally by high inner socket ridges; crura poorly preserved, observed in one specimen, fairly long, divergent, curving ventrally; adductor scars well preserved in one valve (Fig. 9F), impressed, anterior pair subelliptic, slightly divergent anteriorly, posterior pair smaller, strongly elongate, divergent anteriorly, slightly asymmetric.

Remarks.—*Pleuropugnoides calcaris* sp. nov. is morphologically close to, and was probably the ancestor of, *P. pleurodon* (Phillips, 1836) described from the early Viséan of England and Northern Ireland (see Ferguson 1966; Brunton 1984). The Chinese species is readily distinguished from the latter mainly by its smaller shell, stronger, more angular and more numerous costae in the sulcus and on the flanks. Internally *P. calcaris* differs in having a longer median septum in the dorsal valve. It is also similar to *Pleuropugnoides greenleightonensis* Ferguson, 1966 from the late Namurian of British Isles (Ferguson 1966) in attaining comparable shell dimensions and in having angular costae and a long dorsal median septum. The characteristic marginal spurs on the ventral flanks which are formed by strongly reflected anterior ends of costae in ventral direction, appear also to be present in *P. greenleightonensis* (see Ferguson 1966: pl. 23: 11–13). *P. calcaris* differs in having more numerous costae in the sulcus (usually 4 in the former and 2–3 in *P. greenleightonensis*) and on the flanks (usually 7–8 and 3–5, respectively) and a more trapezoidal, rather than rounded tongue.

It is noteworthy that a rhynchonellid similar to the species here described has been widely reported from China as *Ptychomaletoechia kinlingensis* (Grabau, in Chu 1933). The species is known from many localities and from sediments representing the late Famennian through the Tournaisian (e.g., Yang 1964; Tan 1987; Chen and Shi 1999). Unfortunately, Amadeus Grabau never published his description of this species, and Chu (1933) was the first to give a short description with figures of what was then called *Camarotoechia kinlingensis* from the Kinling Limestone (Tournaisian) of Jiansu. Evidently this quite important Chinese form urgently needs taxonomic and nomenclatorial revision, including its generic assignment, which seems problematic because externally it is quite different from the early Famennian *Ptychomaletoechia omaliusi* (Gosselet, 1877), the type species of the genus.

Pleuropugnoides calcaris sp. nov. is generally more finely ribbed than *Ptychomaletoechia kinlingensis* having more ribs on the fold and sulcus (4 and 5 in the former, 3 and 4 in the latter) as well as on flanks (up to 11 and 8, respectively). In the former the flanks of the adult ventral valve are invariably distinctly concave whereas in the latter they are usually convex to flat and only rarely very weakly concave. *Ptychomaletoechia kinlingensis* does not form marginal spurs on its ventral flanks while in the species from Muhua they are characteristic. The ventral sulcus of the new species is less deep than in *P. kinlingensis*.

Stratigraphic and geographic range.—Known only from the type locality and horizon.

Genus *Propriopugnus* Brunton, 1984

Type species: Conchylolithus Anomites pugnus Martin, 1809; Carboniferous Limestone, Viséan; Derbyshire, England.

Propriopugnus? sp.

Fig. 9H.

Material.—Only one fragment of a ventral valve from sample MH1.

Remarks.—This very fragmentary specimen represents an anteromedian portion of ventral valve (i.e., tongue) and shows characteristic well marked radial costae which have a tendency to be gradually weaker posteriorly. The valve margin has a strongly zig-zag commissure. The specimen is 17.8 mm wide suggesting that the shell might attain about 27 mm in width. It does not belong to any other species identified in the Muhua Formation. It cannot be determined taxonomically with confidence but the general aspect of the specimen is suggestive of *Propriopugnus* Brunton, 1984 (see Parkinson 1954; Martínez Chacón 1979; Brunton 1984; Savage and Corlett 1996).

Family Petasmariidae Savage, 1996

Genus *Leiorhynchoidea* Cloud, 1944

Type species: Leiorhynchoidea schucherti Cloud, 1944; Wordian, Middle Permian; southwestern Coahuila, Las Delicias, Mexico.

Leiorhynchoidea? sp.

Fig. 10.

Material.—One almost complete shell, 2 incomplete dorsal and 1 incomplete ventral valves, all from sample MH2. Eight very small fragments of single dorsal valves and shells from sample M2-8 and 10 fragments of dorsal valves from sample MH1 may be also attributed to this species.

Remarks.—The two recovered dorsal valves from the sample MH2 attain approximately 12 and 18 mm in length, respectively. The valves are convex, widely oval in outline, posteriorly with a very shallow, barely perceptible median excavation, which anteriorly changes to gentle fold. Exterior of both valves is smooth in the posterior 8 mm, anteriorly with extremely delicate, simple rounded costae. On larger and better preserved valve (Fig. 10B) there are 4 costae in the fold, 2 parietal costae, and at least 7 almost indistinguishable costae on the partially preserved flank. Interior of both valves shows septalium supported by a thin median septum, the latter reaches much less than a half of the valve length.

Probably to this species can be referred a slightly damaged young shell, as well as a fragment of a ventral valve, both from the same sample as the two dorsal valves described above. The shell (Fig. 10D) is 12.2 mm long, 12.8 mm wide, 5.1 mm thick, broadly oval in outline, lenticular, and equibiconvex in lateral profile. Anterior region of both valves shows a very feeble, almost imperceptible costation and presence of a very shallow sulcus on the ventral valve. The

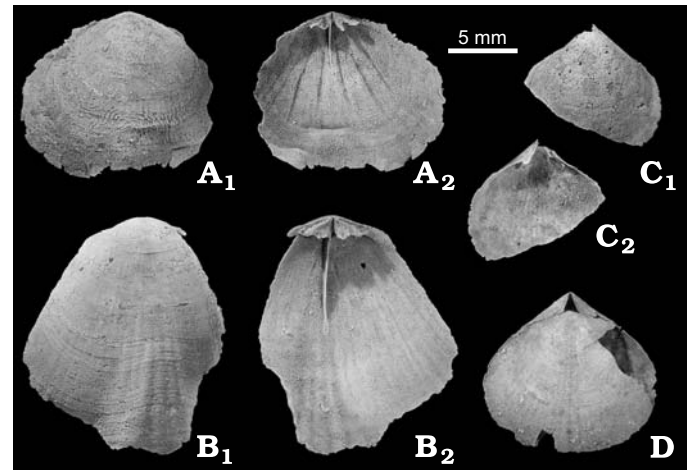


Fig. 10. Pugnacoid brachiopod *Leiorhynchoidea?* sp. from the Tornaisian Muhua Formation, southern China. **A, B.** Two isolated dorsal valves, PKUM02-0422 (**A**) and PKUM02-0423 (**B**), in exterior (**A₁**, **B₁**) and interior (**A₂**, **B₂**) views. **C.** Incomplete ventral valve, PKUM02-0424, in exterior (**C₁**) and interior (**C₂**) views. **D.** Almost complete shell, PKUM02-0425, in dorsal view. Sample MH2.

single broken ventral valve (Fig. 10C) shows also traces of costation as well as a presence of dental plates in its interior.

The described material is very fragmentary and the single shell at our disposal is too immature making the taxonomic determination of this form rather difficult. It bears some general resemblance to the Early Carboniferous–Late Permian genus *Leiorhynchoidea*. Our single complete shell shows some external similarity to *Leiorhynchoidea carbonifera* (Girty, 1911) described from the Chesterian of Idaho (Butts 2007). Other specimens from Muhua show also evident similarity to *L. carbonifera* from the Heath Formation (Mississippian) of Montana, USA (see Easton 1962). Paucity of the present material, however, does not allow for a more detailed determination.

Superfamily Stenoscismatoidea Oehlert, 1887

Family Stenoscismatidae Oehlert, 1887

Subfamily Stenoscismatinae Oehlert, 1887

Genus *Coledium* Grant, 1965

Type species: Coledium erugatum Grant, 1965; Moorefield Formation, Viséan, Carboniferous; Oklahoma, USA.

Coledium bruntoni sp. nov.

Figs. 11, 12.

Etymology: In honour of the late Dr. Howard C.H. Brunton (1935–2008), eminent brachiopodologist.

Holotype: Complete shell PKUM02-0426 illustrated in Fig. 11A.

Type locality: Muhua section, between villages of Muhua and Gedongguan (Guizhou province, South China).

Type horizon: Muhua Formation, correlated with the middle Tornaisian Lower *Siphonodella crenulata* conodont Zone.

Diagnosis.—*Coledium* with subpentagonal outline, flattened or concave ventral flanks, well developed posteriorly but lower anteriorly ventral sulcus, and recurved posterolateral

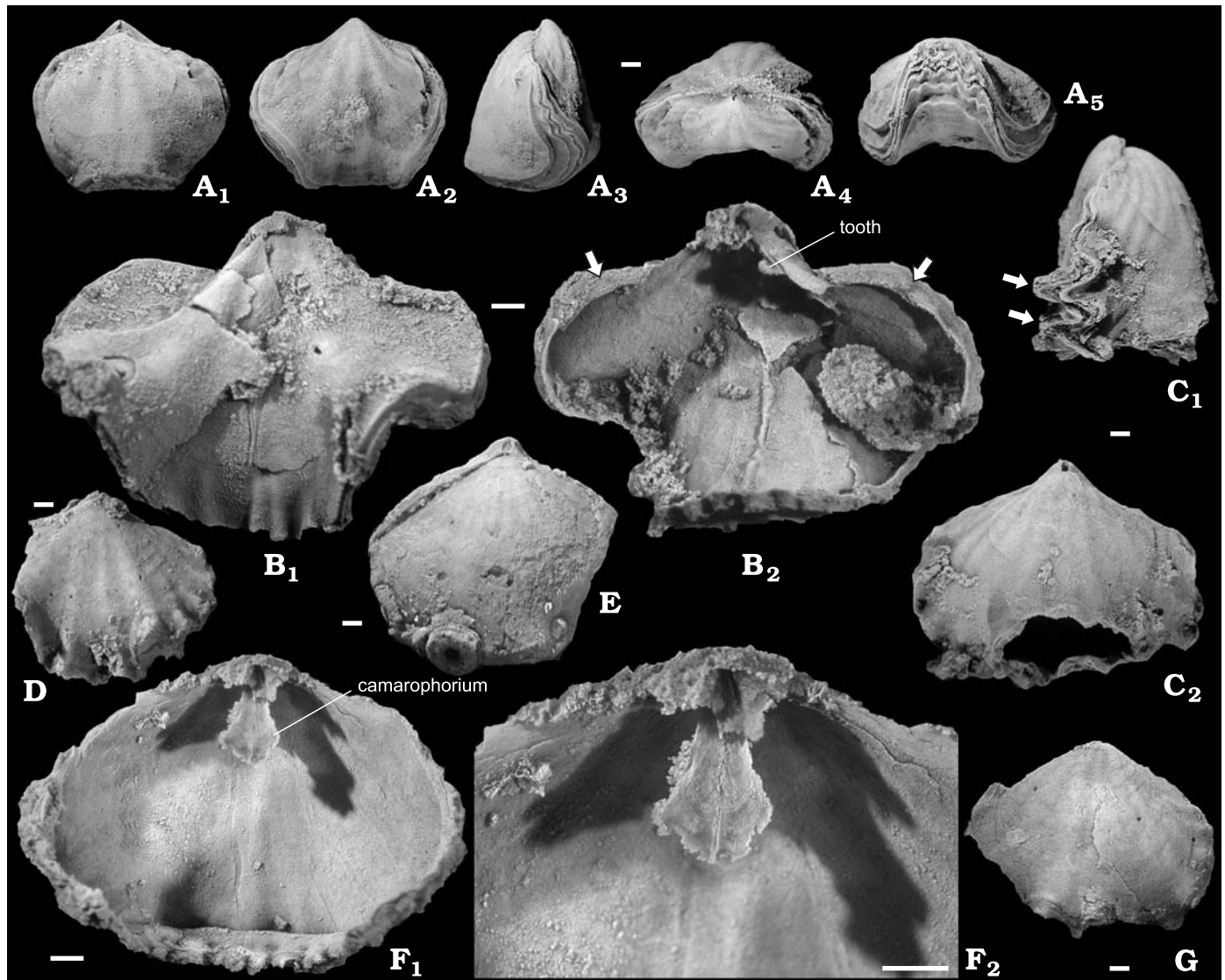


Fig. 11. Stenoscismatoid brachiopod *Coledium bruntoni* sp. nov. from the Tornaisian Muhua Formation, southern China. **A.** Complete shell, holotype PKUM02-0426, in dorsal (A₁), ventral (A₂), lateral (A₃), posterior (A₄), and anterior (A₅) views. **B.** Somewhat deformed ventral valve, PKUM02-0427, exterior (B₁) and interior (B₂); note the recurved postero-lateral valve margins (arrowed). **C.** Shell, PKUM02-0428, in lateral (C₁) and dorsal (C₂) views showing development of spurs (arrowed). **D.** Exterior of incomplete ventral valve, PKUM02-0429. **E.** Slightly damaged shell, PKUM02-0430, in dorsal view. **F.** Interior of the dorsal valve (F₁) and enlargement (F₂) showing camarophorium, PKUM02-0431. **G.** Exterior of incomplete dorsal valve, PKUM02-0432. Sample MH1. Scale bars 1 mm.

ventral margins; dorsal valve about twice as convex as the ventral one, with posteriorly low but anteriorly conspicuous fold; up to 5 ribs on each ventral flank, and up to 3 ribs in the sulcus; flank ribs frequently forms distinct spurs at valve margins. From the most similar *Coledium evexum* Grant, 1965 differs by having a larger, wider, less ventrally inflated shell, and less steep cardinal margins.

Material.—Two complete and two slightly damaged shells and several fragments of disarticulated valves from sample MH1. Dimensions of the holotype (in mm): length 8.6, width 9.6, thickness 6.5.

Description.—Shell attains up to 15.2 mm in width, widest posteriorly at one-third total length, dorsibiconvex, subpen-

tagonal in outline; cardinal extremities smoothly rounded, anterior margin straight or slightly emarginate, anterior commissure uniplicate, valve margins may be slightly geniculate and concentrically undulate because of several growth halts.

Ventral valve pentagonal in outline, slightly convex, with flattened or concave flanks; sulcus begins near the umbo where it is well delineated, more anteriorly it becomes poorly defined; tongue observed in large specimens only; beak suberect, interareas absent, posterolateral margins of the valve strongly recurved and overlapped by the edges of the dorsal valve (Fig. 11B).

Dorsal valve about twice as convex as the ventral one; fold poorly defined, becoming quite conspicuous in the anterior half of the valve.

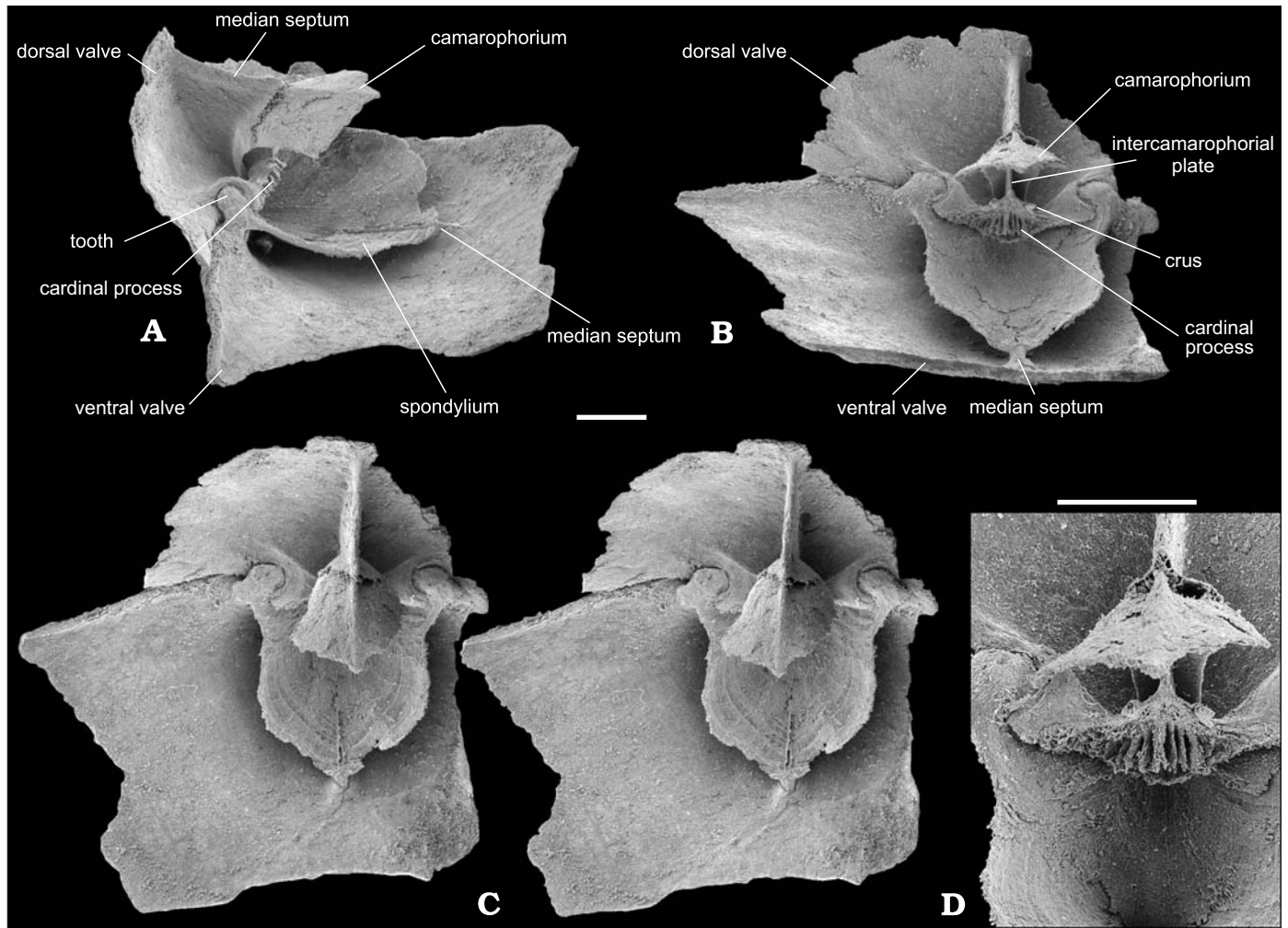


Fig. 12. Stenosismatoid brachiopod *Coledium bruntoni* sp. nov. from the Tornaisian Muhua Formation, southern China. SEM micrographs of the posterior region of a shell PKUM02-0433 showing details of the internal structure viewed laterally (A), anteriorly (B), anterodorsally (C; stereopair), and anteriorly (D; enlargement of B), with labelled morphology. Sample MH1. Scale bars 1 mm.

Interior of ventral valve with a wide, dorsally concave spondylium attaining about 2.5 mm in length and supported by a low median septum. Dorsal interior with a weakly concave camarophorial plate supported by the median septum; median septum highest anteriorly (Fig. 12); intercamarophorial plate and cardinal process (ctenophoridium) present (Fig. 12B, D).

Costae impermanent, very low, delicate and wide, on some specimens they are more strongly developed on the posterior region of the shell; in large specimens flank costae are very strong at the shell margin, where they develop long spurs; when present on both valves they project ventrally and dorsally at right angles to the valve surfaces; up to 5 ribs on each ventral flank, and up to 3 ribs in the sulcus.

Remarks.—The presence of a distinct spondylium and camarophorium indicates that these specimens belong to the stenoscismatoid rhynchonellides. The presence of an intercamarophorial plate in the dorsal valve is important taxonomically. These features, in combination with the general

aspects of the shell and its ornament indicate an assignment to *Atribonium* Grant, 1965 or *Coledium* Grant, 1965. In the latter genus, however, the presence of stolidium is very characteristic, while it is absent in the former. Although this structure is not well preserved on the shells from Muhua, presence of several undulate growth halts (Fig. 11A₅) at the valve margins is indicative of a stolidium and, in consequence, our material is attributed to the genus *Coledium*.

The described form is most similar externally to *Coledium evexum* Grant, 1965 from the Early Mississippian (Kinderhookian) of Central Texas, USA (see Grant 1965: 112–114, pl. 15: 1–10; text-fig. 26). However, the Chinese species can be distinguished readily from the latter by having a larger, wider, less ventrally inflated shell, and less steep cardinal margins. *Coledium bruntoni* sp. nov. is similar in size, general outline, and slightly concave ventral flanks to *Coledium altisulcatum* Carter, 1967 from the Chappel Limestone (Mississippian) of central Texas (see Carter 1967: 308–310, fig. 5, pl. 22: 9–12) but differs in having stronger radial ornament and less inflated dorsal umbo.

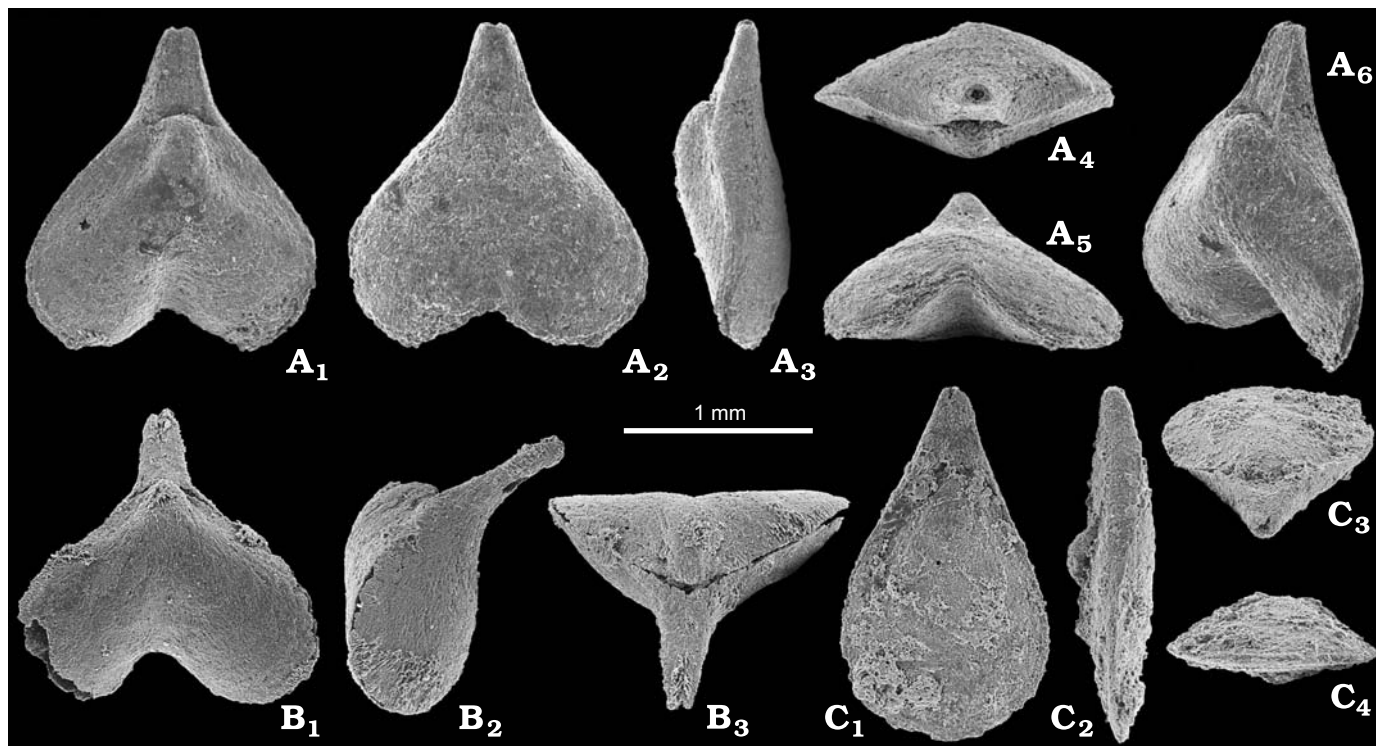


Fig. 13. Lambdarinoidean brachiopods from the Tornaisian Muhua Formation, southern China. **A.** *Lambdarina sinensis* Baliński and Sun, 2008 (figured in Baliński and Sun 2008: fig. 3K–P), holotype ZPAL V.XXVI/26, shell in dorsal (A₁), ventral (A₂), lateral (A₃), posterior (A₄), anterior (A₅), and oblique lateral (A₆) views. **B.** *Hampsia cooperi* Morris, 1994, PKUM02-0434, shell in dorsal (B₁), lateral (B₂), and posterior (B₃) views. **C.** *Dacryrina dziki* Baliński and Sun, 2008, PKUM02-0435, shell in dorsal (C₁), lateral (C₂), posterior (C₃), and anterior (C₄) views. All SEM micrographs. Samples Mu-42 (A), D (B), and GB (C).

