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Authors: Sun, Yuanlin, and Baliński, Andrzej

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YUANLIN SUN and ANDRZEJ BALIŃSKI

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This paper describes 37 species (4 new) belonging to 27 genera (1 new), 14 families, and 6 orders (Lingulida, Craniida, Strophomenida, Productida, Orthotetida, and Orthida) of silicified brachiopods from the middle Tournaisian (Mississippian, lower Carboniferous) of the vicinity of Gedongguan and Muhua villages (southern China). All specimens come from acid etching of detrital and oolitic limestone lenses scattered within grey to black laminated basinal micrite and marl of the Muhua Formation. The formation, which attains about 1–10 meters in thickness, is dated to the *Siphonodella crenulata* Zone. More than 10,000 silicified brachiopod specimens belonging to about 70 species were recovered from over 900 kg of the sampled limestone lenses, the most diverse brachiopod fauna of that age. The characteristic feature of the studied material is the prevailing disarticulation and fragmentation of skeletal parts due to their down slope transportation into a deeper water environment. Within Lingulida, one linguloid and one discinoid species are described. Craniida are represented by five species including *Nematocrania pilea* sp. nov. Strophomenida are represented by fragmentarily preserved specimens belonging to one species. The most diverse are Productida, which are represented by 7 chonetidine and 12 productidine species; new are *Subglobosochonetes gedongguanensis* sp. nov. and *Globosochonetes gracilis* sp. nov. New data on morphology of larval stage of *Argentiproductus margaritaceus* and its mode of attachment are presented. Orthotetida is represented by 5 species including *Lamellispina spinosa* gen. et sp. nov. Orthida is represented by 3, mostly cosmopolitan species. This study of a middle Tournaisian brachiopod fauna from Muhua, together with published data on the Mississippian brachiopods from other regions of South China, allow to study the Devonian–Carboniferous biotic crisis and post-crisis recovery.

Key words: Brachiopoda, silicification, Carboniferous, Mississippian, Tournaisian, China.

Yuanlin Sun [ylsun@pku.edu.cn], Department of Geology, Peking University, Beijing 100871, China;
Andrzej Baliński [balinski@twarda.pan.pl], Instytut Paleobiologii PAN, ul. Twarda 51/55, PL-00-818 Warszawa, Poland.

Introduction

Previous work on the Tournaisian brachiopod fauna in South China has focused mainly on the wide-spread neritic carbonate platform facies (Chu 1933; Yang 1964, 1978; Tong 1978, 1986; Tan 1986, 1987) and few on the relatively deep-water environment (Xu and Yao 1988). This resulted in a widespread opinion that the Tournaisian brachiopod fauna in South China was characterized by endemic forms (such as species belonging to *Yanguania*, *Eochoristites*, *Martiniella*, *Ptychomaletoechia*) and some cosmopolitan genera (representative of *Schuchertella*, *Shizophoria*, *Spirifer*) with relatively low generic diversity (Yang 1964, 1978; Hou 1965; Tong 1986; Tan 1986, 1987).

Baliński (1999) briefly described some interesting and hitherto unknown brachiopods from a detrital limestone lens (sample Mu-42) of the Mississippian (Tournaisian) Muhua Formation at Muhua, Guizhou, China. Although this silicified material was inadequate for detailed study and most fossils were taxonomically determined only to generic level, it clearly showed that the brachiopod fauna at this locality merits detailed investigation. Several further investigations have been carried out around Muhua since 2000. The collected samples were processed with acid and all the silicified and phosphatic remnants were selected. The newly obtained brachiopod fauna from Muhua represents deep-water facies (marginal slope) and is much more diverse than that from the neritic carbonate platform facies. Additionally, the Muhua brachiopod fauna shows strong biogeographical relationship with that of Europe, North America, and Australia. So far only a few new species and genera have been described from this fauna (Sun, Baliński et al. 2004; Sun, Ma et al. 2004; Baliński and Sun 2005, 2008). The rest of brachiopod systematic descriptions, general analysis of the brachiopod fauna from Muhua and its affinity with brachiopods from other regions of China, as well as other continents, will be discussed in another paper being under preparation.