Stratigraphic and geographic range.—Known only from the type locality and horizon.

Superfamily Lambdarinoidea Brunton and Champion, 1974

Family Lambdarinidae Brunton and Champion, 1974

Subfamily Lambdarininae Brunton and Champion, 1974

Genus *Lambdarina* Brunton and Champion, 1974

Type species: *Lambdarina manifoldensis* Brunton and Champion, 1974; early Viséan, Carboniferous Limestone; Staffordshire, England.

Lambdarina sinensis Baliński and Sun, 2008

Fig. 13A.

1999 *Lambdarina* sp.; Baliński 1999: 442, 445, fig. 4I–O, Q, R.

2008 *Lambdarina sinensis* n. sp.; Baliński and Sun 2008: 107–110, figs. 3, 4.

Material.—72 complete to slightly damaged shells, 12 fragments of shells, five dorsal and twelve ventral valves recovered from several samples taken from the Muhua Formation, namely Mu-42, MH1, M2-8, D2, D4, GB, and GT.

Remarks.—This minute species from Muhua has been described and discussed in detail recently by Baliński and Sun (2008). It is the oldest representative of the genus and its proportionally shorter and wider shell lobes seem to be rather primitive feature. In this respect the Chinese species is the closest to the forerunner of the group, i.e., to *Loborina lobata*

Baliński, 1982 from the Famennian of Poland (Baliński 1982, 1995).

Stratigraphic and geographic range.—Known only from the type locality and horizon.

Genus *Hampsia* Morris, 1994

Type species: *Hampsia cooperi* Morris, 1994; Viséan, Carboniferous; Staffordshire, England.

Hampsia cooperi Morris, 1994

Fig. 13B.

1994 *Hampsia cooperi* n. g. n. sp.; Morris 1994: 271–272, fig. 1A–G.

2008 *Hampsia cooperi* Morris, 1994; Baliński and Sun 2008: 112–113, fig. 8.

Material.—Six almost complete shells, one dorsal and one ventral valve slightly covered by adhered grains of silica from samples MH1 and D4.

Remarks.—This species is poorly represented in our collections. It has been described and discussed in detail by Baliński and Sun (2008). Externally, the specimens from China are very similar to *Hampsia cooperi* Morris, 1994 from the Viséan of Staffordshire (England), which is the only known species of the genus.

Stratigraphic and geographic range.—The species is known from the Viséan of Staffordshire, England (Morris 1994) and Tornaisian of southern China (Baliński and Sun 2008 and herein).

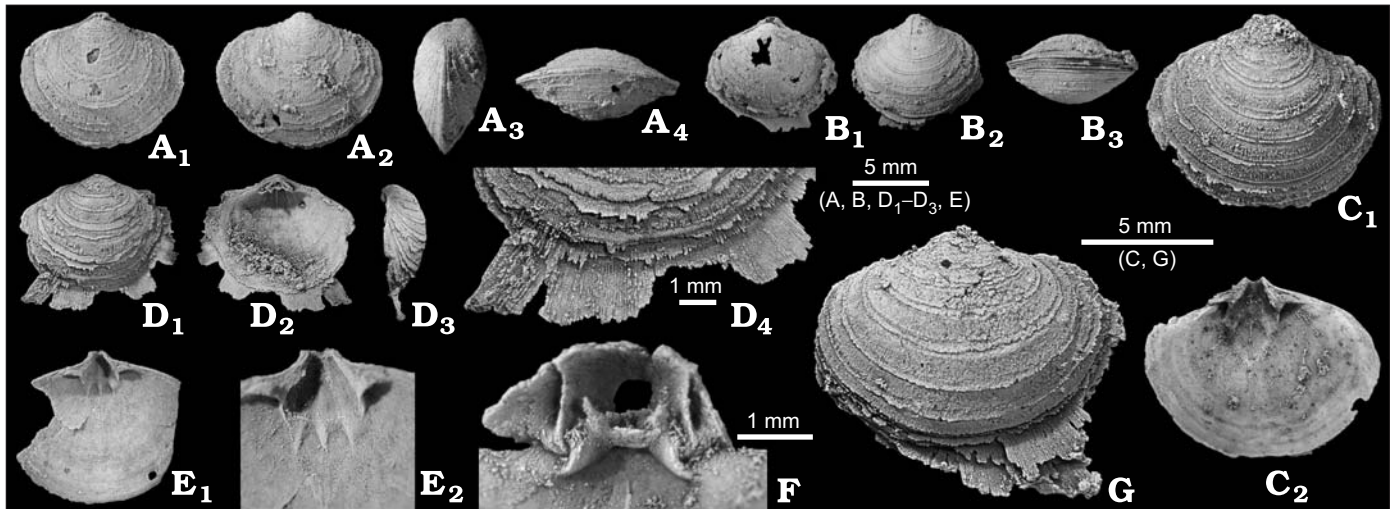


Fig. 14. Athyridoid brachiopod *Actinoconchus* sp. from the Tornaisian Muhua Formation, southern China. A. Complete shell, PKUM02-0436, in dorsal (A₁), ventral (A₂), lateral (A₃), and anterior (A₄) views. B. Shell, PKUM02-0437, in dorsal (B₁), ventral (B₂), and anterior (B₃) views. C. Ventral valve, PKUM02-0438, viewed from exterior (C₁), and interior (C₂). D. Dorsal valve, PKUM02-0439, in exterior (D₁), interior (D₂), and lateral (D₃) views, and enlargement of the external lamellose ornamentation (D₄). E. Incomplete ventral valve, PKUM02-0440, viewed internally (E₁) and enlargement showing dental plates and muscle scars (E₂). F. Umbonal region of a broken shell, PKUM02-0441, showing dental plates and cardinalia (dorsal valve below). G. Exterior of ventral valve, PKUM02-0442, showing well preserved long growth lamellae. All from sample MH1.

Genus *Dacryrina* Baliński and Sun, 2008

Type species: *Dacryrina dziki* Baliński and Sun, 2008; Muhua Formation, Tornaisian, Carboniferous; Muhua, Guizhou Province, China.

Dacryrina dziki Baliński and Sun, 2008

Fig. 13C.

1999 Rhynchonelloid gen. et sp. indet.; Baliński 1999: 445, fig. 4F, G. 2008 *Dacryrina dziki* n. sp.; Baliński and Sun 2008: 111–112, figs. 6, 7.

Material.—22 complete shells, two ventral and two dorsal valves from samples Mu-42, GB, and GT.

Remarks.—For a detailed description of the genus and species see Baliński and Sun (2008). This unusual micromorphic lambdarinoid differs from all members of the superfamily by lacking a bilobed shell outline. Instead, it is characterised by a tear-shaped elongate shell and by having a long, straight, tube-like ventral umbo, which is narrowly triangular in outline as in *Lambdarina*. Internally, the Chinese form is also virtually identical to *Lambdarina*. It is noteworthy that including the genus *Dacryrina* into the superfamily Lambdarinoidea leads to expand the diagnosis of the superfamily in order to include not bilobed, elongate tear-shaped forms. Baliński and Sun (2008) have commented on a presumable life habit of *Dacryrina dziki* and other co-occurring lambdarinids in the Muhua Formation as did Brunton and Champion (1974) for their species from the Viséan of Staffordshire, England.

Order Athyridida Boucot, Johnson, and Staton, 1964
Suborder Athyrididina Boucot, Johnson, and Staton, 1964

Superfamily Athyridoidea Davidson, 1881

Family Athyrididae Davidson, 1881

Subfamily Athyridinae Davidson, 1881

Genus *Actinoconchus* M'Coy, 1844

Type species: *Actinoconchus paradoxus* M'Coy, 1844; Chadian, early Viséan, Carboniferous; Millicent, Kildare County, Ireland.

Actinoconchus sp.

Fig. 14.

Material.—Seven complete shells, 10 ventral, and 9 dorsal valves from sample MH1.

Description.—Shell transversely elliptical to oval in outline, subequally biconvex, sulcus and fold lacking. Ventral interior with short, subparallel and anteriorly divergent dental plates. Inside dorsal valve a small cardinal plate present, with small circular foramen, and postero-laterally bordered by elevated inner socket ridges (cardinal flanges; Fig. 14F); low, sharp myophragm divides medially the dorsal adductor scars (Fig. 14D₂). Externally with strong, widely distributed, concentric growth lines and flat, very long flanges; flanges do not disintegrate to spine-like projections, but are densely longitudinally striated (Fig. 14D₄, G).

Dimensions in mm, shell: length 7.1, width 8.8, thickness 4.7; largest complete ventral valve: length 9.8, width 12.2.

Remarks.—Xu and Yao (1988) described two new and two other species of *Actinoconchus* from the earliest Carboniferous of the Nanbiancun section, Guanxi Province, Southern China. The exterior of these species, as well as the details of ornamentation illustrated for three of those forms strongly suggest that they do not represent *Actinoconchus* but rather *Cleiothyridina*.

The species from Muhua are quite close externally to the type species of the genus, i.e., *Actinoconchus paradoxus* M'Coy, 1844 (see Brunton 1980) having similar shell shape but differing mainly in having less posteriorly protruding umbo of the ventral valve. The former are much less expanded

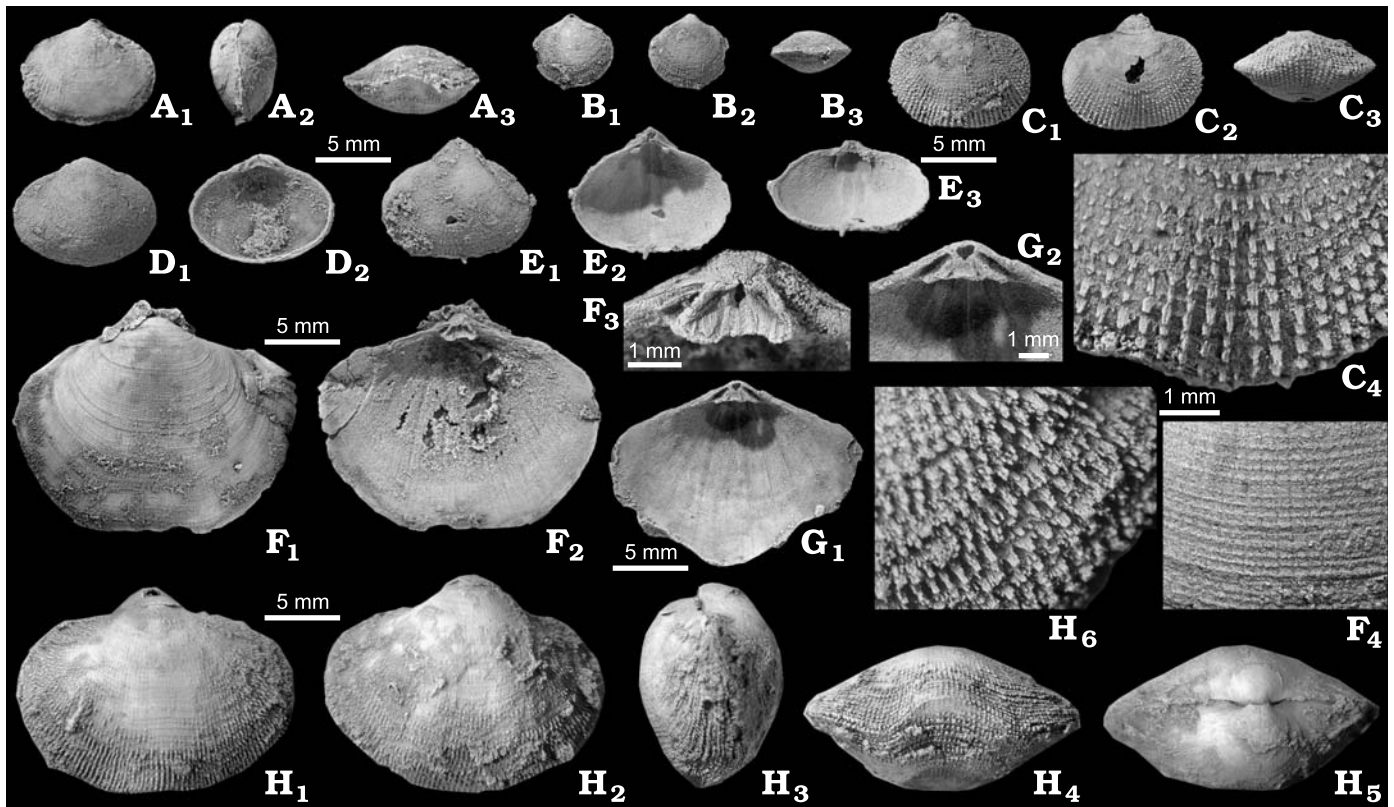


Fig. 15. Athyridoid brachiopod *Cleiothyridina deroissyi* (Léveillé, 1835) from the Tornaisian Muhua Formation, southern China. **A.** Complete juvenile shell, PKUM02-0443, in dorsal (A₁), lateral (A₂), and anterior (A₃) views. **B, C.** Two almost complete shells, PKUM02-0444 (**B**) and PKUM02-0445 (**C**), in dorsal (B₁, C₁), ventral (B₂, C₂), and anterior (B₃, C₃) views, and enlargement of ventral valve showing micro-ornamentation (C₄). **D.** Dorsal valve, PKUM02-0446, viewed externally (D₁) and internally (D₂). **E.** Ventral valve, PKUM02-0447, in exterior (E₁), interior (E₂), and the same inclined anteriorly (E₃) views. **F.** Dorsal valve, PKUM02-0448, in exterior (F₁) and interior (F₂) views and enlarged view of cardinalia (F₃) and corroded surface micro-ornamentation (F₄). **G.** Dorsal valve, PKUM02-0449, interior (G₁) and enlarged view of cardinalia (G₂). **H.** Complete shell, PKUM02-0450, in dorsal (H₁), ventral (H₂), lateral (H₃), anterior (H₄), and posterior (H₅) views, and enlargement showing shell micro-ornamentation (H₆). All from sample MH1.

laterally than *Actinoconchus expansus expansus* (Phillips, 1836) and *A. expansus patulus* Brunton, 1980 but more wide than *Actinoconchus oblongus* (Sowerby, 1840) and *Actinoconchus obtusus* (M'Coy, 1844). Brunton (1980) placed provisionally *A. obtusus* in synonymy with *A. oblongus*. Several other lamellose athyridids similar to *Actinoconchus* but with persistent ventral sulcus were placed by Jin and Fang (1983) within genus *Lamellosathyris* Jin and Fang, 1983.

Subfamily Cleiothyridininae Alvarez, Rong, and Boucot, 1998

Genus *Cleiothyridina* Buckman, 1906

Type species: Atrypa pectinifera J. de C. Sowerby, 1840; Guadalupian, Permian; Durham, England.

Cleiothyridina deroissyi (Léveillé, 1835)

Figs. 4B, C, I, 15, 16A.

1835 *Spirifer De Roissyi*; Léveillé 1835: 39, pl. 2: 18–20.

1980 *Cleiothyridina deroissyi* (Léveillé); Brunton 1980: 228–229, figs. 23–24.

1984 *Cleiothyridina deroissyi* (Léveillé); Brunton 1984: 59–62, figs. 67–73.

Material.—76 complete shells and more than 110 mostly

complete single valves. The majority of the present material came from sample MH1, but several specimens of the species was found also in samples MH2 and M2-8.

Remarks.—The specimens from Muhua are characterised by a strongly transverse elliptical to subcircular outline, strongly biconvex shell profile and a median fold and sulcus. The largest shells reach about 20 mm in width. The shells are ornamented with dense, concentric, thin lamellae projecting anteriorly and anterolaterally as flattened spine-like outgrowths arranged in radial rows (Fig. 15C₄, H₆). On specimens with worn out surface a characteristic reticulate pattern is well seen (Fig. 15F₄).

Internally, an apically perforated cardinal plate and low median myophragm are present in dorsal valves. The dental plates tend to be clearly laterally convex and widely separated when they merge with the valve floor (Fig. 15E₃). The pair of elongate oval adductor scars separated by low median myophragm is easily distinguishable on large specimens. The dorsal median myophragm is relatively short, about one-fourth of the valve length, and does not extend to the anterior margin of the adductor scars. The latter are located clearly posteriorly to the valve midpoint whereas in *Cleiothyridina tenuilineata* described below the scars reach almost a half of

the valve length (Fig. 16). The outer hinge plates are roughly triangular in shape with posterolateral edges (or inner socket ridges) forming cardinal flanges which are slightly postero-ventrally bent. The conjunct inner hinge plates are sub-trapezoidal in shape and have a thin median ridge. In one well preserved dorsal valve a longitudinal striation is visible on the whole surface of the outer hinge plates (Fig. 15F₃). Slightly weaker and oblique striation can be observed on the inner hinge plates of the same valve. Most probably this complex striation marks the attachment scars of the pedicle adjustor muscles. The dorsal foramen is relatively small but frequently it seems enlarged by damage (Fig. 15F₃). The mantle canal system is well impressed especially in large dorsal valves. Four to five pairs of principal canals could be recognised (e.g., 15F₂). The dental plates tend to be laterally convex and widely separated when they merge with the valve floor (Fig. 15E₃). The pair of elongate oval adductor scars, separated by low median myophragm is easily distinguishable on large specimens.

The described specimens are very similar to the Early Carboniferous *Cleiothyridina deroissyi* (Léveillé, 1835) described from the Western Europe (see Brunton 1980, 1984). The species is characterised by a variable shell outline which in adult individuals may be unusually transverse for the genus (Brunton 1984: 59, fig. 73). Similar variability is observed among Chinese specimens.

Feng (1989) described *Cleiothyridina dapoushangensis* Feng, 1989 from Dapoushang section (vicinity of Muhua) on the basis of a single, possibly juvenile and slightly incomplete specimen. Unfortunately, this inadequate material is not sufficient to make any reliable comparison with our specimens. Moreover, the type specimen from Dapoushang seems to be lost (Xueping Ma and Ji Qiang personal communication, December, 2009).

Stratigraphic and geographic range.—According to Brunton (1984) *C. deroissyi* occurs relatively commonly in the Tournaisian of Belgium and less frequently in the Tournaisian-mid-Viséan in the British Isles, now recovered from Tournaisian of southern China.

Cleiothyridina tenuilineata (Rowley, 1900)

Figs. 4D–F, J, 16B, 17.

1900 *Athyris tenuilineata*; Rowley 1900: 264, pl. 5: 31–33.

1967 *Cleiothyridina tenuilineata* (Rowley); Carter 1967: 344–347, pl. 16: 8a–13e; text-fig. 21.

1979 *Cleiothyridina tenuilineata* (Rowley, 1900); Nalivkin 1979: 155, pl. 64: 5.

1987 *Cleiothyridina tenuilineata* (Rowley); Carter 1987: 60, pl. 20: 1–12.

Material.—69 complete shells and nearly 200 separate valves from sample MH1.

Remarks.—The specimens are characterised by their almost equally biconvex, lenticular shell, usually circular to slightly pentagonal outline, and rectimarginate anterior commissure. The shell width is equal to or slightly less than the shell length, but slightly wider specimens can also be found. The largest specimens attain about 14–15 mm in width. They have no evident median fold or sulcus. The ventral interior shows well developed sub-parallel dental plates (Fig. 17C). The dorsal median myophragm extends more than one-third to one-half of the valve length and divides two pairs of well marked, subovate adductor scars (see Figs. 16B, 17H). The anterior margin of the adductor scars is very close to the mid-point of the dorsal valve. The triangular outer hinge plates are postero-laterally bounded by thickened, postero-ventrally projecting cardinal flanges. The conjunct inner hinge plates are subtrapezoidal and pierced apically by a relatively small dorsal foramen. However, the median ridge on the cardinal plate, which is well developed in *Cleiothyridina deroissyi* described above, is usually absent in the present species or weakly marked in the most posterior region of the plate (Fig. 17F). Spirallium, jugum, and jugal stem are preserved in a broken shell shown on Fig. 17N. The external ornamentation consists of dense concentric, partly overlapping growth lamellae which on better preserved specimens may also be fringed with flattened spine-like outgrowths (Fig. 17E, K, O); the latter seem more closely but less regularly spaced than in *C. deroissyi* described above. It is noteworthy that generally the spine-like outgrowths are rarely observable in our specimens whereas short concentric lamellae are the most common.

The general lenticular shell shape and proportion of its external dimensions strongly suggest that the specimens belong to *Cleiothyridina tenuilineata* (Rowley, 1900), described from the Mississippian of North America (Carter 1967, 1987). Externally the specimens from Muhua are also almost identical with *Cleiothyridina fimbriata* (Phillips, 1836) described from late Tournaisian and Viséan strata of the British Isles (see Brunton 1984: 58–59). As Brunton (1984: 58) noted the strik-

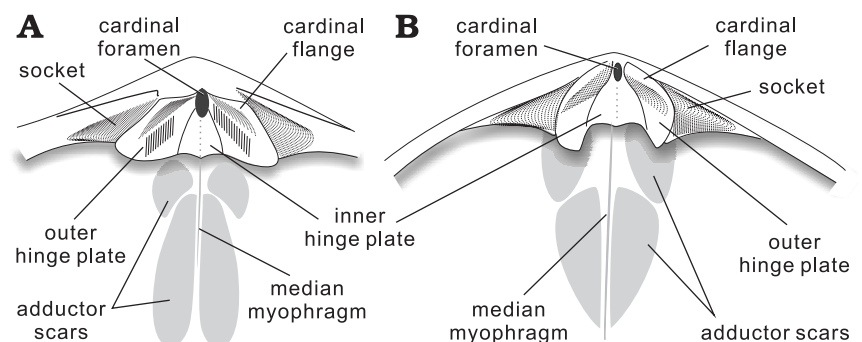


Fig. 16. Reconstruction of the cardinalia of athyridide *Cleiothyridina deroissyi* (Léveillé, 1835) (A) and *Cleiothyridina tenuilineata* (Rowley, 1900) (B).