The middle Tournaisian age of the fauna from Muhua postdates the end Devonian biotic crisis (Devonian–Carboniferous Boundary Event, Hangenberg Event, Terminal De-

Fig. 1. Outcrops of the early Carboniferous (Mississippian) formations between the villages of Muhua and Gedongguan, Guizhou Province, China. **A**. View of the outcrop taken from the road leading from Gedongguan (bottom) to Muhua (far left). **B**. Closer view of the outcrop showing the Devonian–Carboniferous boundary and the Mississippian formations (location of the MH1 and MH2 samples marked). **C**. Oolitic packstone lens of the Muhua Formation and closer location of the MH2 sample. **D**. Outcrop G near Gedongguan village (location of the GB and GT samples marked).

vonian Event; see e.g., Johnson and Sandberg 1989; Sandberg et al. 1989; Walliser 1996; Streel et al. 2000; Kaiser et al. 2006). Since the duration of the Tournaisian stage is estimated for ca. 13.9 Ma (Gradstein and Ogg 2004) it is reasonable to assume that the fauna from Muhua lived about 6 Ma after the D–C Boundary Event. This event is regarded by some researchers as one of the most severe bio-events in Phanerozoic history (e.g., Johnson and Sandberg 1989; Sandberg et al. 1989; Walliser 1996; Streel et al. 2000; Kaiser et al. 2006). As Kaiser et al. (2006) noted the event has to be evaluated in terms of a complex pattern of climate change, resulting in glacial-eustatic sea-level change as well as oceanic shelf anoxia and related perturbations in the carbon cycle, which affected both the marine and the terrestrial ecosystems. The resulting mass extinction affected, among other, green algae, clymenid ammonoids, ostracodes, conodonts, crinoids, and placoderm fishes (e.g., Blumenstengel 1993; Becker 1993; Walliser 1996; Olempska 1997; Głuchowski 2002; Schwark and Empt 2006), but other groups, including shallow-water ostracodes and brachiopods, appear to have been less severely affected (Simakov et al. 1983; Shilo et al. 1984; Simakov 1993; Talent et al. 1993; Casier et al. 2005).

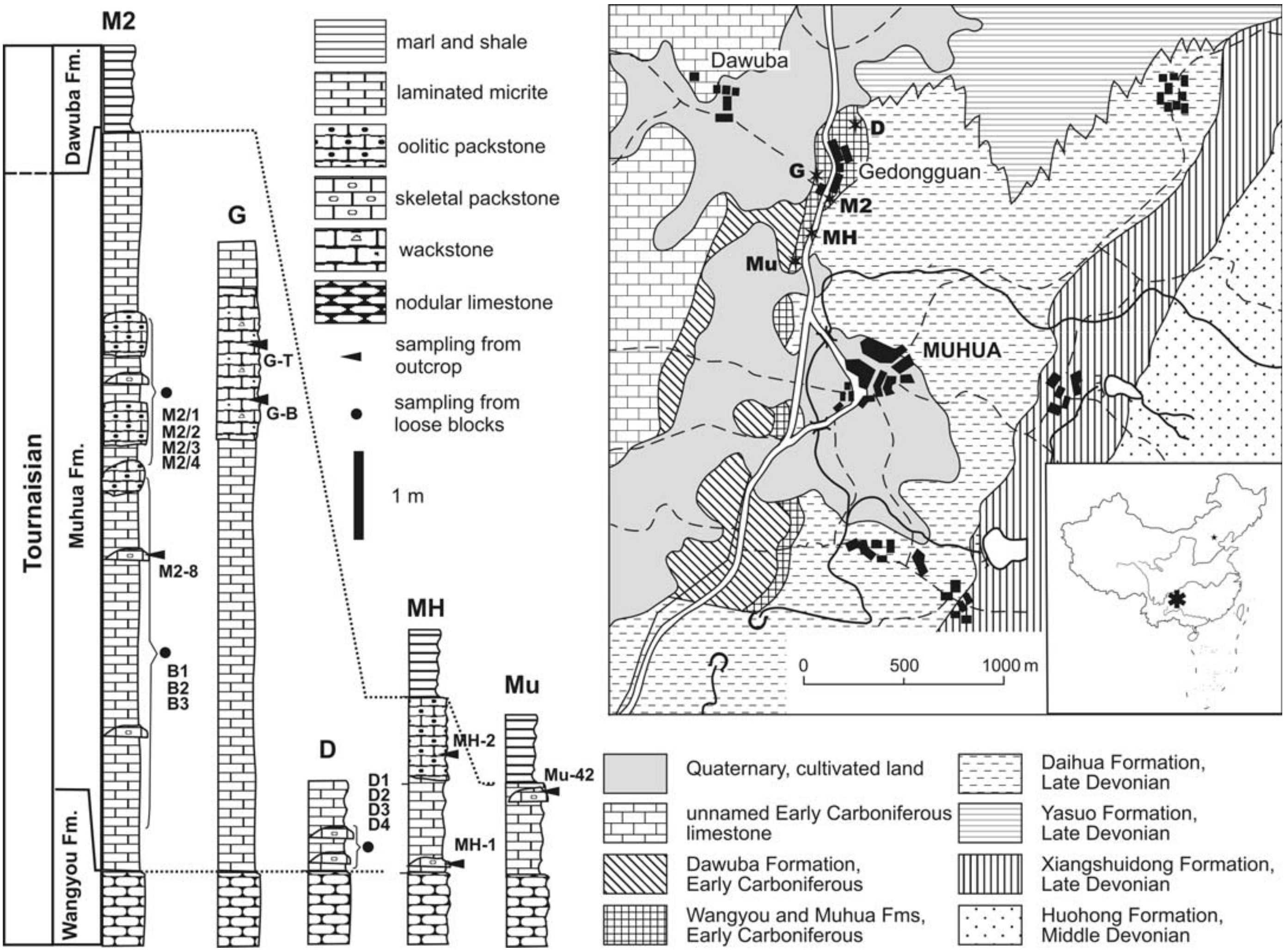


Fig. 2. Lithological sections of the Tournaisian Muhua Formation at five sampling sites around Gedongguan village and their locations near Muhua, Guizhou Province, China (modified after Dzik 1997).

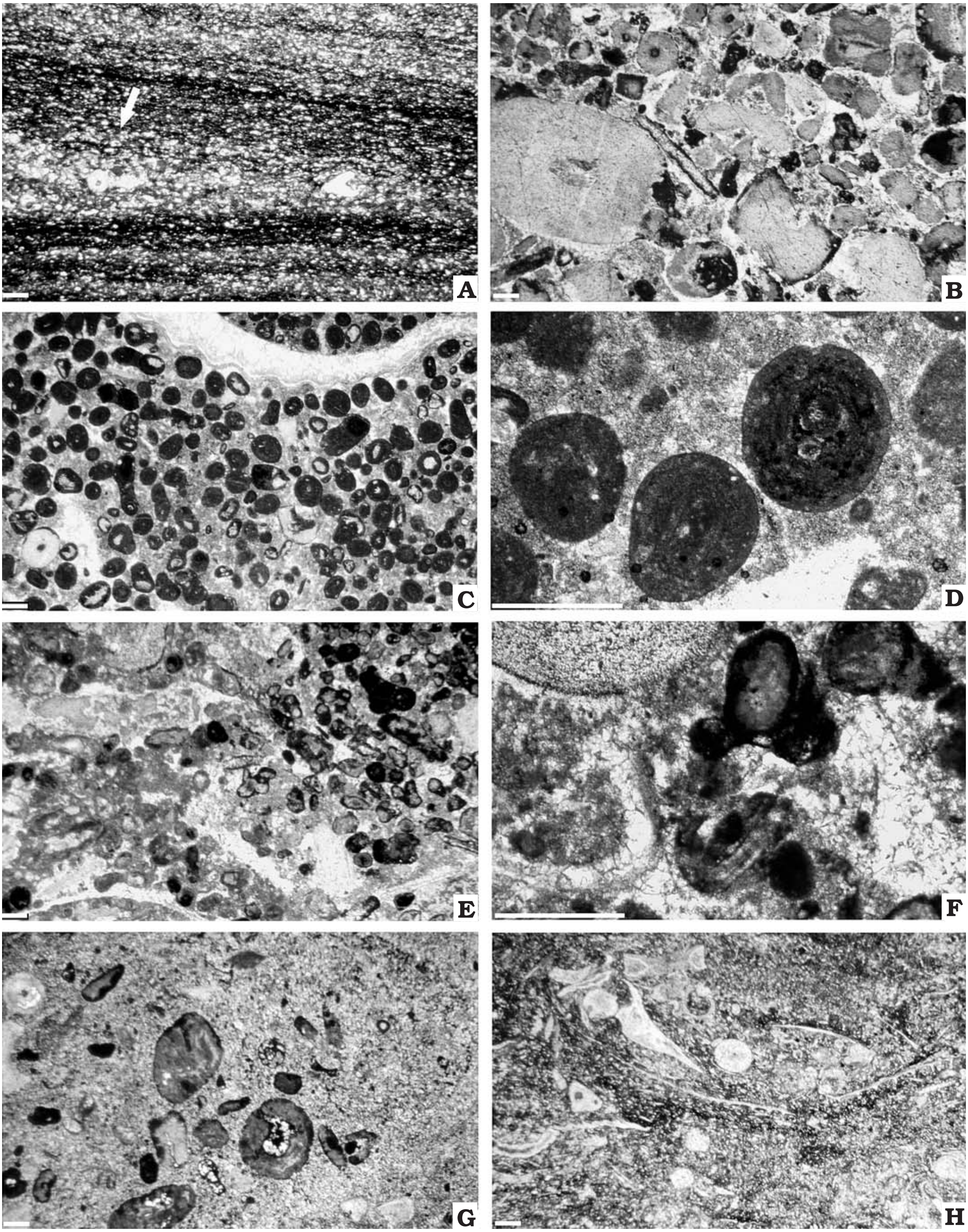
This study of a middle Tournaisian brachiopod fauna from Muhua, together with published data on the early Carboniferous brachiopods from other regions of South China, will contribute to the knowledge of D–C biotic crisis and post-crisis recovery. The results of the study of the Late Famennian–Tournaisian brachiopod faunal dynamic in South China will be published in a separate paper being under preparation.