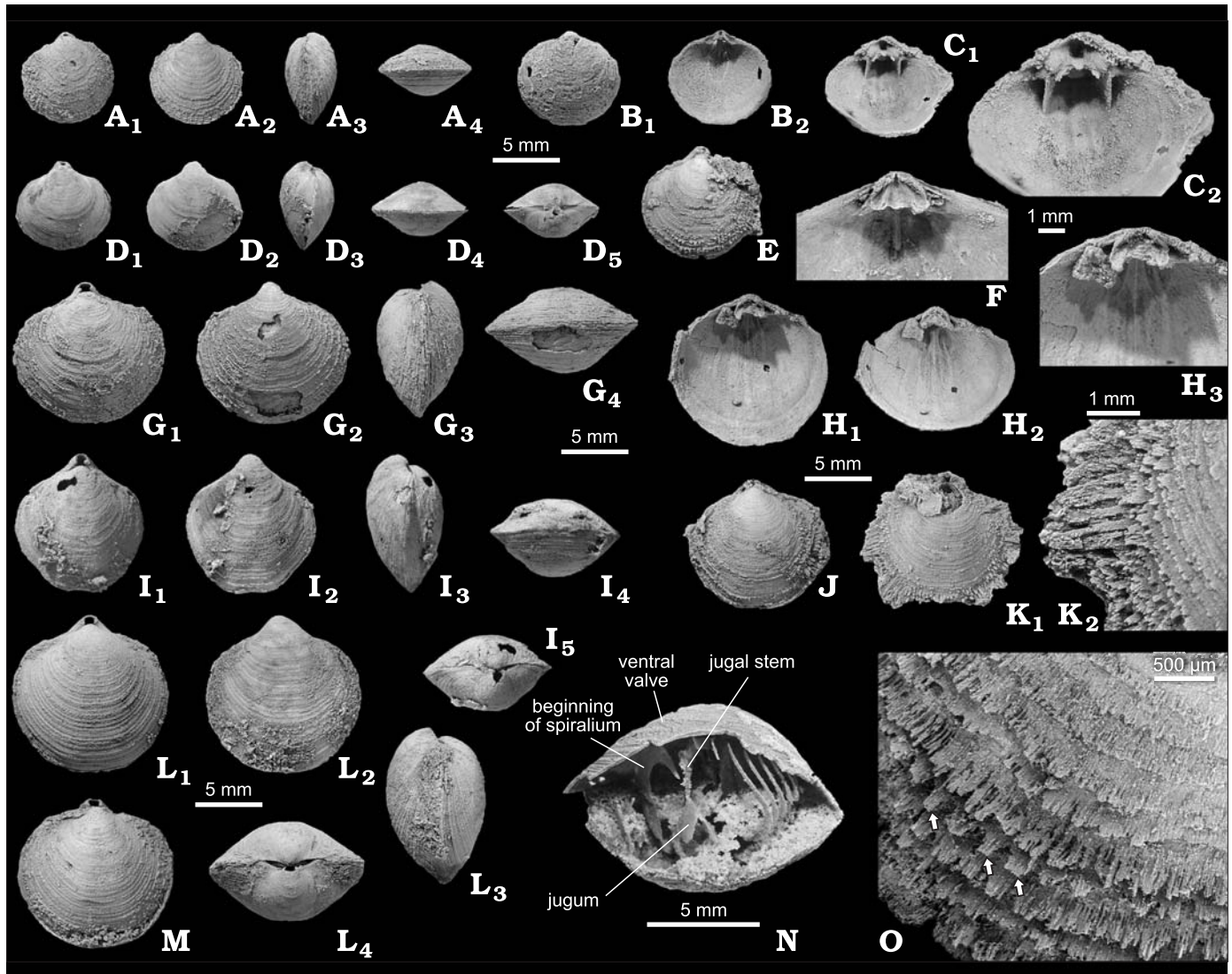


Fig. 17. Athyridoid brachiopod *Cleiothyridina tenuilineata* (Rowley, 1900) from the Tournaisian Muhua Formation, southern China. **A.** Complete juvenile shell, PKUM02-0451, in dorsal (A₁), ventral (A₂), lateral (A₃), and anterior (A₄) views. **B.** Dorsal valve, PKUM02-0452, exterior (B₁) and interior (B₂). **C.** Interior of ventral valve, PKUM02-0453, with preserved broken off umbonal region of the dorsal valve (cardinalia viewed from below), in general (C₁) and enlarged (C₂) views. **D.** Juvenile shell, PKUM02-0454, in dorsal (D₁), ventral (D₂), lateral (D₃), anterior (D₄), and posterior (D₅) views. **E.** Complete shell, PKUM02-0455, with adhered some silica deposits in dorsal view. **F.** Well preserved cardinalia, PKUM02-0456. **G.** Shell, PKUM02-0457, in dorsal (G₁), ventral (G₂), lateral (G₃), and anterior (G₄) views. **H.** Dorsal valve, PKUM02-0458, in interior (H₁), the same slightly inclined anteriorly (H₂), and enlarged (H₃) views. **I.** Shell, PKUM02-0459, in dorsal (I₁), ventral (I₂), lateral (I₃), anterior (I₄), and posterior (I₅) views. **J.** Complete shell, PKUM02-0460, in dorsal view. **K.** Shell, PKUM02-0461, with preserved spine-like outgrowths in dorsal (K₁) and enlarged (K₂) views. **L.** Complete shell, PKUM02-0462, in dorsal (L₁), ventral (L₂), lateral (L₃), and posterior (L₄) views. **M.** Complete shell, PKUM02-0463, in dorsal view. **N.** Damaged shell, PKUM02-0464, viewed from the anterior showing preserved spirallium with labelled details. **O.** Enlargement showing well preserved surface micro-ornamentation; note concentric lamellae desintegrating to spine-like outgrowths (arrowed), PKUM02-0399; see also Fig. 4J. All from sample MH1.

ing feature of the shell of *C. fimbriata* is its spinose ornamentation which consists of very long “spines” attaining up to 5 mm in length. Although the spines on our specimens may be also quite long (up to about 2 mm in specimen shown on Fig. 17K) they seem to be less regularly spaced than in the species from the British Isles.

Stratigraphic and geographic range.—According to Carter (1967, 1987) *Cleiothyridina tenuilineata* is widely distributed in the late Kinderhookian and early Osagian of the central and southwestern USA, as well as in the Banff Formation

(Early Carboniferous) of Canada. This species was also recorded from Kynov horizon (lower Tournaisian) of the Urals (Nalivkin 1979). Comparable specimens were recorded as *C. cf. tenuilineata* by Sour-Touvar et al. (2005) from lower Mississippian of northeastern México. Tournaisian of Muhua section, southern China.

Superfamily Meristelloidea Waagen, 1883

Family Meristidae Hall and Clarke, 1895

Subfamily Rowleyellinae Alvarez and Brunton, 1995

Genus *Muhuathyris* Sun, Ma, Baliński, and Zhang, 2004

Type species: Muhuathyris circularis Sun, Ma, Baliński, and Zhang, 2004; Muhua Formation, Tournaisian, Carboniferous; Muhua, Guizhou Province, China.

Muhuathyris circularis Sun, Ma, Baliński, and Zhang, 2004

Fig. 18.

2004 *Muhuathyris circularis* new species; Sun et al. 2004b: 240–243, figs. 1–3.

Material.—Four ventral and six complete dorsal valves from sample MH1; in addition 14 incomplete ventral and dorsal valves ranging from 4 to 25 mm in width.

Description.—The species was described in detail by Sun et al. (2004b).

Remarks.—*Muhuathyris circularis* is one of the most characteristic athyridid brachiopods in the fauna of the Muhua Formation. Its general morphology as well as details of a complex internal shell structure and its variability were discussed by Sun et al. (2004b). It differs from related *Camorphorella* Hall and Clarke, 1893 in the absence of a dorsal shoe lifter. From the similar genus *Rowleyella* Weller, 1911 the Chinese species differs in having two long subparallel vertical plates lateral to the dorsal median septum (Fig. 18B, C) and extending from the beak to the posterior edges of the dorsal adductor scars. However, these plates could be interpreted as rudimentary cruralium (see Sun et al. 2004b: 243) which in *Rowleyella* is well developed. According to Alvarez (2007) the subfamily affiliation of *Muhuathyris* is somewhat uncertain but our interpretation of the interior of the genus indicates that it can be placed within Rowleyellinae.

Stratigraphic and geographic range.—At present the species (and genus) is known from the type locality only.

Superfamily Nucleospiroidea Davidson, 1881

Family Nucleospiridae Davidson, 1881

Genus *Nucleospira* Hall in Davidson, 1858

Type species: Spirifer ventricosus Hall, 1857; Lochkovian, Lower Helderberg Group, Devonian; New York, USA.

Nucleospira sp.

Fig. 19C–E.

1999 *Nucleospira?* sp.; Baliński 1999: 445, fig. 4H.

Material.—Four fragmentary dorsal valves and 2 shell fragments from samples MH1 and Mu-42.

Remarks.—The species was first noted in the Muhua fauna by Baliński (1999) on the basis of two small fragments of dorsal valves extracted by acid treatment from a 1.5 kg sample from Mu-42. Recently, although several hundreds of kilograms of samples from the Muhua Formation were processed in acid, only three additional fragmentary specimens were found. The specimens show the characteristic posteroventrally projecting cardinal process, with a wide cavity at its internal base. The sockets are shallow, positioned behind the flanks of the cardinal process and crural bases (Fig. 19D, E); the latter run ventrally along the flanks of the cardinal process. Spine bases are clearly seen on only one dorsal valve.

Suborder Retziidina Boucot, Johnson, and Staton, 1964

Superfamily Retzioidea Waagen, 1883

Family Retziidae Waagen, 1883

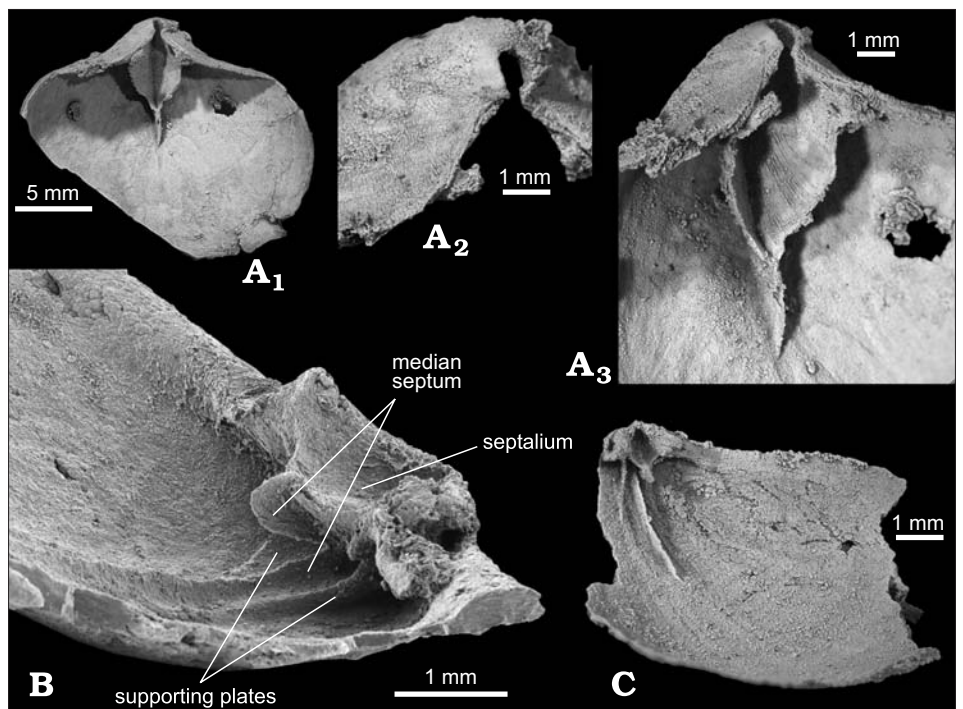


Fig. 18. Meristelloid brachiopod *Muhuathyris circularis* Sun, Ma, Baliński, and Zhang, 2004 from the Tournaisian Muhua Formation, southern China. **A.** Incomplete ventral valve, PKUM02-0465, in general interior view (A_1), enlargement of umbonal region showing left tooth (A_2), and enlarged interior in slightly oblique view showing spondylium supported by median septum (A_3). **B.** SEM micrograph of the interior of an incomplete dorsal valve, PKUM02-0466, in oblique-lateral view with labelled morphology (partly after Sun et al. 2004b: fig. 1–25). **C.** Incomplete dorsal valve, PKUM02-0467, in oblique view showing cardinalia. All from sample MH1.

Genus *Acambona* White, 1865

Type species: Acambona prima White, 1865; Burlington Limestone, Osagean, Mississippian; Iowa, USA.

Acambona sp.

Fig. 19B, F–I.

Material.—One slightly damaged juvenile dorsal valve, 14 very small fragments of umbonal region of dorsal valve, and one incomplete ventral valve from samples MH2, M2-8, M2/2, M2/3, and M2/4.

Remarks.—Although the specimens at our disposal are very fragmentary there is no doubt that they belong to the retziid athyridides. The characteristic internal features of the dorsal valves are: massive cardinal plate without perforation, high postero-ventrally projecting cardinal flanges, and low median septum. The cardinal plate is attached to the valve wall dorsally to the inner socket ridges (Fig. 19G). Of special interest is the presence of a distinct median ridge running on the underside of the cardinal plate, continuing anteriorly from the umbonal cavity also as a median ridge on the valve floor (Fig. 19G). This ridge can be interpreted as a low median septum. A strong median ridge is also observed between high and sharp crural bases on the upper (ventral) surface of the cardinal plate (Fig. 19B₁, F). Inside the ventral valve a short pedicle collar is developed. The presence of a median ridge on the floor of the dorsal valve and median ridges on both the upper and lower surfaces of the cardinal plate distinguish the specimens from Muhua from all known species of *Eumetria* Hall, 1863. The absence of distinct radial costae on our specimens (which usually represent, however, only the umbonal region of the shell) reminds the condition observed in *Acambona* (e.g., Weller 1914: 449; Grunt 1986: 159). Also the presence of distinct pedicle collar in ventral valves from Muhua indicates that they should be included rather in the genus *Acambona*. The specimens clearly represent, at least, a new species, but more material is needed in order to allow a full description.

Family Neoretziidae Dagys 1972

Subfamily Hustediinae Grunt, 1986

Genus *Hustedia* Hall and Clarke, 1893

Type species: Terebratulina mormoni Marcou, 1858; Upper Carboniferous; Nebraska, USA.

Hustedia sp.

Fig. 19A.

1999 *Hustedia* sp.; Baliński 1999: 445, fig. 4A, B.

Material.—Four damaged shells from samples MH2, D4, and Mu-42.

Remarks.—The species was reported from the Muhua Formation by Baliński (1999). It is very rare form in the fauna because the recent intensive acid processing of samples resulted in only one additional specimen (Fig. 19A). A single nearly complete shell from sample MH2 is 2.4 mm long and 2.0 mm wide. There are 12 and 13 radial costae on the dorsal and ventral valves, respectively. The low number of radial

costae resembles the ribbing characteristic of *Hustedia mormoni* (Marcou, 1858), described from the Upper Carboniferous of Nebraska (see Dunbar and Condra 1932). The specimens from Muhua are also similar externally to *Hustedia* cf. *radialis* (Phillips, 1836) described from the Early Carboniferous of Staffordshire by Brunton and Champion (1974). *H. radialis* re-described by Brunton (1984) from Bolland and Fermanagh (Great Britain) is wider and possesses more radial ribs.

Order Spiriferida Waagen, 1883

Suborder Spiriferidina Waagen, 1883

Superfamily Theodossioidea Ivanova, 1959

Family Palaeochoristitidae Carter, 1994

Genus *Palaeochoristites* Sokolskaya, 1941

Type species: Spirifer cinctus Keyserling, 1846; Tournaisian, Lower Carboniferous; Petchora river, northern Russia.

Palaeochoristites cinctus (Keyserling, 1846)

Fig. 20.

1846 *Spirifer cinctus* Keyserling; Keyserling 1846: 229, pl. 8: 2.

1941 *Palaeochoristites cinctus* (Keyserling); Sokolskaya 1941: 29–34, pl. 3: 1–5; pl. 10: 1–3.

1952 *Palaeochoristites cinctus* (Keyserling); Sarytcheva and Sokolskaya 1952: pl. 55: 321.

1979 *Palaeochoristites* cf. *cinctus* (Keyserling, 1846); Nalivkin 1979: 139, pl. 54: 1, 2; pl. 55: 1.

2002 *Palaeochoristites cinctus* (Keyserling, 1846); Sartenaer and Płodowski 2002: pl. 4: 26–30.

Material.—One complete juvenile shell (Fig. 20A; dimensions in mm: length 9.5, width 14.4, thickness 6.0), 3 complete dorsal and one complete ventral valves, and 35 fragments of single dorsal and ventral valves. All from sample MH1.

Description.—Medium sized, elliptical transverse in outline, ventribiconvex; cardinal margin straight but much shorter than the maximum shell width which is located slightly anterior to the hinge line; cardinal extremities well rounded, anterior commissure rectimarginate.

Ventral valve with triangular, concave, but relatively low interarea; delthyrium open; median sulcus almost not distinguishable, but on one juvenile shell a pair of thicker costae suggest the presence of a sulcus (Fig. 20A₂).

Dorsal valve less convex than the ventral one, with well marked umbonal swelling; interarea very low but subtriangular, sockets very narrow, anteriorly diverging at 101–113°; fold not developed, although on one specimen a pair of better marked intercostal, fold bounding spaces can be observed.

Interior of ventral valve with vertically subparallel dental plates. Dorsal valve with very small cardinal process and wide subvertical inner socket ridges which together with crural bases form sub-rectangular, almost flat plates fused with the valve floor only posteriorly, thus forming variably developed crural plates (Fig. 20C–E); anteroventral margin of inner socket ridges high, extending above the plane marked by the surface of the dorsal interarea. On one of the

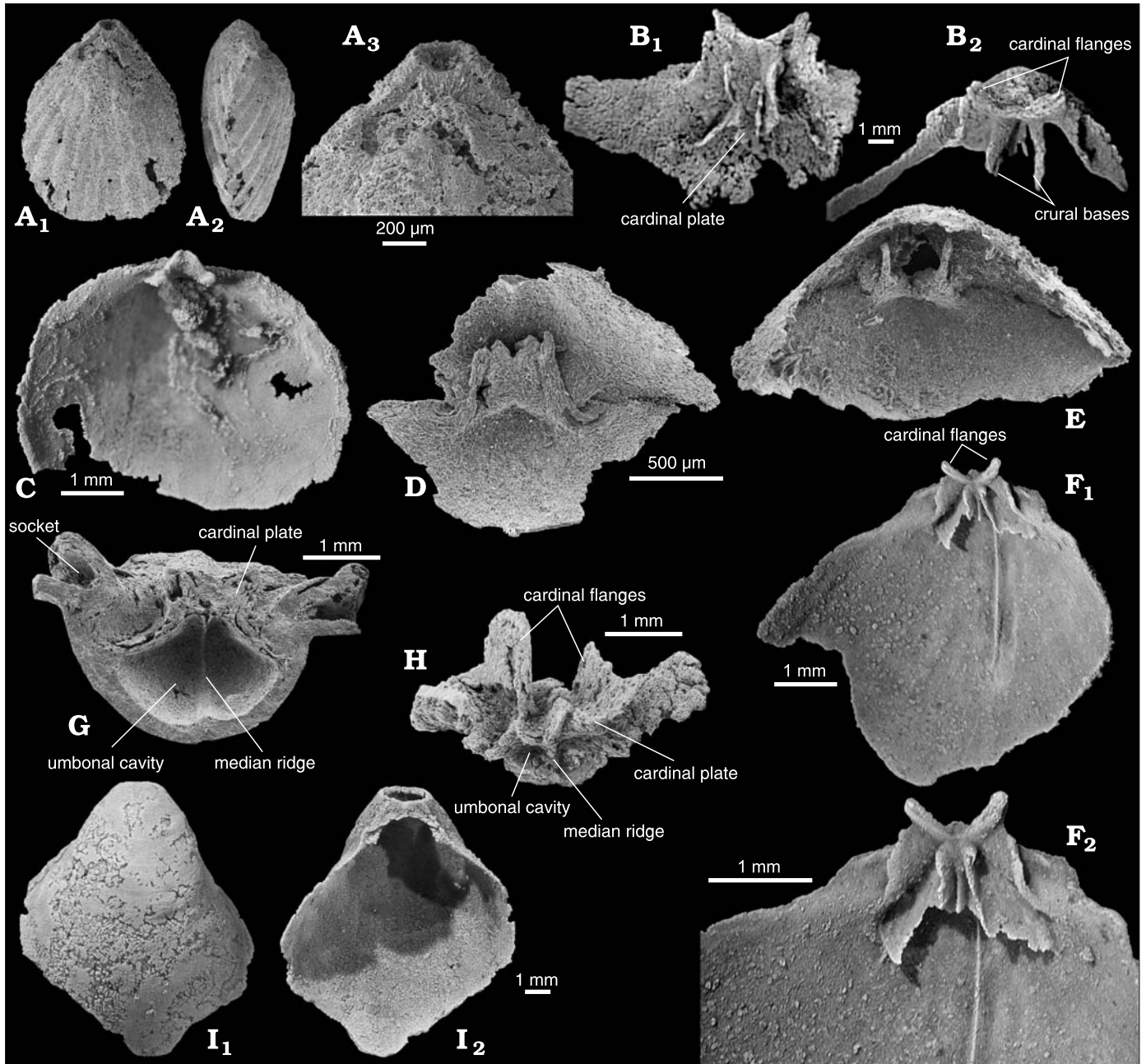


Fig. 19. Retzioid and nucleospiroid brachiopods from the Tornaisian Muhua Formation, southern China. **A.** Retzioid *Hustedia* sp.; nearly complete shell, PKUM02-0468, in dorsal (A_1), lateral (A_2), and enlarged dorsal (A_3) views. **B, F–I.** Retzioid *Acambona* sp. **B.** Umbonal fragment of dorsal valve, PKUM02-0469, in interior (B_1) and posterior (B_2) views showing complexity of cardinalia. **F.** Slightly incomplete dorsal valve, PKUM02-0470, in interior (F_1) and enlarged interior (F_2) views. **G, H.** Umbonal region of two dorsal valves, PKUM02-0471 (**G**) and PKUM02-0472 (**H**), in anterior view with labelled morphology. **I.** Incomplete ventral valve, PKUM02-0473, in exterior (I_1) and interior (I_2) views. **C–E.** Nucleospiroid *Nucleospira* sp. **C.** Interior of incomplete dorsal valve, PKUM02-0474. **D, E.** Two posterior fragments of shell, PKUM02-0475 (**D**) and PKUM02-0476 (**E**), in anterior view showing cardinalia; ventral valve at the top. **A, D, E, G, and H,** SEM micrographs. Samples MH1 (**A, C–E**) and MH2 (**B, F–I**).

dorsal valves two pairs of adductor scars can be recognised (Fig. 20E): short and wide posterior pair and elongate, longitudinally striated anterior one; the scars divided medianly by wide longitudinal ridge.

External surface multicostate, costae rounded to sub-angular, frequently bifurcate, rarely trifurcate.