Institutional abbreviations.—PKUM, Geological Museum of Peking University, Beijing, *China*; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

Geological setting and sampling

All the studied material come from four exposures of the Muhua Formation, namely MH (GPS coordinators 25° 47.991'N and 106°124.186'E), M2 (25°148.050'N and 106° 124.217'E), G (25°148.109'N, and 106°124.205'E), and D (25°148.256'N and 106°124.350'E) which are scattered around Gedongguan village, Muhua, Guizhou (Figs. 1, 2). In this area the Muhua Formation is underlain by ca. 3.4 m thick light-grey bedded limestone of Daihua Formation (Late Famennian) and ca. 4 m thick lenticular limestone, marlstone, and nodular limestone of Wangyou Formation (lower part of Tournaisian; see Ziegler and Sandberg 1984; Hou et al. 1985; Ziegler et al. 1988; Ji 1989), and overlain by the black shale of the Dawuba Formation (Late Tournaisian to Viséan). Muhua Formation is composed of grey to black laminated micrite with sporadic lenses of grey to dark grey skeletal packstone, grainstone, and wackestone containing silicified fossils. These lenses are highly variable in extent from ca. one-half to several meters in width and up to 2 m in thickness. The exposed thickness of the Muhua Formation around Gedongguan village varies from one to over ten meters.

Site MH is in the vicinity of Muhua III Section of Hou et al. (1985), about 40 m to the north of the Mu site mentioned by Baliński (1999). Two samples were collected from this site: MH1 (ca 220 kg in weight) was taken from a light grey-colour crinoid packstone lens that occurs about 20 cm


A
B
C
D
E
F
G
H

above the base of the Muhua Formation and MH2 (ca. 250 kg in weight) was collected from a big block of dark grey oolitic packstone lens, about 1 m above MH1 (Fig. 1A–C).

Site M2 is in the south end of Gedongguan Village. Five samples were collected from this site. M2-8 is taken from a small grey detritic packstone lens about 3.5 m above the base of the Muhua Formation with weight ca 10 kg. M2/1 to M2/4 were taken from loose blocks of dark grey oolitic-detritic packstone and wackestone with weight about 15 kg for each. Judging from the lithology, these loose blocks should come from horizons stratigraphically higher than sample M2-8 from this site.

Site G (Fig. 1D) is near the south edge of a small pond, about 50 m to the west of Gedongguan Village, where GB (ca. 150 kg in weight) and GT (ca. 60 kg in weight) samples were collected from a 1.5–2 m thick dark grey wackestone near the top of the Muhua Formation. GT was located about 1 m above GB.