Remarks.—This species is represented in the material by one juvenile shell and scanty single valves only. Neverthe-

less, characteristic shape and external ornamentation are highly indicative of these valves representing a species of the genus *Palaeochoristites*. The valves are transversely elliptical in outline with rounded cardinal extremities and either lack a fold and sulcus or these are weakly developed. Crural bases form sub-rectangular, almost flat plates fused with the valve floor only posteriorly, thus forming variably developed crural plates.

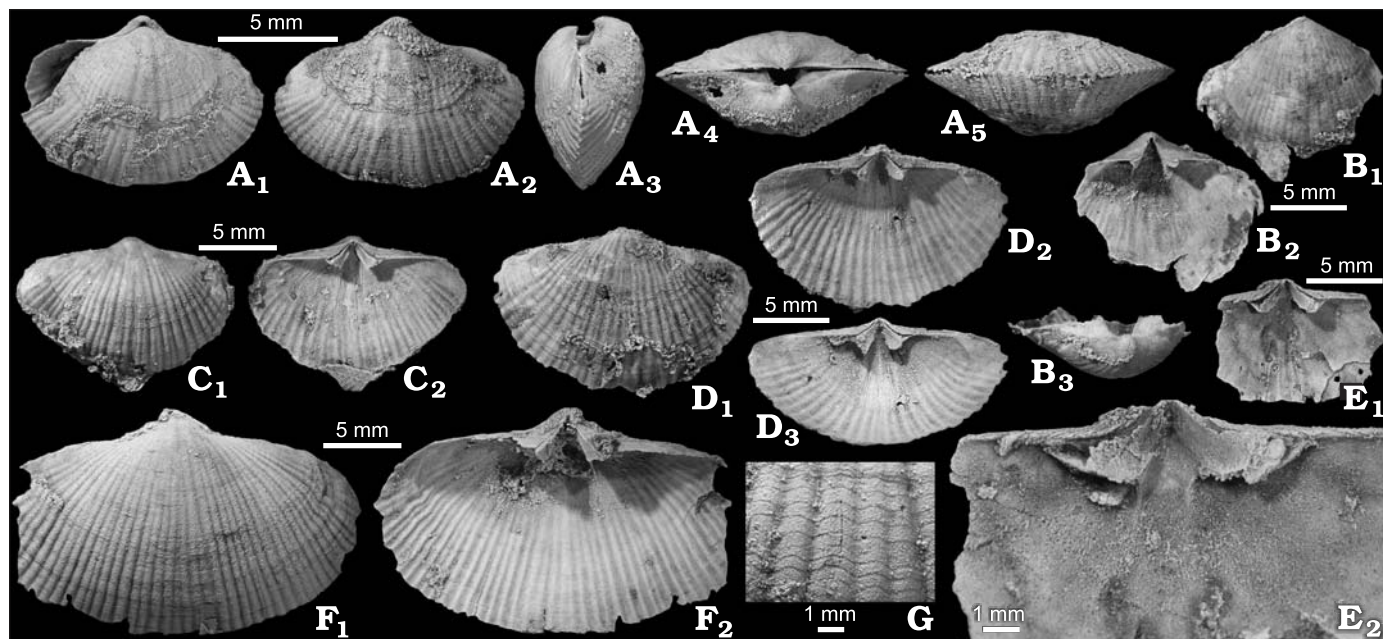


Fig. 20. Palaeochoristitid brachiopod *Palaeochoristites cinctus* (Keyserling, 1846) from the Tournaisian Muhua Formation, southern China. **A.** Complete young shell, PKUM02-0477, in dorsal (A₁), ventral (A₂), lateral (A₃), posterior (A₄), and anterior (A₅) views. **B.** Ventral valve, PKUM02-0478, viewed from the exterior (B₁), interior (B₂), and posterior (B₃). **C.** Dorsal valve, PKUM02-0479, in exterior (C₁) and interior (C₂) views. **D.** Dorsal valve, PKUM02-0480, in exterior (D₁), interior (D₂), and the same inclined anteriorly (D₃) views. **E.** Interior of incomplete dorsal valve, PKUM02-0481, in general (E₁), and enlarged (E₂) views showing cardinalia with crural plates. **F.** Ventral valve, PKUM02-0482, in exterior (F₁) and interior (F₂) views. **G.** Detail of external ornamentation, dorsal valve, PKUM02-0483. All from sample MH1.

The specimens are identical with *Palaeochoristites cinctus* described from the Tournaisian of the European Russia and the Urals (Sokolskaya 1941; Sarytcheva and Sokolskaya 1952; Nalivkin 1979). A single specimen described as *Palaeochoristites cinctus* from Kunlun Mountains (China) by Chen and Shi (2003: 164, pl. 10: 21–25) most probably does not represent the species nor the genus because it possesses well marked dorsal fold and ventral sulcus. The type material of *Palaeochoristites mediatius* Liao, 2006 described from the early Carboniferous of Jinbo, Hainan Island, China (Liao and Zhang 2006), is so fragmentary that no reliable comparison can be made. Also, shell costation in our specimens is much thinner.

Stratigraphic and geographic range.—The species is known from the Tournaisian of Europe, the Urals, and China. According to Sartenaer and Plodowski (2002) *Spirifer cinctus* Keyserling, 1846 reported previously from Belgium actually represents *Mesochorispira konincki* (Dewalque, 1895).

Genus *Eochoristites* Chu, 1933

Type species: *Eochoristites neipentaiensis* Chu, 1933; Kinling Limestone, Tournaisian, Early Carboniferous; Tangshan, Jiangsu Province, China.

Eochoristites neipentaiensis Chu, 1933

Figs. 6G, H, 21, 22.

1933 *Eochoristites neipentaiensis* Chu (gen. et sp. nov.); Chu 1933: 31–37, pl. 3: 23–37; pl. 4: 1–4, 6–11, pl. 5: 6, 7.

1933 *Eochoristites neipentaiensis* mutation *alpha*; Chu 1933: 36–37, pl. 3: 39, pl. 4: 5, 43.

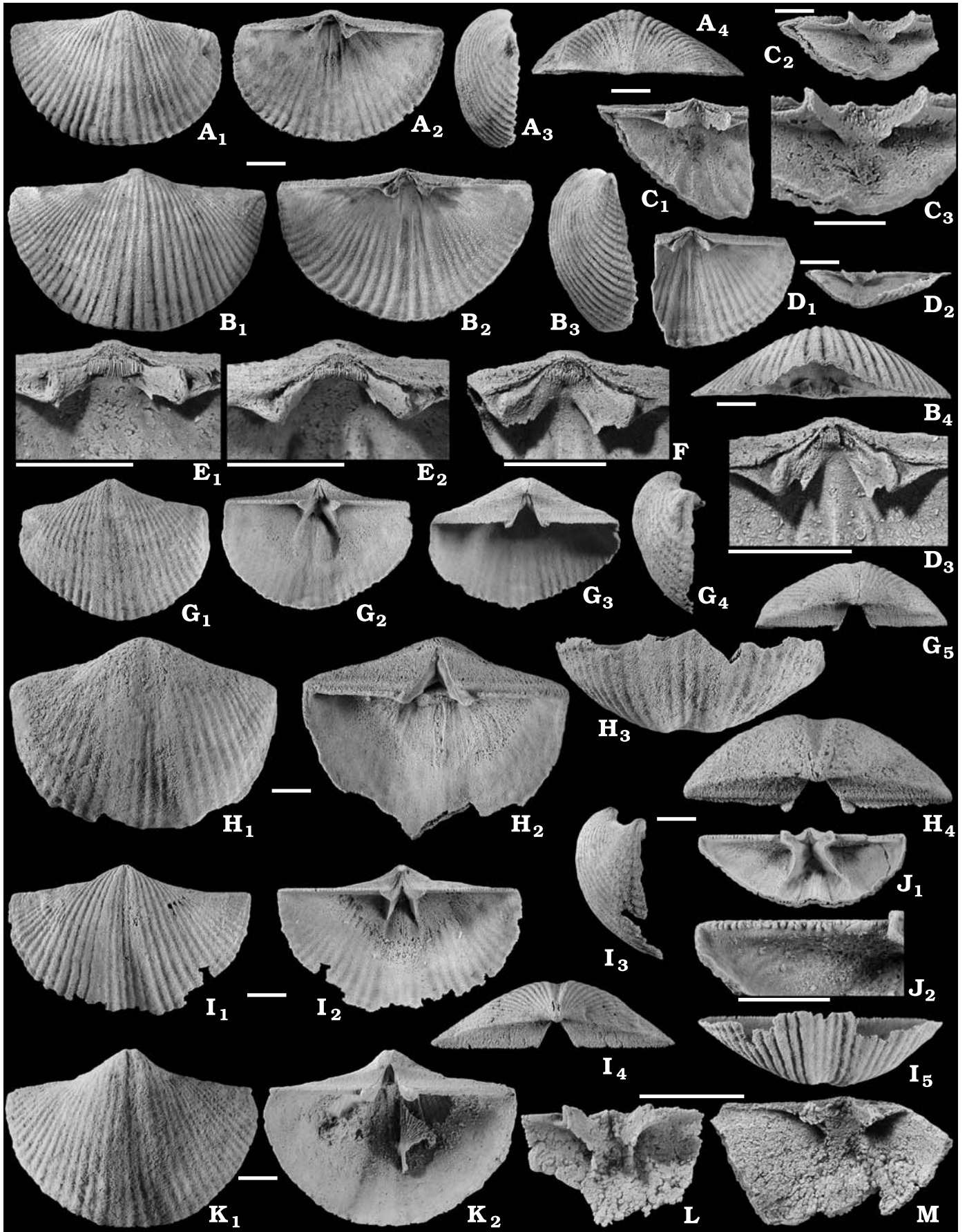
1933 *Eochoristites neipentaiensis* mut. *transversa* Chu (mut. nov.); Chu 1933: 37–39, pl. 4: 34–37.

1933 *Eochoristites neipentaiensis* var. *lungtanensis* Chu (var. nov.); Chu 1933: 39–40, pl. 4: 25–33.

1977 *Eochoristites neipentaiensis* Chu, 1933; Yang et al. 1977: 443, pl. 177: 6.

1982 *Eochoristites neipentaiensis* Chu, 1933; Wang et al. 1982: 240, pl. 76: 8.

Fig. 21. Palaeochoristitid brachiopods from the Tournaisian of Guizhou Province. **A–K.** *Eochoristites neipentaiensis* Chu, 1933 from the Muhua Formation, Muhua. **A.** Complete dorsal valve, PKUM02-0484, in exterior (A₁), interior (A₂), lateral (A₃), and posterior (A₄) views. **B.** Complete dorsal valve, PKUM02-0485, in exterior (B₁), interior (B₂), lateral (B₃), and anterior (B₄) views. **C.** Interior of incomplete dorsal valve, PKUM02-0486, in general (C₁), anterior (C₂), and enlarged anterior (C₃) views showing short dorsal adminicula. **D.** Interior of incomplete dorsal valve, PKUM02-0487, in general (D₁) and anterior (D₂) views, and enlargement showing cardinalia (D₃). **E.** Enlargement of the posterior region of the dorsal valve, PKUM02-0488, showing cardinalia in ventral (E₁), and slightly inclined anterior (E₂) views. **F.** Enlargement of the posterior region of the dorsal valve, PKUM02-0489, showing cardinalia. **G.** Ventral valve, PKUM02-0490, in exterior (G₁), interior (G₂), posterodorsal (G₃), lateral (G₄), and posterior (G₅) views. **H.** Slightly incomplete ventral valve, PKUM02-0491, in exterior (H₁), interior (H₂), anterior (H₃), and posterior (H₄) views. **I.** Almost complete ventral valve, PKUM02-0492, in exterior (I₁), interior (I₂), lateral (I₃), posterior (I₄), and anterior views (I₅). **J.** Interior of ventral valve, PKUM02-0493, in anterior view (J₁) and enlargement of internal edge of interarea showing accessory denticles (J₂). **K.** Ventral valve, ZPAL V.XXVI/69, viewed from the exterior (K₁), and interior (K₂). **L, M.** *Eochoristites neipentaiensis* from Dushan; interior of two incomplete dorsal valves, PKUM02-0494 (L) and PKUM02-0495 (M), showing development of distinct dorsal adminicula. Samples MH2 (A–I), D3 (K), and Dushan (L, M). Scale bars 5 mm.



1986 *Eochoristites neipentaiensis* Chu; Tan 1986: 441, pl. 3: 4–7.
 1987 *Eochoristites neipentaiensis* Chu; Tan 1987: 128, pl. 19: 14–16.
 1995 *Eochoristites neipentaiensis* Chu; Chen 1995: pl. 1: 24–27.
 1999 *Eochoristites neipentaiensis* Chu, 1933; Chen and Shi 1999: 238,
 figs. 4A–C, E–N, R, 5A, B.

Material.—About 40 single mostly complete and more than 500 incomplete valves from sample MH2.

Description.—Shell medium sized, attaining usually 18–25 mm in length and 25–38 mm in width, semicircular to sub-pentagonal in outline, more transverse in juveniles, subequally biconvex, with the greatest width at the hinge or, rarely, slightly anteriorly to it; cardinal extremities meet at about a right angle, rarely with very small and very short mucrons.

Ventral valve with massive umbo and suberect to incurved beak; interarea anacline to apsacine, wide, broadly triangular, concave near umbo to almost flat near hinge line; delthyrium open, in large specimens its apical part becomes closed by callosity resulted from thickened dental flanges; valve flanks convex viewed laterally, in posterior profile convex to slightly flattened; sulcus moderately wide, well marked posteriorly, widens and shallows anteriorly, usually not clearly delimited from flanks anteriorly although the sulcus bounding costae are typically wider than other lateral costae.

Dorsal valve semicircular in outline, regularly convex in lateral profile, with slightly swollen umbonal region and convex to slightly flattened, rarely weakly concave near the cardinal extremities; interarea low, 1.3–1.5 mm high, rectangular, slightly concave; fold indistinct in height but well separated from the flanks by more prominent intercostal spaces.

Interior of ventral valve with strong, extrasinal dental adminicula, widely divergent anteriorly, thickened in adults but with sharp anterior edges, fused umbonally infilling the apical part of the delthyrium (Fig. 21G₂, I₂); teeth subtriangular to suboval in cross-section extending up to 1.3 mm beyond the hinge line; secondary denticulation developed on about one third of specimens (Fig. 21J₂); adductor scars deeply impressed posteriorly and laterally between dental adminicula, less evidently delimited anteriorly, longitudinally striated (Fig. 21G₂, H₂). Dorsal valve interior with very deep sockets diverging at approximately 114–123°; hinge plates nearly vertical to slightly inclined, crural plates frequently not observed, but on some specimens (less than half) short supports for crura are developed posteriorly (Fig. 22) where they join the elongated anteriorly base of the cardinal

process (Fig. 21C₂, C₃, D₂); cardinal process longitudinally striated, subtriangular in ventral view; adductor muscle scars narrow but quite long reaching about the valve midlength, divided by sharp and low myophragm (Fig. 21A₂, B₂, D₁).

Shell usually ornamented by 13–17 (exceptionally up to 19) rounded radial costae on each flank; costae simple, diminishing in size and strength laterally, slightly wider than intercostal grooves; sulcus bordering costae wider than those on flanks, extending from the umbo; one, most often simple, intercalated median costa appears at some distance from the beak; usually 4 simple lateral sulcal costae bifurcate from the sulcus bounding costae; fold with 7–8 bifurcating costae. Growth lines and other details of micro-ornamentation usually not observed due to the inadequate preservation of external shell surface but one specimen reveals slightly imbricate growth lamellae.

Remarks.—The specimens show internal structures of both valves characteristic for palaeochoristitids, but their external ornament and the development of a fold and sulcus is different from those in *P. cinctus* described above. The wider costae and more clearly developed fold and sulcus allow the specimens to be assigned to a species of the genus *Eochoristites* Chu, 1933.

Chu (1933) established several new species, varieties, and mutations belonging into his new genus *Eochoristites*. Aside from the typical form, to the species *Eochoristites neipentaiensis* (type species of the genus) he included *Eochoristites neipentaiensis* mut. *transversa*, *E. neipentaiensis* mut. *alpha*, and *E. neipentaiensis* var. *longtanensis* (Chu 1933). Each of the first two “mutations” was founded on a single fragmentary specimen. The variety was “represented by not less than ten specimens, none of which [was] complete” (Chu 1933: 39). It is also noteworthy that all three forms occur in the same horizon and locality as the typical specimens of *E. neipentaiensis*. Although the three forms listed above are treated by some authors as separate species (e.g., Chen and Shi 1999) it seems more probable that they represent rather an intraspecific variability of *E. neipentaiensis*. We prefer that the three forms be included in the synonymy list of the latter species. It should be mentioned that type material of these forms, described and figured by Chu (1933), seem inadequate quantitatively and qualitatively to create new taxa. Two other species of the genus, i.e., *Eochoristites leei* Chu, 1933 and *Eochoristites elongata* Chu, 1933 that co-occur with *E. neipentaiensis* in the Kinling

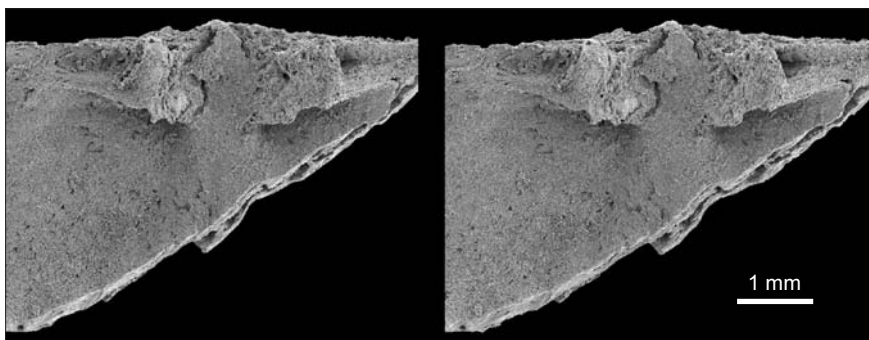


Fig. 22. Palaeochoristitid *Eochoristites neipentaiensis* Chu, 1933 from the Tornaisian Muhua Formation, southern China. SEM stereopair of incomplete dorsal valve, ZPAL V.XXVI/70, showing development of short dorsal adminicula. Sample D3.

Limestone are generally similar to the latter and may represent a spectrum of its intraspecific variability. Thus, the taxonomic validity of all eochoristitids from the Kinling Limestone should be confirmed by detailed re-study of more representative topotype material.

The specimens from the Muhua Formation are very similar in external morphology to *E. neipentaiensis* which is a characteristic and quite widely recognised guide brachiopod species for the Early Carboniferous (Tournaisian) deposits of Southern China. In general shape, dimensions and ornamentation of the shell the material described here shows remarkable similarity with the type specimens described by Chu (1933) and material from the Liujiatang Formation of Central Hunan (Tan 1986). Some of the specimens of Chu (1933: pl. 3: 30–33), however, are more elongated and have much shorter cardinal margin than specimens from Muhua. In respect to the shell proportion our specimens strictly correspond to the Chu's mut. *transversa* which, as it was mentioned above, should be regarded as morphotype of *E. neipentaiensis*. From *E. leei* and *E. elongata* our specimens are generally wider, have wider cardinal margin and less swollen ventral umbonal region of the ventral valve. The latter are similar in wide outline of the shell to *Eochoristites chui* Yang, 1964 from the late Tournaisian Tangbagou Formation of Dushan (Guizhou Province). Our material differs in having evidently greater shell dimensions and much thicker shell ornamentation.

Although we do not have topotype material of Chu's species (his original collection cannot be found) some comparisons of the internal structure of the dorsal valve with presumably conspecific material from Dushan (Guizhou Province) can here be made. One of the diagnostic features of the cardinalia of *Eochoristites neipentaiensis* (as well as the genus *Eochoristites*) is the presence of dorsal adminicula. These plates are well developed and quite long in the dorsal valve from Dushan illustrated here for comparison (Fig. 21L, M) but rather short and sometimes even difficult to recognise or apparently absent in specimens from Muhua (Figs. 21C–F, 22). This inclines us to assume that development of the dorsal adminicula in *Eochoristites* might be a subject of significant, both spatial and temporal, intraspecific variability.

A problem of morphological relationships between the present species from sample MH2 with a spiriferoid from samples GB and GT described below as *Parallelora* sp. is worth comment. There is no doubt that both forms at first glance are very similar externally and internally despite the fact that they represent different superfamilies in the recently proposed taxonomy of Spiriferida (Carter et al. 1994; Carter and Gourvenec 2006). The differences are not essential and are expressed mainly by the triangular ventral interarea and non-bifurcating flank costae in the species from MH2 whereas in *Parallelora* sp. the interarea usually is sub-rectangular and rare bifurcations of lateral costae occur. Of great importance for taxonomy of the order Spiriferida is the denticulation of the hinge line which occurs in Spiriferoidea but is unknown in Theodossioidea, which includes *Eochoristites*.

Our material shows that denticulation of the hinge line is present in *Parallelora* sp. which is characteristic of the superfamily. In the majority of *Eochoristites* from MH2 the secondary denticulation is not developed but on about one-third of ventral valves small and delicate secondary denticles are easily recognisable (Fig. 21J₂). This suggests that palaeochoristitids on one hand and *Parallelora*- or *Prospira*-like forms on the other appear to be much more closely related than it is revealed in the present systematics of the Spiriferida.

Stratigraphic and geographic range.—*E. neipentaiensis* Chu, 1933 is a quite widespread guide species for the Early Carboniferous (lower part of the Tournaisian) strata of Southern China (e.g., Chen 2004). In Muhua this is a characteristic species for the assemblage of the sample MH2.

Superfamily Ambocoelioidea George, 1931

Family Ambocoeliidae George, 1931

Subfamily Ambocoeliinae George, 1931

Genus *Crurithyris* George, 1931

Type species: *Spirifer urei* Fleming, 1828; Viséan (Carboniferous) of Strathaven, Lanarkshire, Scotland.

Crurithyris cf. *nastus* Brunton and Champion, 1974

Figs. 4G, H, 23.

Material.—About a hundred shells and more than 500 single valves from samples D1, D2, GB, GT, MH1, and MH2-8.

Description.—Shell small, strongly ventribiconvex, rectangular to sub-circular in outline, usually wider than long, with hinge line about two-third of the shell width; lateral margins rounded, anterior margin slightly emarginate. Ventral valve deep, posteriorly inflated; interarea apsacline and concave; shallow median sulcus appears near the umbo. Dorsal valve transversely elliptical in outline with very short interarea; sulcus present but very weak to imperceptible.

Inner socket ridges, crural bases, crura and cardinal process are figured on well preserved dorsal valve in Figure 23C, D (see also Fig. 23I). Sockets diverge from hinge line at about 23–25°. Inside the ventral valve there is a low median ridge extending about one-half of the valve length (Fig. 23B₁, G).

Although the majority of the specimens from Muhua display smooth shell surfaces (Fig. 23A) well preserved specimens show a spinose micro-ornamentation. On the ventral valve here figured (Fig. 23F) two sizes of micro-spines are well seen, similar to the condition observed by, e.g., George (1931) in *Crurithyris magnispina* and by Brunton (1984) in *Crurithyris urei*.

Remarks.—This species is the most numerous in the fauna of the Muhua Formation. It is especially dominant in the sample MH1 which is characterised by the highest taxonomic diversity of all samples studied from this area.