Site D is located on top of a small hill about 100 m to the northeast of Gedongguan Village and in the vicinity of the Daposhang Section of Ji (1989), where only the basal part of the Muhua Formation (about 1 m thick) crops out due to the natural weathering. Four samples (D1–D4) were collected from loose blocks of grey packstone and grainstone at this site with weight 3, 5, 6, and 150 kg, respectively.

According to Olempska (1999) the lenses were formed by skeletal debris sliding down the slope into a deeper water environment. Thin section analysis shows that formation of the lenses and surrounding rock are related with turbidite (Fig. 3). The difference in content and type, as well as abrasion of the skeletal grains among these lenses might be related to the position where they were deposited. Abundance and weak abrasion of skeletal debris and grains in MH1, MH2, and some samples from the D and M2 sites suggest that they were deposited proximal to the source area (Fig. 3B–D) while the skeletal material of thin shelled forms are dominant in the wackestone of GB and GT (Fig. 3G, H), strongly suggesting that they were distal deposits of a turbidite. Ostracodes, brachiopods, and echinoderm ossicles predominate. Some lenses are composed almost exclusively of crinoid debris, while some other are oolitic. Subordinate are fish remains (Ginter and Sun 2007), tetracorals, bryozoans, gastropods, *Cornulites*, trilobites, conodonts, and some problematic fossils (Baliński 1999). Recently, foraminifers, tabulate corals, phyllocarids, machaeridians, ammonites, and bivalves (Fang et al. 2006) were also recovered. It is possible that the Muhua fauna might have lived around the mud mounds but their presence in the vicinity is not supported by direct evidence. The fossils obtained from studied lenses suggest that they lived in a marine shelf environment with normal salinity.

Conodont analysis indicates that MH1 and the samples from Site D (D1–D4) unquestionably represent the Lower *Siphonodella crenulata* Zone which is represented here by abundant *Siphonodella duplicata*, *S. quadruplicata, S. crenulata*, and *S. lobata*. However, the conodont assemblage from other samples is characterized by elements of *Polygnathus, Pseudopolygnathus*, and *Spathognathodus*, and deficiency of *Siphonodella*. The lack of *Gnathodus delicatus* in the conodont assemblages of these latter samples collected from stratigraphically higher locations than MH1 and the samples from Site D may suggest that they are still in the Lower *Siphonodella crenulata* Zone, however, the possibility that they belong to the Upper *Siphonodella crenulata*–*Siphonodella isosticha* Zone cannot be fully excluded. Baliński (1999) described one specimen of *Mestognathus* sp. from sample Mu-42 which represents the topmost part of the Muhua Formation. As it was suggested by Baliński (1999) this species is probably phylogenetically the oldest representative of the genus. According to Bełka (1983) and von Bitter et al. (1986) *Mestognathus* originated within the Upper *Siphonodella crenulata–Siphonodella isosticha* Zone. The species from the top of the Muhua Formation could also be coeval, or somewhat older from the oldest known species of the genus. It can be assumed then that the formation on a whole represents the middle Tournaisian.

Material and methods

Thirteen samples of detrital and oolitic limestone, collected from the Mississippian Muhua Formation at four nearby sites around Gedongguan Village (including 8 from loose blocks) with a total weight over 900 kg were processed with acetic and formic acids. In a result, more than ten thousand silicified brachiopod specimens belonging to about 70 species were recovered from these samples. The most characteristic feature of the studied material is the evident disarticulation of skeletal parts and their fragmentation. Usually, only specimens smaller than 5 mm are well preserved, frequently with conjoined valves. A good example are micromorphic species which are represented by well preserved shells or single valves with retained details of the internal structures. Larger specimens above 5–10 mm are fragmented partly before final deposition, partly in sediment through compaction, and partly because of incomplete silicification. As noted by Olempska (1999) and Ginter and Sun (2007) the skeletal debris of the limestone lens of the Muhua Formation was probably transported down the slope into a deeper water environment. It can be expected that the brachiopod material from the Muhua Formation represents space-averaged associa-

← Fig. 3. Thin sections of some typical rocks in the Muhua Formation. **A**. Laminated micrite surrounding MH1 sample at the MH site with graded bedding (arrowed). **B**. Crinoid packstone from MH1 sample. The content of skeletal grains reaches over 90%. **C**, **D**. Oolitic packstone from MH2 sample with a few of skeletal fragments representing brachiopods, crinoid stems, and foraminiferans. **E**, **F**. Packstone from M2-8 sample. Note the grains mainly consisting of pelloids and skeletal fragments of brachiopod shell and crinoid stems. **G**, **H**. Wackestone from GB sample. The bioclasts, consisting of crinoid ossicles and some thin shelled organisms such as brachiopods and ostracodes, are scattered within a fine micritic matrix. Scale bars 5 mm.