The specimens show great similarity to *Crurithyris nastus* described from the Early Carboniferous (Viséan) of Staffordshire, British Isles (see Brunton and Champion 1974: 830–

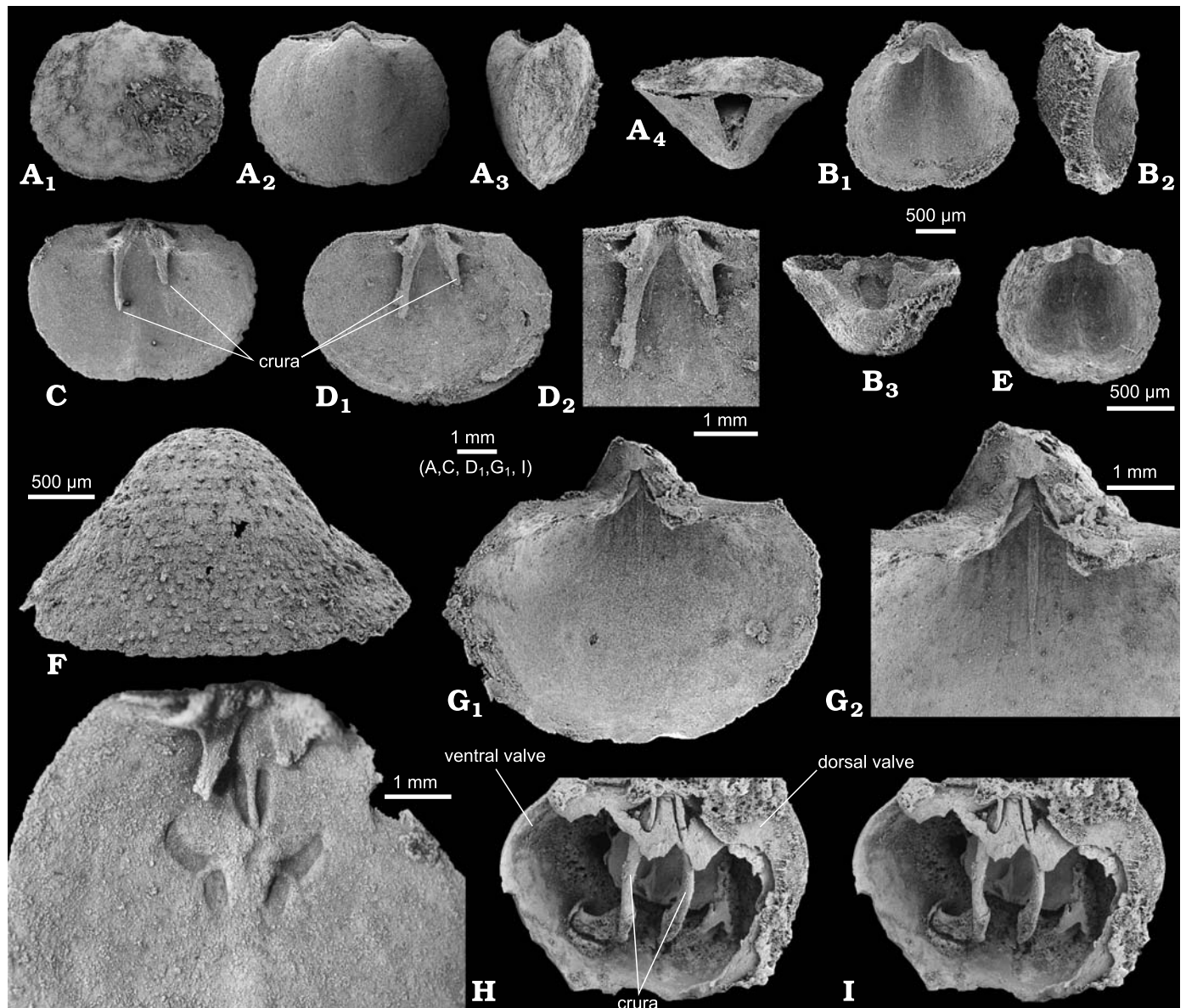


Fig. 23. Ambocoeliid brachiopod *Crurithyris* cf. *nastus* Brunton and Champion, 1974 from the Tournaisian Muhua Formation, southern China. **A.** Complete shell PKUM02-0496 in dorsal (A_1), ventral (A_2), lateral (A_3), and posterior (A_4) views. **B.** Small ventral valve, PKUM02-0497, in interior (B_1), lateral (B_2), and posterior (B_3) views. **C, D.** Interior of two dorsal valves (C, D_1) and enlarged view of cardinalia (D_2), PKUM02-0498 (C) and PKUM02-0499 (D). **E.** Interior of very small ventral valve, PKUM02-0500. **F.** Anterior view of ventral valve, PKUM02-0501, exterior showing spinose micro-ornamentation. **G.** Interior of ventral valve (G_1) and enlargement of the umbonal region (G_2), PKUM02-0502. **H.** Enlargement of the interior of dorsal valve, PKUM02-0503, showing cardinalia and muscle scars. **I.** Stereomicrographs of shell, PKUM02-0504, in dorsal view with much of the dorsal valve removed showing crura and the beginning of the spiralium; another small dorsal valve is seen deep behind crura. A–G, I, SEM micrographs. All from sample MH1.

833, pl. 110: 6–16; text-fig. 6). The former shows some external resemblance to *Crurithyris parvus* Xu and Yao, 1988 described from the Tournaisian of Nanbiancun section, Guilin Province, China (Xu and Yao 1988: 287, pl. 72: 6–9) but differs in having wider shell and higher ventral interarea.

Stratigraphic and geographic range.—*C. nastus* was described from rocks of probably early Viséan age (Chadian) of the Manifold valley, Staffordshire. The very similar specimens described herein are from Tournaisian of Muhua, southern China.

Family Verneuliidae Schuchert, 1929

Genus *Changshunella* Sun, Baliński, Ma, and Zhang, 2004

Type species: *Changshunella yangi* Sun, Baliński, Ma, and Zhang, 2004; Muhua Formation, Tournaisian, Carboniferous; Muhua, Guizhou Province, China.

Changshunella yangi Sun, Baliński, Ma, and Zhang, 2004

Fig. 24.

2004 *Changshunella yangi* gen. et sp. nov.; Sun et al. 2004a: 269–273, figs. 2–6.

2008 *Changshunella yangi* Sun, Baliński, Ma, and Zhang, 2004a; Baliński and Sun 2008: 113–114, fig. 9.

Material.—15 ventral valves and 26 dorsal valves from Muhua III section (Hou et al. 1985) where it was found in sample MH1 taken from the base of the Muhua Formation.

Description.—See Sun et al. (2004a) and Baliński and Sun (2008) for detailed descriptions of the genus and species.

Remarks.—This bizarre micro-spiriferid is one of the most interesting discoveries in the Muhua fauna. Its small size and unique external form of the shell, invariably dominated by three very strong and opposed (not alternating) plications on both valves are very characteristic features (Fig. 24). Its length generally does not exceed 4 mm although these shells unquestionably represent mature or even gerontic, individuals. The type of shell plication in *C. yangi* indicates that it may be close to some other verneuliid spiriferoids, such as *Verneulia* Hall and Clarke, 1893 and *Nugushella* Tiazheva, 1960. Noteworthy is also a certain external similarity between *C. yangi* and *Scenesia extensa* Cooper and Grant, 1976, the later being described from the Permian of West Texas (Cooper and Grant 1976: 2756–2758, pl. 724: 36–66) and included by Carter et al. (1994) in the superfamily Paeckelmanelloidea.

Stratigraphic and geographic range.—Known exclusively from the type locality and horizon.

Superfamily Martinoidea Waagen, 1883

Family Martinidae Waagen, 1883

Subfamily Eomartiniopsinae Carter, 1994

Genus *Merospirifer* Reed, 1949

Type species: *Martinia (Merospirifer) insolita* Reed, 1949; Charleston Main Limestone, Viséan, Carboniferous; Roscobie, Scotland, England.

Merospirifer sp.

Fig. 25.

Material.—Very fragmentary six ventral and three dorsal valves.

Remarks.—This smooth shelled spiriferoid is characterised by the presence of thin subparallel dental adminicula and absence of ventral median septum and crural plates. In the apical region of the delthyrium there is a small, strongly indented anteriorly plate which is attached to the dental flanges slightly below the interarea, but sometimes becomes strongly convex (Fig. 25A₂, A₄). Dental adminicula bent medially just below the delthyrial margin then slightly diverge to the valve floor (Fig. 25D₁) similarly as it was noted in *Merospirifer linguifera* (Phillips, 1836) by Brunton (1984). The surface micro-ornamentation is well preserved on one specimen in the form of elongated, densely packed exopunctae (Fig. 25A₆).

The present very fragmentary material differs from *Eomartiniopsis* Sokolskaya, 1941 by having very weak ven-

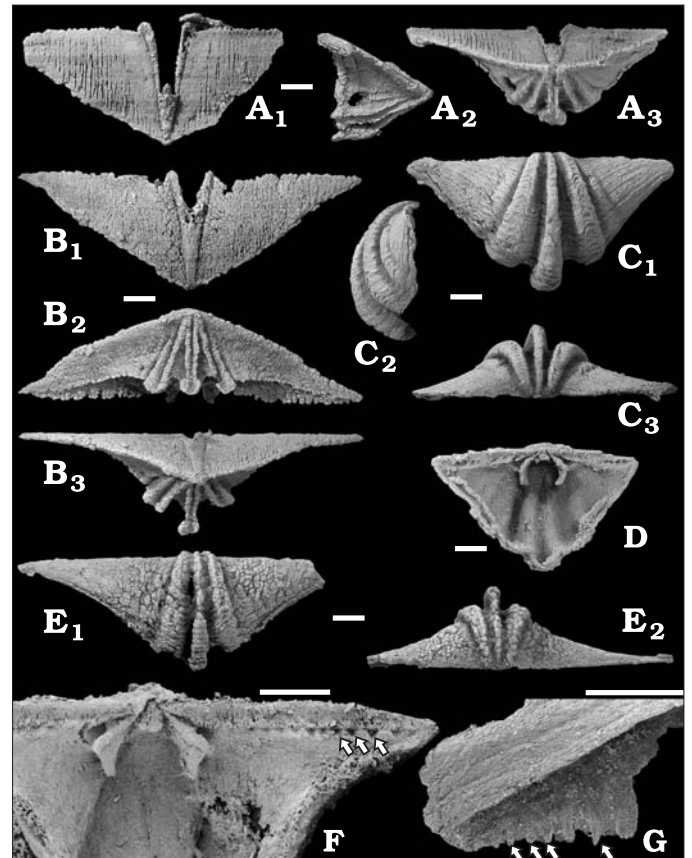


Fig. 24. Verneuliid brachiopod *Changshunella yangi* Sun, Baliński, Ma, and Zhang, 2004 from the Tournaisian Muhua Formation, southern China. **A.** Ventral valve, PKUM02-0505, in posterior (A₁), lateral (A₂), and ventral (A₃) views. **B.** Ventral valve, PKUM02-0506, in posterior (B₁), anterior (B₂), and ventral (B₃) views. **C.** Dorsal valve, PKUM02-0507, in exterior (C₁), lateral (C₂), and posterior (C₃) views. **D.** Dorsal valve, PKUM02-0508, viewed internally. **E.** Dorsal valve, PKUM02-0509, in exterior (E₁) and posterior (E₂) views. **F.** SEM micrograph of the dorsal valve, PKUM02-0510, interior showing cardinalia and accessory sockets (arrowed). **G.** SEM micrograph of the incomplete ventral valve, PKUM02-0511, viewed from the interior (antero-ventral view) showing partially preserved interarea and accessory denticles (arrowed). All from sample MH1. Scale bars 1 mm.

tral sulcus. The former differs also from *Globispirifer* Tachibana, 1964 in having not elongated shell and from *Kisilia* Nalivkin, 1979 in having smooth shell and strong and long dental adminicula. The specimens are also similar in general shape of the shell to *Crassumbo* Carter, 1967 but differ in having well differentiated dental adminicula which are not buried in the umbonal callus. The specimens from the Muhua Formation are the most similar both externally and internally to *Merospirifer* Reed, 1949 which was re-described by Brunton (1984).

Stratigraphic and geographic range.—According to Brunton (1984: 96) the genus occurs throughout the Viséan in the British Isles but some closely related species have been also reported from the Tournaisian. The present material is very poor and comes from samples MH1, MH2, M2–8, and GB.

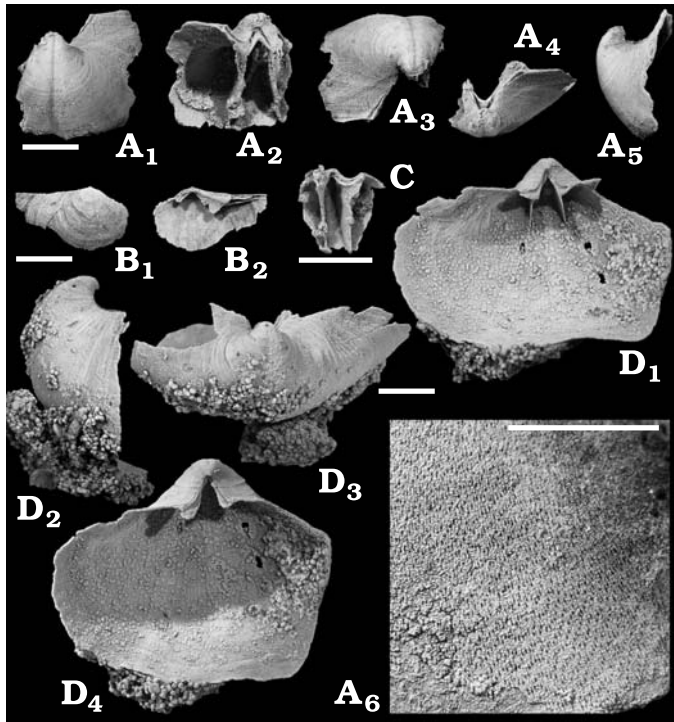


Fig. 25. Martiniid brachiopod *Merospirifer* sp. from the Tournaisian Muhua Formation, southern China. **A.** Fragment of ventral valve, PKUM02-0512, in exterior (A₁), interior (A₂), posterior (A₃), posterodorsal (A₄), and lateral (A₅) views, and enlargement of the surface exopunctate micro-ornamentation (A₆). **B.** Fragment of dorsal valve, PKUM02-0513, in exterior (B₁) and interior (B₂) views, and enlargement of the interior showing cardinalia (B₃). **C.** Fragment of ventral valve, PKUM02-0514, viewed from the interior showing subparallel, thin dental plates. **D.** Incomplete ventral valve, PKUM02-0515, in inclined interior (D₁), lateral (D₂), posterior (D₃), and interior (D₄) views. Samples MH1 (A), M2–8 (B, C), and MH2 (D). Scale bars 2 mm.

Superfamily Spiriferoidea King, 1846

Family Spiriferidae King, 1846

Subfamily Spiriferinae King, 1846

Genus *Spirifer* Sowerby, 1816

Type species: *Conchylolithus (Anomia) striatus* Martin, 1793; early Carboniferous; England.

Subgenus *Spirifer (Mesochorispira)* Carter, 1992

Type species: *Spirifer grimesi* Hall, 1858; upper Tournaisian, Carboniferous; Oklahoma, USA.

Spirifer (Mesochorispira) sp.

Fig. 26L.

Material.—One fragment of anterior part of ventral valve and two small fragments of ventral umbonal part from sample MH1.

Remarks.—This species is extremely rare in the Muhua's fauna being represented by three very incomplete specimens. The best preserved of them is a fragment of a large ventral valve showing well developed median sulcus, short tongue, and numerous radial costae which bi- or trifurcate (Fig. 26L). Growth lines preserved on the specimen indi-

cate rather rounded, not angular cardinal extremities in the adult stage. All these features suggest that this material represents a species of the subgenus *Spirifer (Mesochorispira)*.

Subfamily Prospirinae Carter, 1974

Genus *Finospirifer* Yin, 1981

Type species: *Finospirifer taotangensis* Yin, 1981; Tournaisian, Carboniferous; Hunan Province, Southern China.

Finospirifer sp.

Fig. 26K.

Material.—One incomplete ventral valve from sample GB.

Remarks.—Although we have only one fragmentarily preserved ventral valve at our disposal (Fig. 26K) it is possible to determine it to the genus level quite convincingly. The valve is ornamented with about 20 simple costae on its flank. Sulcus is narrow, quite deep, with a few bifurcating costae. The median sulcal plication is very strong, disproportionately high, and carinate, extending much above the valve flanks in anterior profile. Although the specimen is incomplete and the general outline of the shell difficult to assess, the growth lines reveals that this form is characterised by strongly transverse outline. The latter feature precludes its assignment to the very similar Carboniferous genus *Subspirifer* Shan and Zhao, 1981. According to Carter (2006: 1777) the genus *Subspirifer* may be a junior synonym of *Finospirifer* Yin, 1981.

Finospirifer is a rare form found up to now only in Hunan and western Guizhou provinces, China (Wu et al. 1974; Yin 1981; Tan 1986). Our specimen from Muhua (southern Guizhou Province) extends the geographic range of the genus. The ribbing pattern as well as the shape of the shell which can be traced according to the growth lines suggest that the specimens may represent *F. taotangensis* Yin, 1981 or *F. shaoyangensis* (Ozaki, 1939), both from the early Carboniferous of Central Hunan (Yin 1981). Tan (1986) described two other new species of *Finospirifer* from the early Carboniferous of central Hunan.

Genus *Parallelora* Carter, 1974

Type species: *Spirifer marionensis* Shumard, 1855; Louisiana Limestone, late Famennian, Late Devonian; upper Mississippi Valley, Missouri, USA.

Parallelora sp.

Figs. 6E, 26A–J.

Material.—More than 50 fragments of dorsal and 150 fragments of ventral valves from samples GB and GT. Although all specimens are highly crushed they preserve details of surface ornamentation in great detail.

Description.—Shell medium sized for the genus, subpentagonal to semicircular in outline; juvenile shells up to about 10 mm in length, less than twice to three times as wide as long, extended subtrapezoid in outline, and mucronate; adults less transverse; greatest width at the hinge line, cardinal extremities form short but distinct mucrons.

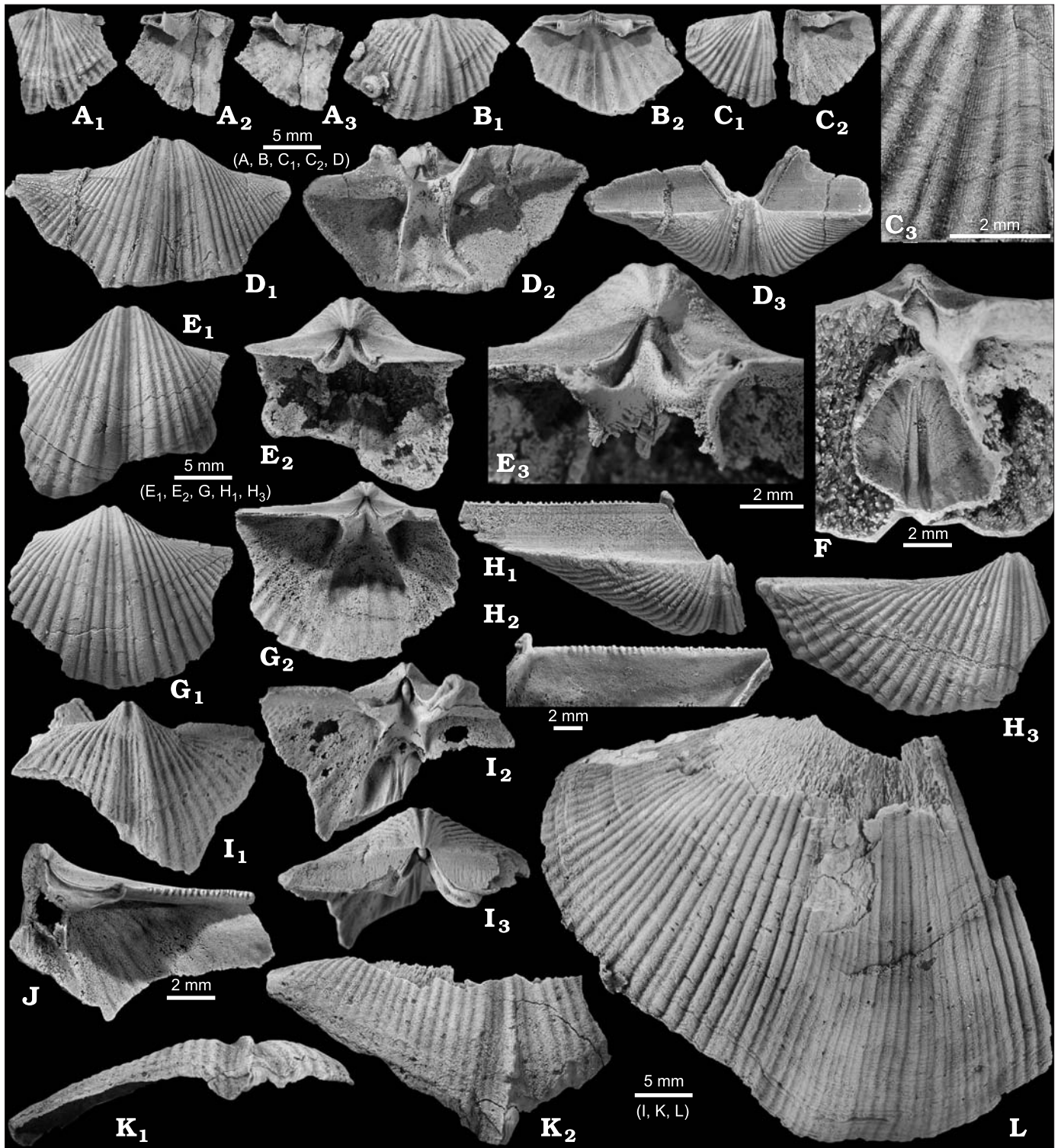


Fig. 26. Spiriferide brachiopods from the Tornaisian Muhua Formation, southern China. **A–J.** *Parallelora* sp. **A.** Incomplete dorsal valve, PKUM02-0516, in exterior (A_1), interior (A_2), and inclined interior (A_3) views. **B.** Incomplete dorsal valve, PKUM02-0517, in exterior (B_1) and interior (B_2) views, and enlargement of cardinalia (B_3). **C.** Incomplete dorsal valve, PKUM02-0518, in exterior (C_1), interior (C_2), and enlarged exterior (C_3) views showing surface micro-ornamentation. **D.** Incomplete ventral valve, PKUM02-0519, in exterior (D_1), interior (D_2), and posterior (D_3) views. **E.** Incomplete ventral valve, PKUM02-0520, in exterior (E_1) and interior (E_2) views, and enlarged posterior region (E_3). **F.** Interior of incomplete ventral valve, PKUM02-0521, showing partly preserved muscle scars. **G.** Incomplete ventral valve, PKUM02-0522, in exterior (G_1) and interior (G_2) views. **H.** Incomplete ventral valve, PKUM02-0523, in posterior (H_1 ; showing subrectangular interarea), fragmentary interior (H_2 ; showing denticulate hinge line), and exterior (H_3) views. **I.** Incomplete ventral valve, ZPAL V.XXVI/71, in exterior (I_1), interior (I_2), and posterior (I_3) views. **J.** Interior of incomplete ventral valve, PKUM02-0524, showing accessory denticulation. **K.** *Finospirifer* sp., incomplete ventral valve, PKUM02-0525, in anterior (K_1) and exterior (K_2) views. **L.** *Spirifer* (*Mesochorispira*) sp., exterior of incomplete ventral valve, PKUM02-0526; note numerous ctenostomate borings. Samples GB (A–H, J, K), GT (I), and MH1 (L).