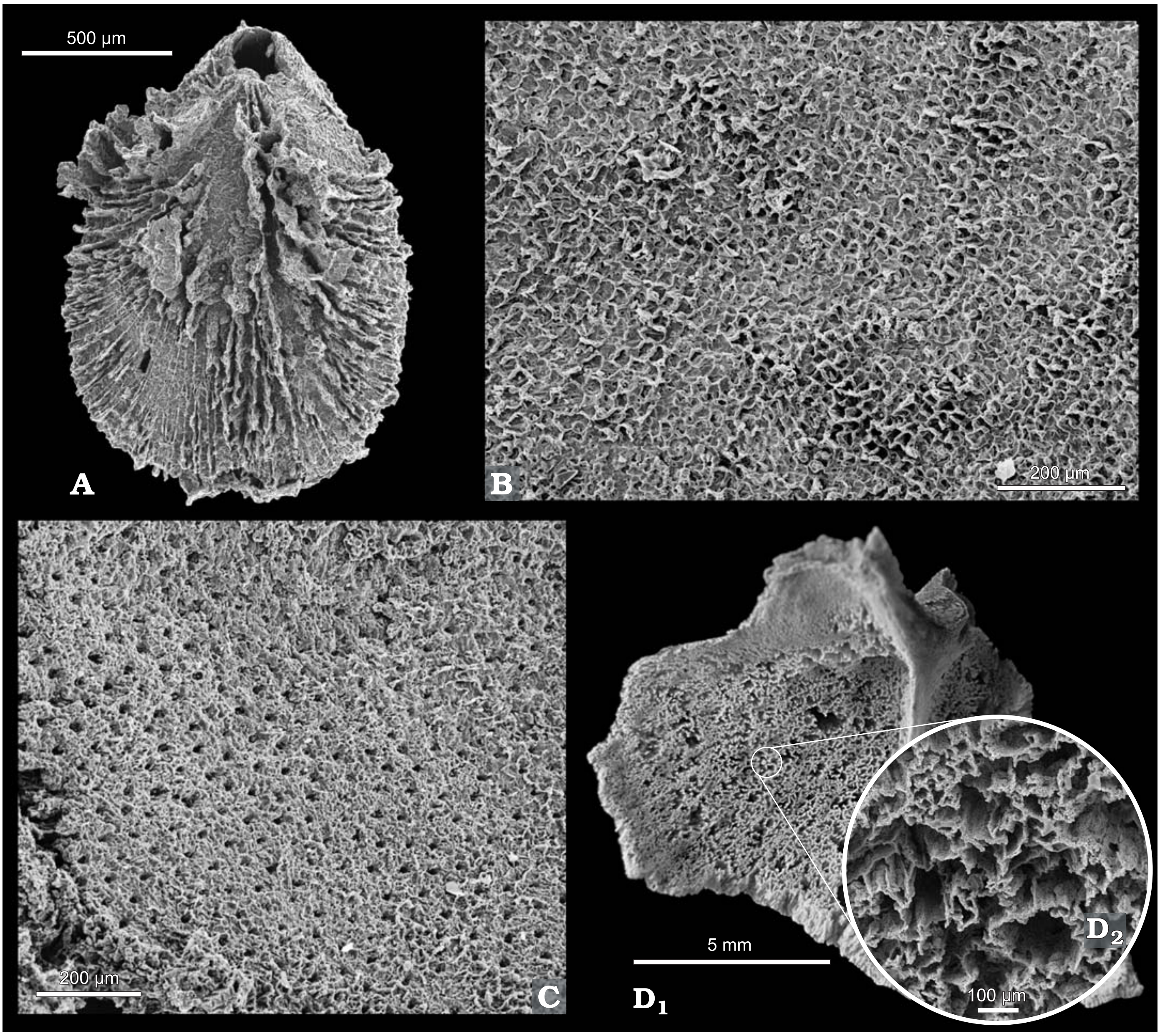


Fig. 4. Different results of the silicification of brachiopod valves from the Muhua Formation. **A**. Subradial lamellae of silica arising along fibres of the secondary shell layer as seen on the external surface of shell. **B**. Net-like pattern formed by silica on the internal surface of the terebratulid valve reflecting the mosaic of the terminal faces of fibres (see text for further explanation). **C**. Punctate shell microstructure preserved on a silicified terebratulid valve. **D**. Spiriferoid ventral valve silicified with "spongy" silica; general view (D_1) and enlargement (D_2).