Ventral valve with massive umbo and strongly incurved beak; beak ridges sharp, subparallel to the hinge line; interarea apsacline, slightly concave to flat at the hinge and strongly concave near the umbo, with curvature reaching about 180°, usually subrectangular (Fig. 26H₁), rarely low-triangular, wide, weakly striated longitudinally; delthyrium wide and open, with the delthyrial angle attaining 48–67°, in large specimens apically closed by callosity of thickened posterior regions of the dental adminicula; the callosity may form a more or less subdelthyrial triangular plate below the level of the interarea or may be convex with distinct median ridge or thickening (Fig. 26E₂, E₃, F, G₂, I₂); flanks moderately convex, in posterior view flattened to concave, especially near the cardinal extremities; sulcus moderately wide, evident, deep and grove-like in the umbonal region, shallower anteriorly, bordered by a pair of clearly wider costae.

Dorsal valve transverse subelliptical to semicircular in outline, with low fold, well delimited by deep fold-bounding intercostal furrows; interarea rectangular, usually up to 1.3 mm high; umbo small, low; flanks convex but in posterior profile flattened to slightly concave near cardinal extremities.

Interior of ventral valve with strong extrasinal, anteriorly widely divergent dental adminicula, thickened and fused posteriorly in adults, but with sharp anterior edges (Fig. 26D₂, F, G₂, I₂); in large specimens with high and concave interarea the teeth are supported distally only by dental ridges; teeth well marked but rather small, triangular in cross-section extending about 1 mm beyond the hinge line; secondary denticulation delicate but well visible along the hinge line except the nearest 2 mm from the teeth (Fig. 26H₁, H₂, J); muscle scars suboval in outline, deeply impressed posteriorly and posterolaterally between thickened dental adminicula, weakly delimited anteriorly, frequently divided medially by slightly elevated myophragm (Fig. 26F, I₂); ontogenetically older valves markedly thickened posteriorly with space between dental adminicula infilled noticeably with callus (Fig. 26D₂, E₃, G₂, I₂).

Interior of dorsal valve with rather deep but narrow sockets diverging at 125–138°; hinge plates subrectangular, converging with the wide base of the cardinal process; crural plates not developed; cardinal process longitudinally striated (Fig. 26A₂, A₃, B₂, C₂); adductor scars narrow, elongate, with sharp median ridge or myophragm (Fig. 26A₂, B₂).

Shell ornamented by 14–17 costae on each flank; costae usually simple, but sporadically bifurcate on one out of three or four specimens, rounded in cross-section, widen markedly anteriorly, separated by narrow interspaces; sulcus bordering costae bifurcate 2–3 times; median costa usually present, appearing within a few mm from the beak; about 6 bifurcating costae on fold. External micro-ornamentation of fine, sinuous, imbricating lamellae with frequency of about 4 per mm; very faint radial capillae densely packed, of about 16 ridges per mm, terminating at growth lamellae in the form of very small tubercles (Fig. 26C₃).

Remarks.—This species is represented in our material by invariably highly crushed single valves despite their massive,

thick-shelled structure. On the contrary, these specimens are characterised by surprisingly well preserved surface micro-ornamentation. This is in striking contrast with equivalent spiriferid species *Eochoristites neipentaiensis* Chu, 1933 from sample MH2 which is represented by mainly well preserved complete single valves but with completely worn out micro-ornamentation as well as partly abraded surface costation. These preservational characteristics between different samples are most likely a result of complex hydrodynamics and post depositional conditions on one hand and variability in the diagenetic (mainly silicification) processes on the other.

The shell shape and its ornamentation as well as details of the interior of both valves suggest that the described species represents a prospirinin spiriferoid. The shell proportions, its pattern of costation, capillate and imbricate micro-ornamentation, and presence of wide, usually subrectangular ventral interarea suggest generic affiliation with *Parallelora*. Unfortunately, the very fragmented material lacks the characters needed for specific identification. The species from Muhua differs, however, from the late Famennian *Parallelora marionensis* Schumard, 1855 and the early Mississippian *Parallelora nupera* Carter, 1988 by having slightly higher ventral interarea, more massive ventral umbonal callosity, and less numerous, thicker costae (see Carter 1988). *P. marionensis* was reported also from the uppermost Famennian–early Tournaisian of the Urals by Nalivkin (1979) and from the Tournaisian of Southern Tianshan Mountains, NW China by Chen and Archbold (2000). Specimens from Muhua differ clearly from *Spirifer subavis* Plodowski, 1968 (= *Parallelora subavis*) from Étroeung zone of Afghanistan (Plodowski 1968) by having greater shell and much thicker costae. It seems that the specimens are similar to *Parallelora obesa* Xu and Yao, 1988 from the latest Famennian–earliest Mississippian of Nanbiancun section (Guanxi Province, Southern China) but differ at least in having non-carinate dorsal fold. Unfortunately, *P. obesa* is inadequately figured (see Xu and Yao 1988: 296–297, pl. 77: 16–19, text-fig. 96b) and its specific characteristic difficult to assess.

Feng (1989) established a new species *Brachythyrina originalis* Feng, 1989 from the lower part of the Muhua Formation of the Dapoushang section. He founded the species on a single fragmentary ventral valve which seems generally similar to the species here described. Unfortunately, Feng's (1989) description and figures of *B. originalis* are not adequate to warrant any reliable comparison and his species should be considered as nomen dubium until better topotype materials becomes available.

Superfamily Paeckelmannelloidea Ivanova, 1972

Family Strophopleuridae Carter, 1974

Subfamily Strophopleurinae Carter, 1974

Genus *Voiseyella* Roberts, 1964

Type species: *Strophopleura anterosa* Campbell, 1957; Late Tournaisian, Carboniferous; New South Wales, Australia.

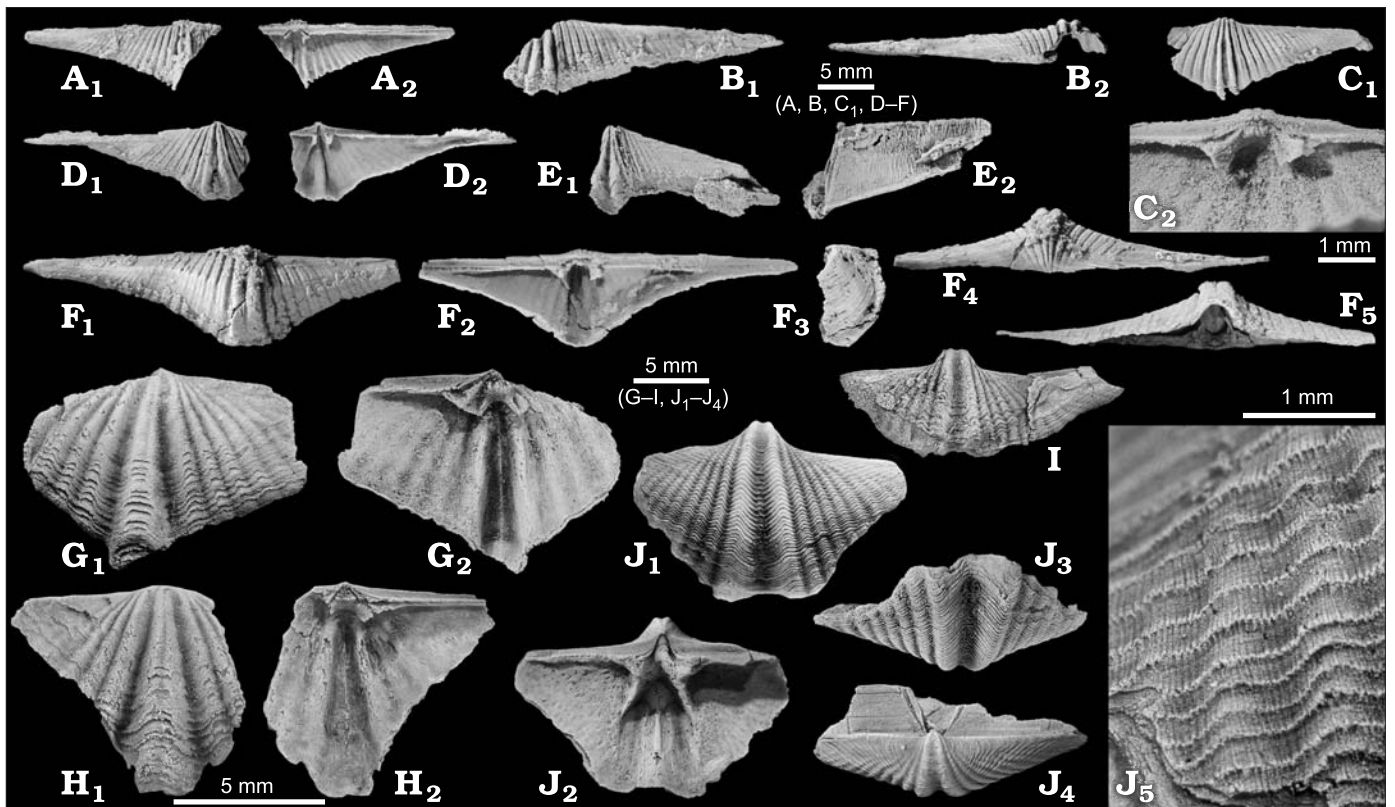


Fig. 27. Strophopleurid brachiopods from the Tornaisian Muhua Formation, southern China. **A–F.** *Voiseyella bruntoni* Baliński and Sun, 2010a. **A.** Incomplete dorsal valve, PKUM02-0527, in exterior (A_1) and interior (A_2) views. **B.** Incomplete dorsal valve, PKUM02-0528, in exterior (B_1) and posterior (B_2) views. **C.** Slightly damaged dorsal valve, PKUM02-0529, showing exterior (C_1) and enlargement of cardinalia (C_2). **D.** Incomplete ventral valve, PKUM02-0530, in exterior (D_1) and interior (D_2) views. **E.** Incomplete ventral valve, PKUM02-0531, in exterior (E_1) and posterior (E_2) views. **F.** Almost complete dorsal valve, PKUM02-0532, in exterior (F_1), lateral (F_2), posterior (F_3), and anterior (F_4) views. **G–J.** *Voiseyella cf. texana* (Carter, 1967). **G, H.** Two incomplete dorsal valves, PKUM02-0533 (**G**) and PKUM02-0534 (**H**), in exterior (G_1, H_1) and interior (G_2, H_2) views and enlargement of the interior showing cardinalia (G_3). **I.** Exterior of ventral valve, PKUM02-0535. **J.** Incomplete ventral valve, PKUM02-0536, in exterior (J_1), interior (J_2), anterior (J_3), and posterior (J_4) views, and enlargement showing external micro-ornamentation (J_5). Sample MH1 (A–F), GB (G, H, J), and GT (I).

Voiseyella bruntoni Baliński and Sun, 2010a

Fig. 27A–F.

2010 *Voiseyella bruntoni* sp. nov.; Baliński and Sun 2010a: 93–96, figs. 2, 3.

Material.—Four complete and 14 damaged ventral valves, 4 complete and 22 damaged dorsal valves from sample MH1.

Remarks.—This species has been recently described and discussed in detail by Baliński and Sun (2010a). It differs from all other species of the genus in having an exceptionally transverse, fusiform outline and a characteristically shaped fold and sulcus. The ventral sulcus is narrow, deep, and V-shaped in cross section (Fig. 27D, E), but frequently shallows anteriorly in large specimens. Dorsal fold is distinct, initially appearing as a single costa which bifurcates early within 1–2 mm of the umbo and thus forms two very strong costae divided by a deep median groove (Fig. 27A–C, F). Each flank of the shell is ornamented by 6 to 14 wide and simple radial costae which diminish in size and strength laterally and commonly disappear completely towards the lateral extremities.

Stratigraphic and geographic range.—Known exclusively from the type locality and horizon.

Voiseyella cf. texana (Carter, 1967)

Fig. 27G–J.

Material.—Four incomplete ventral and two incomplete dorsal valves from sample GB, and one incomplete ventral valve from GT.

Description.—This small and fragmentary material reveals quite satisfactory the detail of the internal shell structure as well as external shell ornamentation and micro-ornamentation. The species is characterised by strongly extended laterally shell, with pointed mucrons, narrow but quite deep ventral sulcus bounded laterally by a pair of very thick and high costae, very prominent dorsal fold delimited by deep intercostal furrows and bearing a faint medial groove, simple rounded lateral costae, prominent ventral umbo with incurved beak overhanging the apex of the delthyrium, and having strongly developed imbricate concentric lamellae. Dental adminicula are anteriorly diverging, thin, follow margins of sulcus, or are extrasinal (Fig. 27J₂). In ontogenetically old specimens ventral valve becomes thick posteriorly and thickened dental adminicula occlude apical region of the delthyrium. Dental adminicula embrace posterior part of the

longitudinally striated muscle scars which are deeply impressed posteriorly, weakly delimited anteriorly, and medially divided by a thin ridge (Fig. 27J₂). On some ventral valves the ovarian pitting may be observed laterally of dental adminicula. Cardinal process of ctenophoridium type, quite wide, triangular in ventral view, with thickened base which extends to the proximal dorsal margins of wide plates formed by inner socket ridges and crural bases (Fig. 27H₂). There is a low but sharp and long dorsal median ridge which continues from the umbonal region quite far anteriorly (broken anterior part of valves limits the observation). Besides prominent, regularly disposed concentric imbricating lamellae the micro-ornament consists of well defined radial, densely packed capillae (Fig. 27J₅). The incompleteness of the specimens does not allow examining the condition of denticulation.

Remarks.—The general aspect of the shell as well as the details of its internal structure and external ornament strongly suggest that the described species belongs to the genus *Voiseyella*. Although the specimens are very incomplete they can be easily distinguish from *Voiseyella bruntoni* Baliński and Sun, 2010a from sample MH1 by having longer shell, lower and more concave ventral interarea, wider ventral sulcus, simple dorsal fold without deep median furrow, and markedly thickened posterior shell tissue.

The specimens agree in most characters to *Voiseyella texana* from the Chappel Limestone (Mississippian) of central Texas (Carter 1967). Both forms have similar size and shell shape, costation, and micro-ornamentation. It is also worth of noting that in both forms occurs the characteristic thickening of the posterior shell tissue. The only discrepancy between our material and that from Texas is in the strength of sulcus bounding costae which in the former appears to be stronger. The present specimens are also quite similar in general shell shape and ornamentation to *Voiseyella anterosa* (Campbell, 1957) from the Lower Carboniferous of New South Wales (see Campbell 1957; Roberts 1964) and *Voiseyella novamexicana* (Miller, 1881) from the Chappel Limestone (Mississippian) of Texas. Our specimens differ from the both species by having less expanded laterally shell.

Stratigraphic and geographic range.—*Voiseyella texana* occurs in the Mississippian Chappel Limestone of central Texas (Carter 1967) and the upper Tournaisian Banff Formation (lower Carboniferous) of western Alberta, Canada (Carter 1987). Here we report very similar specimens from the Tournaisian of Muhua, southern China.

Subfamily Bashkiriinae Nalivkin, 1979

Genus *Bashkiria* Nalivkin, 1979

Type species: *Bashkiria gemma* Nalivkin, 1979; upper Tournaisian, Carboniferous; Usujli river, the Urals, Russia.

Bashkiria? sp.

Fig. 28.

Material.—Four incomplete ventral and 3 incomplete dorsal valves from samples GB and GT.

Remarks.—The characteristic features of this species include strongly transverse shell with pointed cardinal extremities, weak ventral sulcus bounded by thick plicae, distinct in umbonal region but barely perceptible anteriorly, weak dorsal fold, better defined posteriorly by deep and wide furrows, smooth, non-costate flanks, except for one pair of weakening anteriorly, rounded plicae on dorsal valve, wide, low triangular ventral interarea with denticulate hinge line, small dental adminicula, confined to the umbonal region only, rather small ventral muscle scars, absent crural plates, triangular ctenophoridium supported by plate-like ridges which join the dorsal edge of the inner socket ridges and crural bases (Fig. 28D₃). The most characteristic features of the species which allow to distinguish it easily from other forms of the Muhua fauna are the smooth, not ribbed, expanded laterally shell and the evident concentric imbricating lamellae. These features, together with internal structure of the shell suggest that the species represents a paeckelmanelloid spiriferid. It shows some similarity with the Tournaisian genus *Bashkiria* expressed especially in the strongly transverse shell outline and the development of fold and sulcus. Moreover, *Bashkiria* has a very weak, sometimes even difficult to observe shell costation, which may resemble the smooth flanks of the species from Muhua. Unfortunately, inadequate present material does not allow a more detailed description and comparison.

Genus *Celsiformix* Carter, 1974

Type species: *Celsiformix rowleyi* Carter, 1974; Lower Burlington Limestone, Tournaisian, Carboniferous; upper Mississippi Valley, USA.

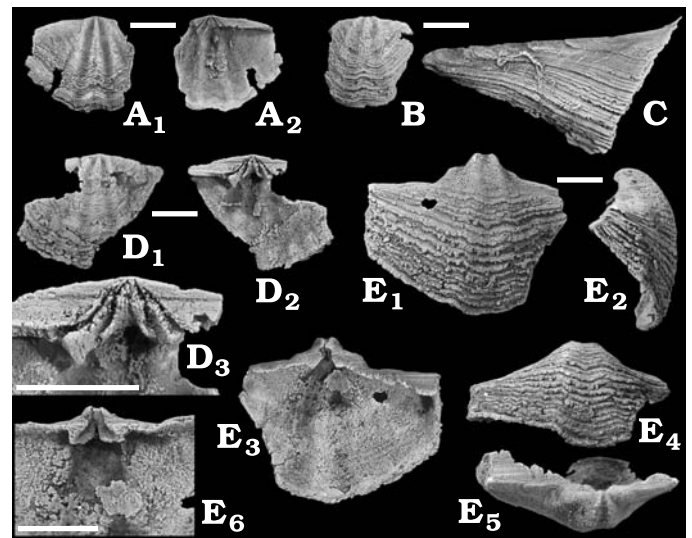


Fig. 28. Strophopleurid brachiopod *Bashkiria?* sp. from the Tournaisian Muhua Formation, southern China. **A.** Incomplete dorsal valve, PKUM02-0537, in exterior (A₁) and interior (A₂) views. **B.** Exterior of incomplete dorsal valve, PKUM02-0538. **C.** Left flank of incomplete ventral valve, PKUM02-0539. **D.** Incomplete dorsal valve, PKUM02-0540, in exterior (D₁), interior (D₂), and enlarged (D₃; showing details of cardinalia) views. **E.** Slightly damaged ventral valve, PKUM02-0541, in exterior (E₁), lateral (E₂), interior (E₃), anterior (E₄), posterior (E₅), and enlarged internal (E₆) views. Sample GB (A–D) and GT (E). Scale bars 2 mm.

Celsiformix carteri Baliński and Sun, 2010a

Figs. 4K, L, 5A, B, D, 6D, F, 29.

2010 *Voiseyella carteri* sp. nov.; Baliński and Sun 2010a: 96–97, pl. 1: 1–33, text-fig. 5.

Material.—43 single ventral and 88 dorsal valves, generally well preserved. All specimens from sample MH1 apart from a single ventral valve was found in sample M2-8.

Remarks.—This species was recently described in detail by Baliński and Sun (2010a: pl. 1, text-fig. 4). It is distinguished from the other species of the genus by its strongly transverse outline (dorsal valve width to length ratio varies from 2.2 to 5.0; Fig. 29A–E). This great variability is connected mainly with a very variable development of cardinal extremities which in some exceptionally fusiform specimens may be ex-

tremely expanded and delicate (Fig. 29C). It is noteworthy that the great variability in the shell width to length ratio is associated with similar variability in the number of lateral costae which varies from 14 to 32: generally the wider valves have more radial costae.

Stratigraphic and geographic range.—Known exclusively from the type locality and horizon. One of the most numerous spiriferids in the Muhua Formation.

Superfamily Brachythyridoidea Frederiks, 1924

Family Brachythyrididae Frederiks, 1924

Genus *Brachythyris* M' Coy, 1844

Type species: *Spirifera ovalis* Phillips, 1836; Viséan, Carboniferous; Bolland, Yorkshire, England.

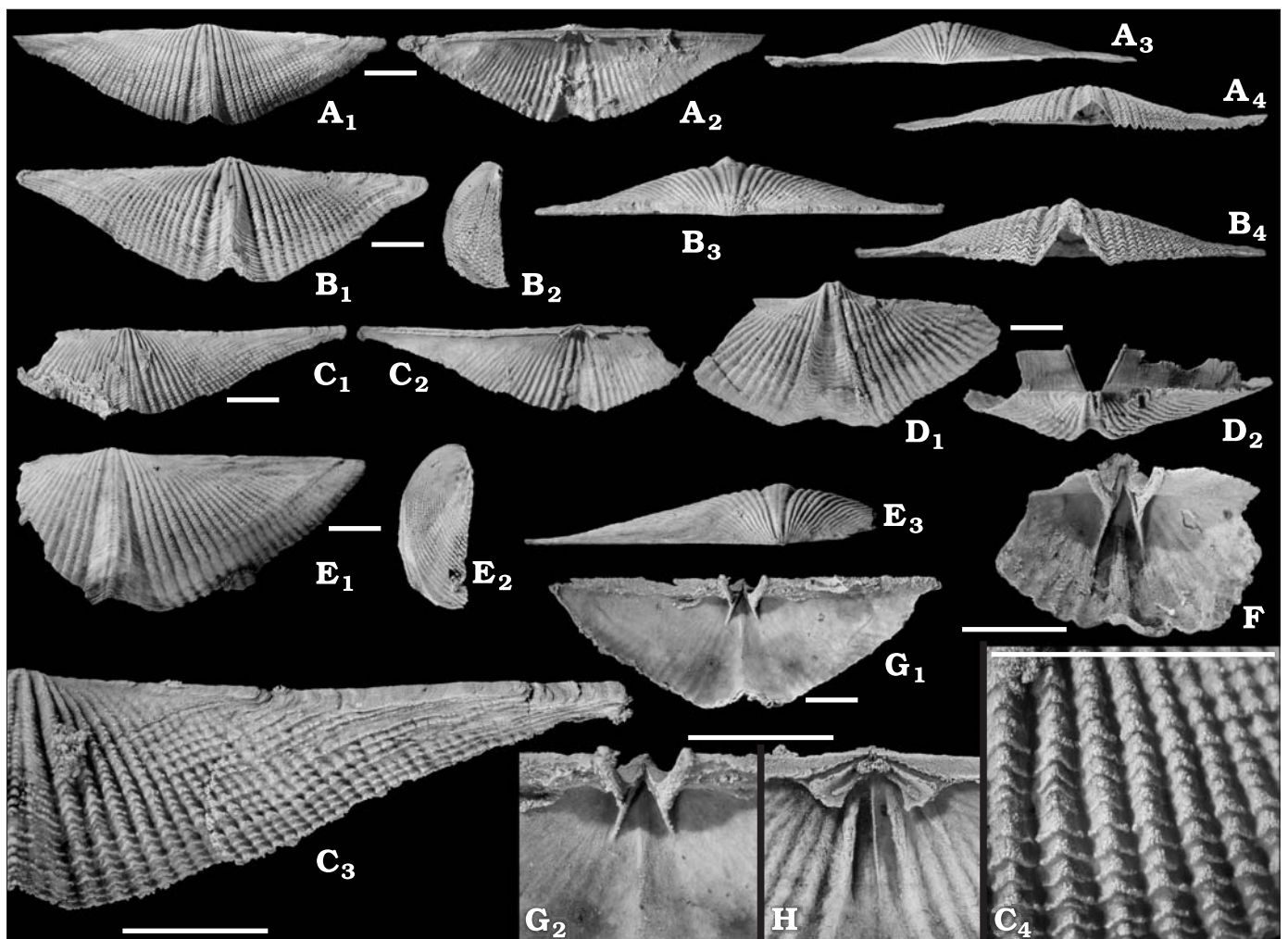


Fig. 29. Strophopleurid brachiopod *Celsiformix carteri* Baliński and Sun, 2010a from the Tornaisian Muhua Formation, southern China. **A.** Complete dorsal valve, PKUM02-0542, in exterior (A₁), interior (A₂), posterior (A₃), and anterior (A₄) views. **B.** Complete dorsal valve, PKUM02-0543, in exterior (B₁), lateral (B₂), posterior (B₃), and anterior (B₄) views. **C.** Incomplete dorsal valve, PKUM02-0544, showing exterior (C₁), interior (C₂), enlarged right half of the valve (C₃), and enlargement of surface ornamentation (C₄); note distinct growth lamellae on C₃ showing development of the cardinal extremities during ontogeny. **D.** Incomplete ventral valve, PKUM02-0545, in exterior (D₁) and posterior (D₂) views. **E.** Incomplete dorsal valve, PKUM02-0546, in exterior (E₁), lateral (E₂), and posterior (E₃) views. **F.** Interior of a damaged ventral valve, PKUM02-0547, showing partially closed delthyrium by the umbonal callosity and dental adminicula. **G.** Interior of a complete ventral valve, PKUM02-00382 (G₁) and enlargement showing open delthyrium and dental adminicula (G₂); specimen illustrated by Baliński and Sun 2010a: pl. 1: 24–26, new photographs. **H.** Enlargement of the posterior region of the holotype PKUM02-0381 (figured by Baliński and Sun 2010a: pl. 1: 22–23; new photograph), viewed internally, showing cardinalia. All from sample MH1. Scale bars 5 mm.

Brachythyris sp.

Fig. 30A–E.

Material.—Five very fragmentary ventral valves from sample MH1 and one incomplete ventral valve from sample MH2.

Remarks.—Assignment of this scarce material to the genus *Brachythyris* is based on external characters, including the presence of a narrow sulcus, weak, rounded and simple radial costae, as well as on the absence of dental adminicula in the interior of the ventral valve (Fig. 30A–E). The median costa which can be observed in the specimens described below as *Skelidorygma* sp. does not occur in the form here described suggesting that it should be better placed in the genus *Brachythyris*.

Family Skelidorygmidae Carter, 1994

Genus *Skelidorygma* Carter, 1974

Type species: *Spirifer subcardiformis* Hall, 1858; Viséan, Carboniferous; Illinois, USA.

Skelidorygma sp.

Fig. 30F–I.

Material.—One incomplete shell, 4 incomplete ventral valves and 1 fragmentary dorsal valve from samples GB and GT.

Remarks.—The specimens are characterised by a brachythyrid, suboval shell outline with short hinge line and smoothly rounded postero-lateral margins. The ventral sulcus is bordered by a pair of stronger and wider costae. The sulcal ribbing pattern can be assessed on one of the studied specimen

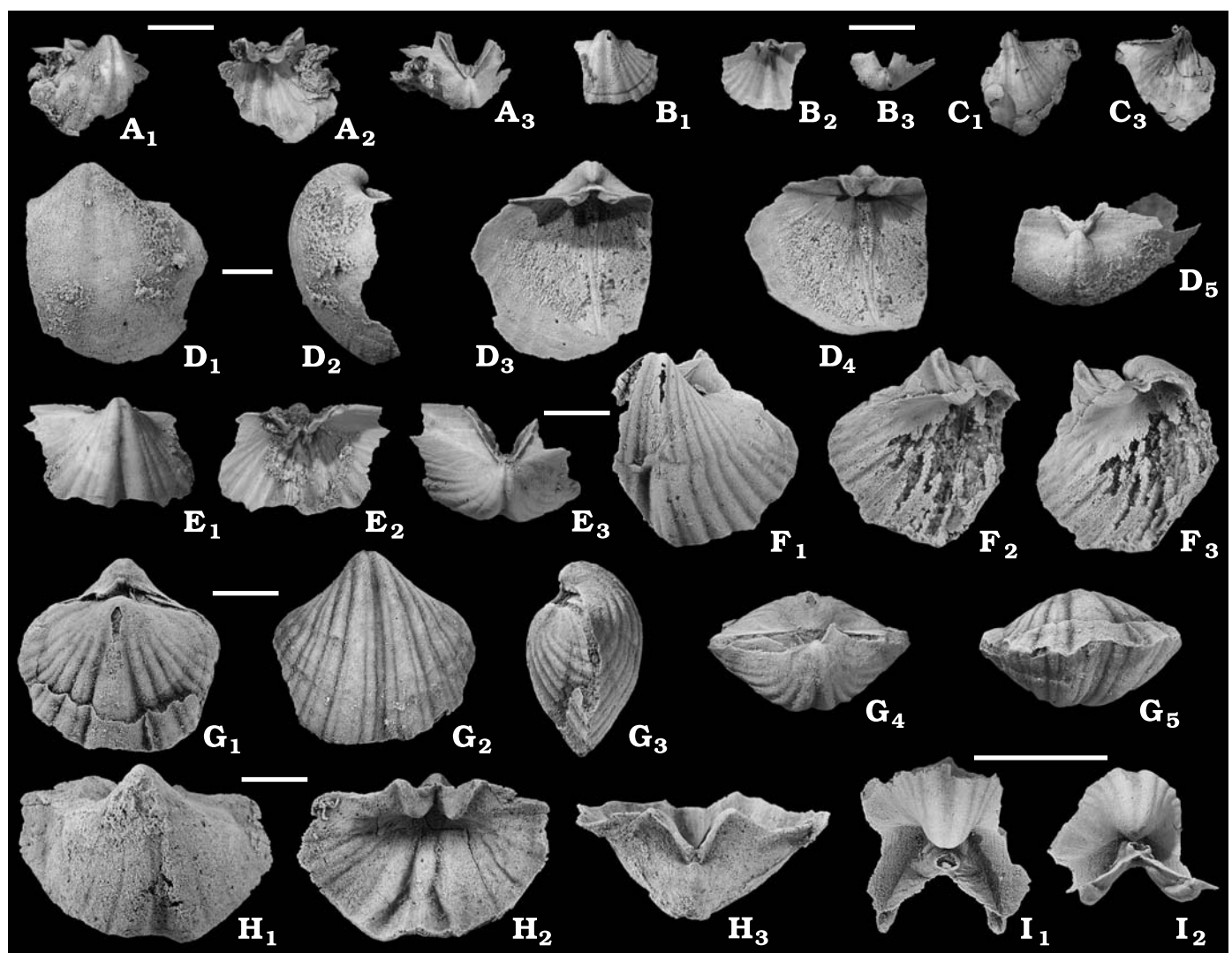


Fig. 30. Brachythyrid brachiopods from the Tornaisian Muhua Formation, southern China. A–E. *Brachythyris* sp. A, B, E. Three incomplete ventral valves, PKUM02-0548 (A), PKUM02-0549 (B), and PKUM02-0550 (E), in exterior (A₁, B₁, E₁), interior (A₂, B₂, E₂), and posterior (A₃, B₃, E₃) views. C. Incomplete ventral valve, PKUM02-0551, in exterior (C₁) and interior (C₂) views. D. Slightly broken ventral valve, PKUM02-0552, with heavily abraded surface costation in exterior (D₁), lateral (D₂), interior (D₃), inclined interior (D₄), and posterior (D₅) views. F–I. *Skelidorygma* sp. F. Incomplete ventral valve, PKUM02-0553, in exterior (F₁), interior (F₂), and lateral (F₃) views. G. Almost complete shell, PKUM02-0554, in dorsal (G₁), ventral (G₂), lateral (G₃), posterior (G₄), and anterior (G₅) views. H. Ventral valve, PKUM02-0555, in exterior (H₁), interior (H₂), and posterior (H₃) views. I. Umbonal region of a ventral valve, PKUM02-0556, in posterior (I₁) and posterodorsal (I₂) views, showing delthyrial cover and pedicle opening. Sample MH1 (A–C), MH2 (D), GB (E, G, H), and GT (F). Scale bars 5 mm.

only (Fig. 30G). Besides the sulcal median costa there are two narrow costae on each slope of the sulcus which arise by bifurcation from the sulcus-bounding costae. The latter, however, bifurcate once also laterally. The costae on flanks are broad, rounded, and either simple (single ventral valve on Fig. 30F), or with a tendency to bifurcate (single incomplete shell on Fig. 30G). The dorsal fold on the latter specimen appears to be smoothly rounded without any evident costation (in contrast to the costate ventral sulcus; see Fig. 30G). Interior of four incomplete ventral valves show no dental plates but thickened dental ridges are well visible (Fig. 30F₂, F₃, H₂). Delthyrium covered by a convex delicate deltidial plate which is medially deeply angularly indented. A single well preserved deltidial plate reveals a presence of an elliptical, ca. 0.7 mm in greater diameter pedicle opening with a short tube-like collar extending externally (i.e., dorsally; Fig. 30I).

Unfortunately, the condition of secondary denticulation, which is characteristic and diagnostic for some brachythyridid species cannot be ascertain on the material due to its preservational constrains. The bifurcate lateral costae which can be observed on one of the specimens are not typical for *Skelidorygma* and many other brachythyridids but in some species bifurcation can be observed, e.g., in *Brachythyris chouteauensis* (Weller, 1909) (Carter 1967: pl. 39: 1), *Meristorygma arctica* Carter, 1974 (Carter 1974: pl. 3: 21–24), *Brachythyris atbasarica* Nalivkin, 1937 (Litvinovich et al. 1969: pl. 67: 2, 3), *Litothyris alticostata* Roberts, 1971 (Roberts 1971: 238, fig. 77), *Brachythyris cobarkensis* Peou, 1980 (Peou 1980: 13), and *Brachythyris suborbicularis* (Hall, 1858) (Xu and Yao 1988: pl. 79: 7).

Suborder Delthyridina Ivanova, 1972

Superfamily Delthyridoidea Phillips, 1841

Family Mucrospiriferinae Boucot, 1959

Subfamily Tylothyridinae Carter, 1972

Genus *Tylothyris* North, 1920

Type species: Spirifer laminosa M'Coy, 1841; Tournaisian, lower Carboniferous; Hook Head, Ireland.

Tylothyris laminosa (M'Coy, 1841)

Figs. 7C, 31.

1841 *Spirifera laminosa* M'Coy; M'Coy 1841: 26.

1844 *Cyrtia laminosa* (M'Coy); M'Coy 1844: 137, pl. 21: 4.

1969 *Tylothyris laminosus* (Mc'Coy); Litvinovich et al. 1969: 280, pl. 69: 4, 5.

1979 *Tylothyris laminosa* (M'Coy, 1844); Nalivkin 1979: 131, pl. 49: 15.

1984 *Tylothyris laminosa* (M'Coy); Brunton 1984: 77–83, figs. 108–119.

2006 *Tylothyris laminosa laminosa* (M'Coy, 1841); Bassett and Bryant 2006: 518–520, pl. 12: 1–8, pl. 14: 1–18, pl. 15: 1–19, pl. 16: 1–6.

2006 *Tylothyris laminosa* (M'Coy); Liao and Zhang 2006: pl. 5: 1–6.

2010 *Tylothyris laminosa* (M'Coy, 1841); Mottequin 2010: 270–271, pl. 6: 4–26; fig. 13.

Material.—About 90 single valves, most of them well preserved. All specimens from sample MH1 apart a few fragments found in sample Mu-42

Description.—This species has been described in great detail and abundantly illustrated by North (1920), Brunton (1984), and Bassett and Bryant (2006).

Remarks.—This is one of the most characteristic spiriferoid brachiopods in the Muhua fauna. Its shell shape, ornamentation and details of the internal structures are very similar to *Tylothyris laminosa* from the Tournaisian and Viséan of the British Isles (see Brunton 1984; Bassett and Bryant 2006). The only difference observed between the specimens from Europe and China is the occasionally developed weak costation on the dorsal fold of the valves here studied.

The specimens from Muhua have greater number of costae than *Tylothyris clarksvillensis* (Winchell, 1865) described by Rodriguez and Gutschick (1967) from the early Mississippian of Western Montana, and *Tylothyris missouriensis* (Weller, 1914) from the early Mississippian of Illinois (see Carter 1988). The specimens described here are much less transversally expanded than *Tylothyris transversa* Roberts, 1971 described from the Tournaisian of Northwestern Australia (see Roberts 1971).

Stratigraphic and geographic range.—The species is known from the late Tournaisian and Viséan of western Europe, the Middle East, the Urals, Kazakhstan, Australia, Japan, and China (see Litvinovich et al. 1969; Nalivkin 1979; Brunton 1984; Tazawa et al. 1984; Liao and Zhang 2006; Mottequin 2010; and herein). Related forms were described as *Tylothyris* sp. aff. *laminosa* from the Tournaisian of Morocco (Brice et al. 2005) and as *Tylothyris* (?) cf. *laminosa* from the lower Carboniferous of Rudny Altai, Russia (Bublichenko 1976).

Superfamily Reticularioidea Waagen, 1883

Family Elythidae Frederiks, 1924

Subfamily Elythinae Frederiks, 1924

Genus *Kitakamithyris* Minato, 1951

Type species: Tornyifer (Kitakamithyris) tyoanjiensis Minato, 1951; Lower Carboniferous; Kitakami Mountains, Honshu, Japan.

Kitakamithyris sp.

Fig. 32.

Material.—One almost complete and 13 fragments of ventral valves, and 7 fragmentary preserved dorsal valves, as well as 16 small fragments of valves showing characteristic micro-ornamentation, all from sample MH1. Two fragments of ventral valves and one incomplete dorsal valve from sample GT. Some small fragments of valves with well preserved micro-ornamentation come also from sample M2-8.

Remarks.—Of special interest are very sparse and fragmentary specimens, but with well preserved characteristic elythide micro-spinose ornamentation. These specimens (sample MH1 and M2-8) show concentric rows of elaborate double-barrelled, densely distributed spines (about 36 spines in 10 mm) similar to those illustrated by, e.g., Kozłowski (1914: fig. 18d) in *Reticularia lineata* var. *perplexa* (Mac Chesney, 1860) (= *Martinothyris lineata*) and by Samtleben (1971: pl. 11: 11) in

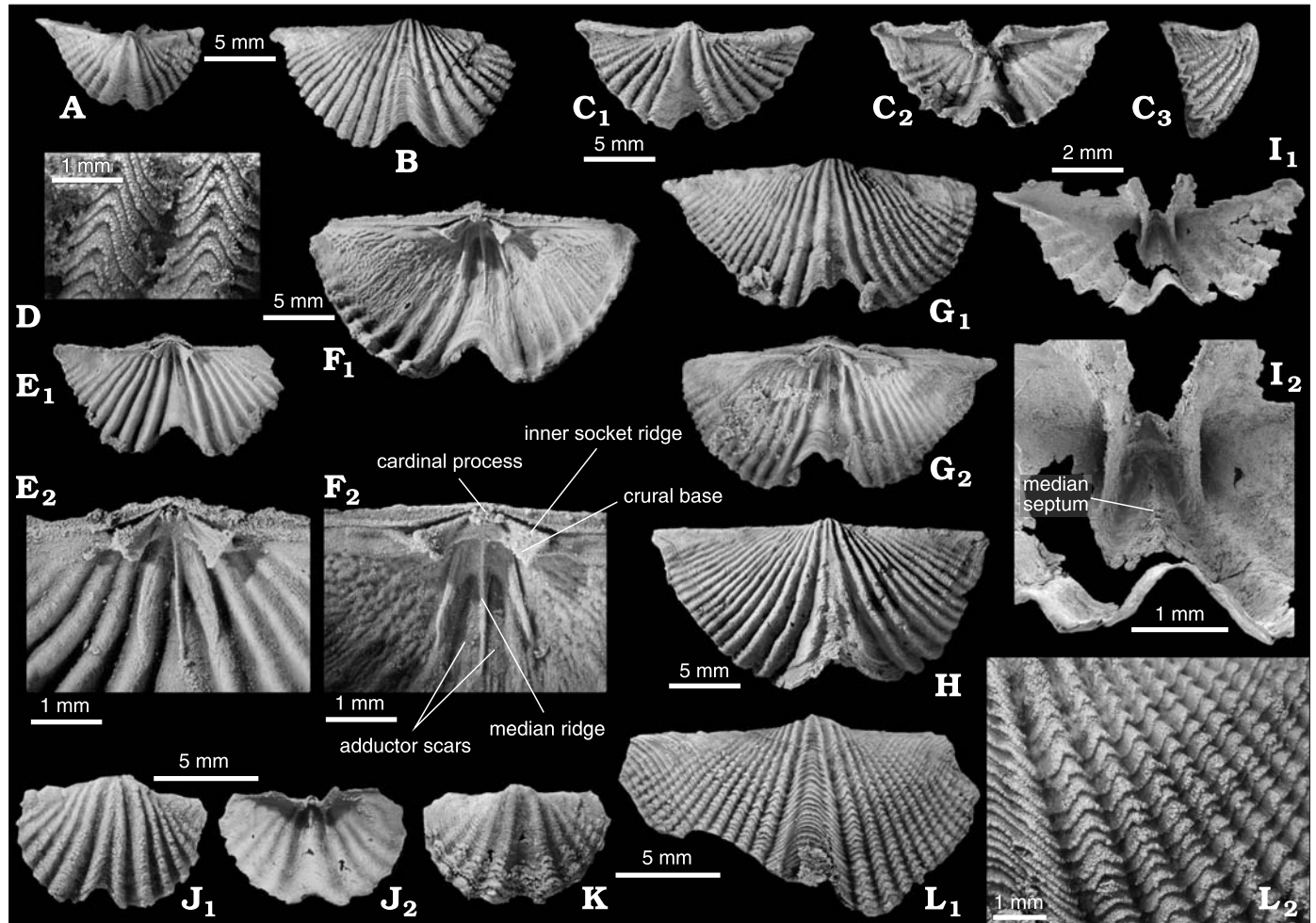


Fig. 31. Delthyridoid brachiopod *Tylothyris laminosa* (M' Coy, 1841) from the Tornaisian Muhua Formation, southern China. **A, B.** Exterior of ventral (A) and dorsal (B) valves, PKUM02-0557 (A) and PKUM02-0558 (B). **C.** Ventral valve, PKUM02-0559, in exterior (C₁), interior (C₂), and lateral (C₃) views. **D.** Detail of external shell micro-ornamentation, PKUM02-0560. **E, F.** Interior of two dorsal valves, PKUM02-0561 (E) and PKUM02-0562 (F), in general (E₁, F₁) and enlarged (E₂, F₂) views. **G.** Dorsal valve, PKUM02-0563, in exterior (G₁) and interior (G₂) views. **H.** Exterior of dorsal valve, PKUM02-0564. **I.** Slightly damaged ventral valve, PKUM02-0565, in anterior (I₁) and enlarged (I₂) views; SEM micrographs. **J.** Juvenile ventral valve, PKUM02-0566, in exterior (J₁) and interior (J₂) views. **K.** Exterior of juvenile ventral valve, PKUM02-0567. **L.** Incomplete dorsal valve, PKUM02-0568, with well preserved lamellose ornamentation, in general (L₁) and detailed (L₂) views. All from sample MH1.

Phricodothyris guadalupensis (Schumard, 1859). Unfortunately, our specimens with well preserved spines are so fragmentary that none of the internal shell features could be assessed. However, some co-occurring ventral valves are almost undoubtedly conspecific, because they also reveal a few preserved double-barrelled spines. These valves, the largest of which attains nearly 25 mm in length, show the presence of a medial sulcus, and internally well developed dental adminicula and median septum. Incomplete dorsal valves from sample MH1, representing probably the same species, has narrow inner socket ridges and ctenophoridium. Two fragments of ventral valves and one incomplete dorsal valve from sample GT also reveal elythid relations by having smooth shell with concentrically distributed scars marking the bases of broken off spines (Fig. 32B). The interior of these two ventral valves reveals the presence of well marked slightly divergent dental adminicula and strong and long median ridge. The growth

lamellae preserved on a single dorsal valve indicate that this species was characterised by transverse shell and rounded cardinal extremities. However, the interior of the dorsal valve from sample GT shows shorter and wider inner socket ridges than the specimens described above from sample MH1. It seems not unlikely that the elythid from sample GT may represent a different species.

This very fragmentary material from samples MH1, M2-8, and GT can be attributed quite convincingly to the genus *Kitakamithyris* mainly because of the ornamentation and general shell shape (indicated by growth lines) as well as the internal structure of both valves. Its very poor preservation, however, precludes a more detailed description and taxonomic assignment.

Stratigraphic and geographic range.—The species of *Kitakamithyris* are known from the Tornaisian of Japan, Russia, Australia, and North America.

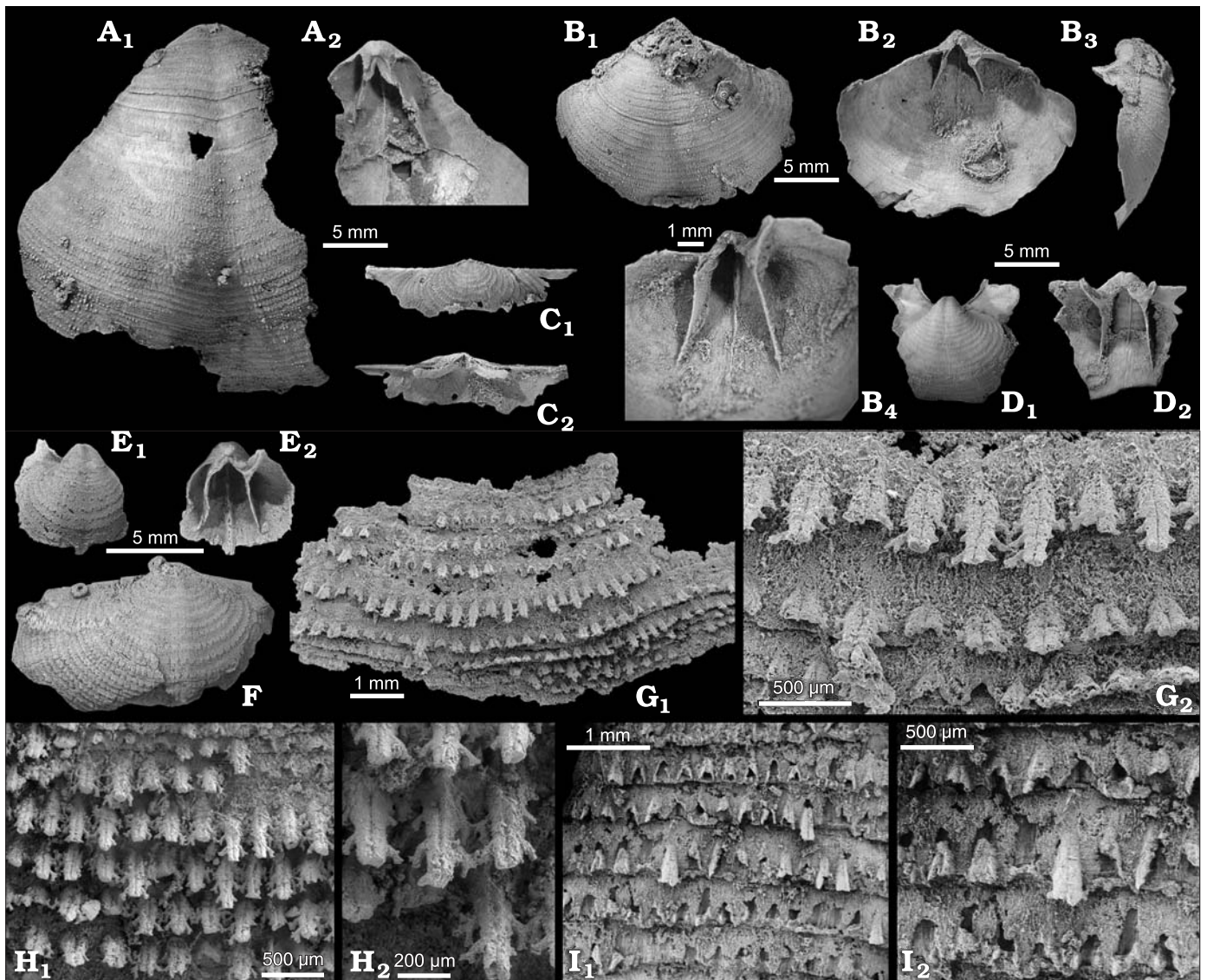


Fig. 32. Reticularioid brachiopod *Kitakamithyris* sp. from the Tornaisian Muhua Formation, southern China. **A**. Incomplete ventral valve, PKUM02-0569, exterior (**A**₁) and interior of the posterior region (**A**₂). **B**. Ventral valve, PKUM02-0570, in exterior (**B**₁), interior (**B**₂), and lateral (**B**₃) views, and enlargement of the interior showing well developed dental adminicula and median septum (**B**₄). **C**. Posterior region of an incomplete dorsal valve, PKUM02-0571, in exterior (**C**₁) and interior (**C**₂) views. **D**, **E**. Two umbonal fragments of the ventral valve, PKUM02-0572 (**D**) and PKUM02-0573 (**E**), in exterior (**D**₁, **E**₁) and interior (**D**₂, **E**₂) views, showing concentric micro-ornamentation, dental adminicula, and median septum. **F**. Incomplete dorsal valve, PKUM02-0574, in exterior view. **G**. Fragment of ventral valve, PKUM02-0575, with well preserved external micro-ornamentation, in general view (**G**₁) and enlargement (**G**₂). **H**, **I**. Two specimens, PKUM02-0576 (**H**) and PKUM02-0577 (**I**), showing well preserved spinose micro-ornamentation, in general (**H**₁, **I**₁) and enlarged (**H**₂, **I**₂) views. **G**–**I** SEM micro-graphs. Samples MH1 (**A**–**D**, **I**), GT (**E**, **F**), and M2-8 (**G**, **H**).

Order Spiriferinida Ivanova, 1972

Suborder Spiriferinidina Ivanova, 1972

Superfamily Pennospiriferinoidea Dagens, 1972

Family Spiriferellinidae Ivanova, 1972

Genus *Spiriferellina* Frederiks, 1924

Type species: Terebratulites cristatus von Schlotheim 1816; Zechstein, Permian; Thüringen, Germany.

Spiriferellina cf. *insculpta* (Phillips, 1836)

Figs. 7B, 33.

Material.—One complete and 2 damaged ventral valves, and

one slightly incomplete dorsal valve from the sample MH2. One damaged dorsal valve and a fragment of ventral valve from the sample GB.

Description.—The single complete ventral valve is 7 mm long, 12 mm wide, and 6.4 mm thick, semicircular in outline, slightly subpyramidal in shape, with a high, almost flat, transversely striated triangular interarea; lateral margins of the interarea slightly rounded; cardinal extremities slightly rounded, hinge line almost equal the greatest width of the valve; sulcus very deep, rounded, bounded by a pair of very high, subangular plicae; delthyrium open, delthyrial angle 24°.

Dorsal valve semicircular in outline, with a very high, an-

gular fold and tree high, angular plicae on each flank, diminishing in size rapidly toward lateral extremities; interarea low, almost linear, slightly concave, rectangular.

Ventral interior with short dental adminicula joining the valve floor in the umbonal region along the bottom of interspaces next to the sulcus-bounding plicae, continuing anteriorly as sharp lamellae decreasing gradually in height and becoming distally barely strong dental ridges; median septum thin, sharp, increasing in height anteriorly and reaching about the mid-valve.

Interior of dorsal valve with strong inner socket ridges diverging at 110° ; inner socket ridges and crural bases forming slightly concave plates, elevated above valve floor, and converging with the base of ctenophoridium; ctenophoridium distinct, subtriangular in dorsal view; adductor scars bordered by distinct ridges running more or less radially along the bottom of the fold-bounding interspaces.

Shell strongly plicate, 6 plicae on each of the two figured ventral valves (Fig. 33A, D), and 3 and 7 (including fold) on two dorsal valves, respectively (Fig. 33B, C). On a single dorsal valve two plicae bifurcate near the anterior margin (Fig. 33C₁) but the bifurcation takes place anterior to a marked arrest of growth caused probably by some serious disturbance during the life of the animal. Concentric growth lamellae prominent, imbricate, with frequency of about 4 per mm; pustules nor observed, shell substance distinctly punctate.

Remarks.—The specimens from Muhua show great resemblance to *Spiriferellina insculpta* (Phillips, 1836) and *Spiriferellina octoplicata* (Sowerby, 1827), both from the Lower Carboniferous of England and Ireland. The latter species are also morphologically similar to each other differing slightly mainly in the general shell outline and character of the shell plication (North 1920; Brunton 1984; Bassett and Bryant 2006). Most of our specimens are very close to *S. insculpta* having the same number and shape of radial plicae (Fig. 33A, B, D). Only one slightly incomplete dorsal valve from Muhua shown on Figure 33C has at least 7 plicae thus resembling the condition of *S. octoplicata*. Unfortunately, the insufficient material does not allow for a satisfactory taxonomic comparison.

Stratigraphic and geographic range.—*Spiriferellina insculpta* is known from the Tournaisian–Viséan of the British Isles, Belgium, and doubtfully from the Moscow Basin of Russia (see Brunton 1984). Here we report similar form Tournaisian of Muhua, southern China.

Order Terebratulida Waagen, 1883

Suborder Terebratulidina Waagen, 1883

Superfamily Cryptonelloidea Thomson, 1926

Family Cryptonellidae Thomson, 1926

Subfamily Cryptonellinae Thomson, 1926

Genus *Cryptonella* Hall, 1861

Type species: *Terebratula rectirostra* Hall, 1860; Lower–Middle Devonian; western New York, USA.

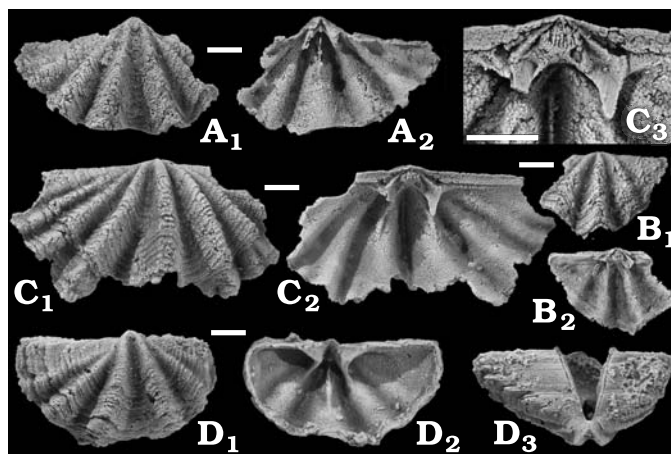


Fig. 33. *Spiriferellina* cf. *insculpta* (Phillips, 1836) from the Tournaisian Muhua Formation, southern China. **A.** Ventral valve, PKUM02-0578, in exterior (A₁) and interior (A₂) views. **B, C.** Two incomplete dorsal valves, PKUM02-0579 (B) and PKUM02-0388 (C, same as in Fig. 7B), in exterior (B₁, C₁) and interior (B₂, C₂) views, and enlargement of cardinalia (C₃). **D.** Ventral valve, PKUM02-0580, in exterior (D₁), interior (D₂), and posterior (D₃) views. Sample MH2 (A, B, D) and GB (C). Scale bars 2 mm.

Cryptonella sp. 1

Fig. 34A, B, D–F, J.

Material.—Four incomplete shells and 2 fragmentarily preserved dorsal valves from samples MH1, MH2, and GT.

Remarks.—There is no doubt that several representatives of terebratulidins are present in the Muhua fauna. Unfortunately the material is very fragmentary and it is not possible to determine how many and which taxa are actually present. Some of the specimens show a densely punctate, elongate shell, nearly straight and long ventral umbo, thin dental plates, and slightly concave, undivided and unsupported hinge plate with an apical perforation (Fig. 34A, B, D–F, J). The two almost complete shells attain 9.3 and 4.4 mm in length and 6.2 and 2.6 mm in width, respectively (Fig. 34 A, B). These internal and external characteristics suggest that the specimens should be placed within genus *Cryptonella*. Although the genus is known mainly from the Devonian, at least two species were recorded from the Carboniferous, i.e., *C. minranensis* Brunton, 1984 (Viséan, lower Carboniferous, Co. Fermanagh, Ireland; Brunton 1984) and *C. simplex* Pérez-Huerta, 2004 (late Moscovian, Pennsylvanian, Nevada, USA; Pérez-Huerta 2004).

Cryptonella sp. 2

Fig. 34C, G, I.

Material.—Two incomplete dorsal valves and one fragment of ventral valve from sample MH1.

Remarks.—Among the terebratulid material there are several fragmentary specimens which resemble the form described above, especially in the internal structure of both valves, but they differ noticeably from *Cryptonella* sp. 1 in having proportionally wider shell (Fig. 34C, G, I). It may also represent a species of the genus *Cryptonella*.

Cryptonellinae gen. et sp. indet.

Fig. 34H, K.

Material.—Several fragments of single valves from samples MH1 and MH2, some of them with fragmentarily preserved internal details.

Remarks.—A few specimens from the sample MH-1 are distinguished by wider shell, unsupported and divided hinge plates. They resemble internally some Pseudodielasmatidae but the lack of the inner hinge plates may be caused by an incomplete preservation of these very fragile structures.

Specimens of uncertain affinity

Fig. 35.

Remarks.—There are two groups of specimens in the investigated material which, for the time being, remain as unassigned to any known genus and species. The first group includes fragments of disarticulated valves or shells which are too incomplete to preserve diagnostic features enough for reli-

able taxonomic determination. The other group, although consists of well preserved single valves and complete shells, represents juvenile stages of growth and are too immature to reveal reliable diagnostic characters of adults.

Among the first group of the fragmentary specimens mentioned above there are several broken dorsal and ventral valves which show well preserved internal structure but cannot be assigned to any species from the Muhua Formation. Some of these specimens are illustrated on Fig. 35O–U. The illustrated dorsal valves show well developed, deep and apparently uncovered septalium, long and high median septum, and absence of cardinal process. The interior of two ventral valves show the presence of thin but long, ventrally convergent dental plates. It seems probable that these specimens represent some camarotoechioid or pugnacoid rhynchonellides.

Several small-sized specimens, ranging from less than one to a few mm in width, represent the other group of forms difficult to determined taxonomically. Some of them represent adult micromorphic brachiopods and have been recently studied in detail (Sun et al. 2004a; Baliński and Sun 2005,

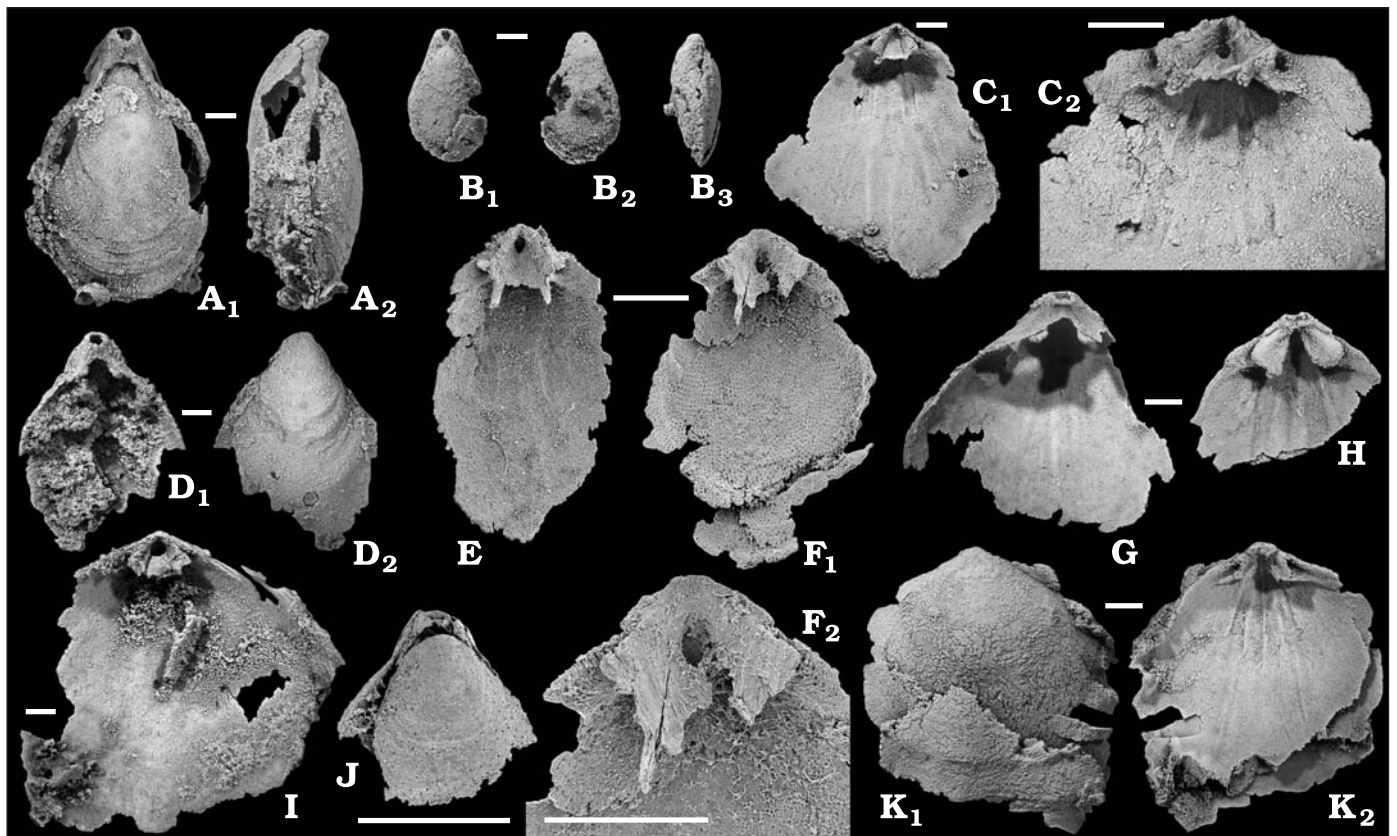


Fig. 34. Terebratulide brachiopods from the Tornaisian Muhua Formation, southern China. **A, B, D–F, J.** *Cryptonella* sp. 1. **A.** Slightly damaged shell, PKUM02-0581, in dorsal (A_1) and lateral (A_2) views. **B.** Incomplete juvenile shell, PKUM02-0582, in dorsal (B_1), ventral (B_2), and lateral (B_3) views. **D.** Incomplete ventral valve, PKUM02-0583, in interior (D_1) and exterior (D_2) views. **E.** Interior of incomplete dorsal valve, PKUM02-0584, showing well preserved cardinal plate and crural bases. **F.** Incomplete dorsal valve, PKUM02-0585, viewed from the interior (F_1) and enlargement of the posterior region showing cardinalia (F_2). **J.** Incomplete juvenile shell, PKUM02-0586, with well visible endopunctae. **C, G, I.** *Cryptonella* sp. 2. **C.** Interior of incomplete dorsal valve, PKUM02-0587, in general view (C_1) and enlargement of slightly tilted posterior region showing cardinal plate, sockets and elongate muscle scars. **G.** Incomplete ventral valve, PKUM02-0588, viewed from the interior showing conjunct deltidial plates, teeth, and pedicle foramen. **I.** Interior of incomplete dorsal valve, PKUM02-0589, showing unsupported cardinal plate. **H, K.** Cryptonelloid gen. et sp. indet. **H.** Interior of incomplete dorsal valve, PKUM02-0590, showing divided hinge plates (damaged cardinal plate?). **K.** Incomplete dorsal valve, PKUM02-0591, in exterior (K_1) and interior (K_2) views showing probably damaged cardinal plate. **E, F, J,** SEM micrographs. Samples MH1 (**A–E, G–I, K**), MH2 (**F**), and GT (**J**). Scale bars 1 mm.

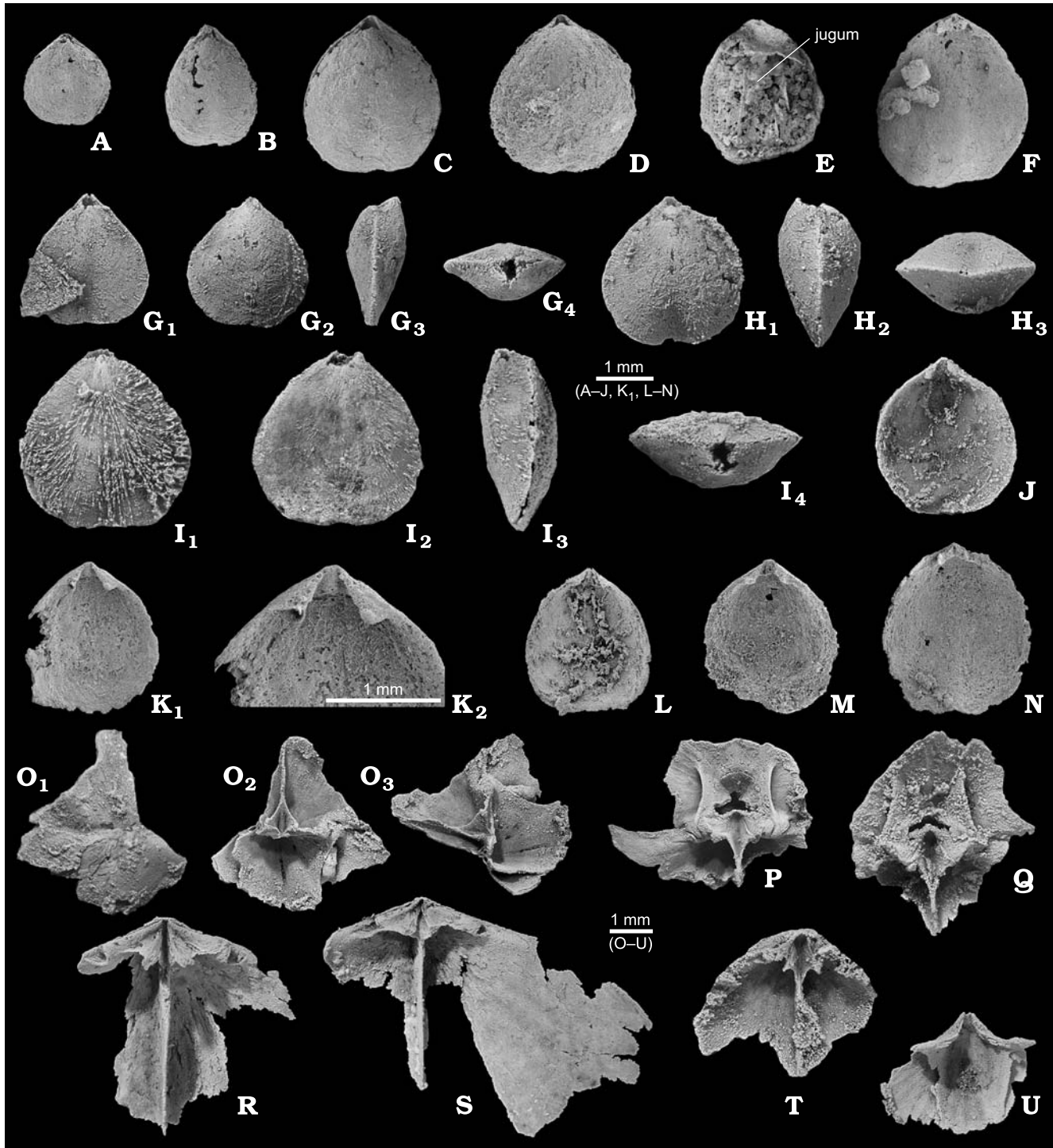


Fig. 35. Fragmentary and juvenile undetermined brachiopods from the Tornaisian Muhua Formation, southern China. A–N. Small shells and single valves probably representing juveniles of athyrididoids. A–D. Four complete shells in dorsal view, PKUM02-0592 (A), PKUM02-0593 (B), PKUM02-0594 (C), and PKUM02-0595 (D). E. Shell PKUM02-0596 with damaged dorsal valve in dorsal view showing partially preserved spirillum and jugum (arrowed). F, N. Two dorsal valves, PKUM02-0597 (F) and PKUM02-0598 (N), viewed from the interior. G, I. Two shells, PKUM02-0599 (G) and PKUM02-0600 (I), in dorsal (G_1, I_1), ventral (G_2, I_2), lateral (G_3, I_3), and posterior (G_4, I_4) views. H. Complete shell, PKUM02-0601, in dorsal (H_1), lateral (H_2), and anterior (H_3) views. J, L, M. Three ventral valves viewed internally, PKUM02-0602 (J), PKUM02-0603 (L), and PKUM02-0604 (M). K. Slightly damaged ventral valve, PKUM02-0605, interior (K_1) and enlargement of the posterior region (K_2). O–U. Fragmentary specimens probably representing juvenile rhynchonellids. O. Umbral region of conjoined valves, PKUM02-0606, in posterior (O_1), anterior (internal) (O_2), and oblique lateral (O_3) views, showing convergent ventrally dental plates and cardinalia. P, Q. Interior of two fragmentary umbral regions of conjoined valves showing convergent ventrally dental plates and cardinalia, PKUM02-0607 (P) and PKUM02-0608 (Q). R–T. Interior of three fragmentary dorsal valves, PKUM02-0609 (R), PKUM02-0610 (S), and PKUM02-0611 (T), showing cardinalia and long median septum. U. Interior of umbral fragment of the ventral valve, PKUM02-0612, showing well developed dental plates. A–F, K, L–N SEM micrographs. All from sample MH1.

2008), but others evidently are juvenile stages of large adults. The latter are most numerous in sample MH1 (see Fig. 35A–N). A shortage of specimens representing transitional growth stages makes impossible their reliable taxonomic assignment but it is highly probable that they represent one or more athyridide species co-occurring in the assemblage.

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