tions, i.e., it may contain forms which dwelt in slightly different locations or niches on the sea floor. The time-averaging seems to be much less important in the case of brachiopods from Muhua.

The skeletal debris obtained by acid treatment of limestone samples yield phosphatic remnants of fish, conodonts, and lingulids, as well as silicified skeletal remnants of various invertebrates which were originally calcitic, e.g., ostracodes, articulate brachiopods, echinoderms, tetracorals, trilobites, and bryozoans (Baliński 1999). Those skeletons thought to originally have been aragonitic are almost absent in the silicified material from Muhua. Bivalves and gastropods are very rare but the occurrence of the well preserved archaeogastropod *Platycereas*, with its originally calcitic shell (e.g., Batten 1984), is characteristic. According to Cherns and Wright (2000) paucity of aragonitic shells among many fossil faunas may be largely an early taphonomic effect. Although the relation between skeletal mineralogy and shell microstructure and silicification is not well understood (Schubert et al. 1997) it can be assumed that they played a very important role in the taphonomic process (Holdaway and Clayton 1982; Brunton 1984; Daley and Boyd 1996; Butts 2007). The relation of shell microstructure to silicification can be also observed in the material from Muhua. The fibrous structure of the secondary shell layer of some articulated brachiopods led to the development of characteristic net-like patterns seen on internal surfaces of valves and thin subradial lamellae on the exterior (Fig. 4A, B). It seems that silica crystallisation followed intercrystalline spaces resulted from the decay of organic sheets which originally enveloped calcitic fibres. From the exterior the crystals of the secondary shell are seen as subradial long fibres, but on the internal surface of valves there are characteristic mosaics of orthodoxly stacked terminal faces of the fibres.

The silicification process might lead to very different results. Usually the process helped to preserve very fine details of the shell ornamentation and sometimes even shell microstructure as, e.g., shell punctation of craniids and terebratulids (Figs. 4C, 5Q). By contrast, some specimens reveal very profound obliteration of surface details and shell structure as a result of crystallisation to a "spongy" textured silica (Fig. 4D). This kind of silicification is rarely observed in brachiopod shells but very often in originally aragonite shells of gastropods and bivalves (see also Butts 2007). In the studied material, however, we cannot recognize taphonomic bias between rhynchonellate and strophomenate silicification, despite the differences in their original shell mineralogy.

Systematic palaeontology

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

Phylum Brachiopoda Duméril, 1806

Subphylum Linguliformea Williams, Carlson, Brunton, and Popov, 1996

Class Lingulata Gorjansky and Popov, 1985

Order Lingulida Waagen, 1885

Superfamily Linguloidea Menke, 1828

Family Lingulidae Menke, 1828

Genus *Langella* Mendes, 1961

Type species: *Lingula imbituvensis* de Oliveira, 1930; Tubarâo Series, Permian; Paraná, Brazil.

Langella sp.

Fig. 5A, B.

1999 *Lingula* sp.; Baliński 1999: 441, fig. 3B.

Material.—Twenty two small fragments of both valves, non-silicified.

Description.—Ventral valve is elliptical in outline with triangular posterior region. Propareas are quite prominent, triangular, elevated; flexure lines present. Pedicle groove narrow, deep and well-defined. Interior characters weakly impressed; very shallow, long, and narrow groove, slightly widening anteriorly, can be revealed. Dorsal valve is elongate elliptical with gently curved posterior margin. Dorsal pseudointerarea is raised, undivided, developed as rounded, arched thickened margin. Interior characters not visible except very weak median ridge which bifurcates at the anterior end. Ornamentation in form of dense concentric growth lines.

Remarks.—The available material is fragmented and some general morphological characters can be only outlined here. General shape of both valves, character of the ventral pseudointerarea as well as some internal markings suggest that the specimens may represent either *Barroisella* Hall and Clarke, 1892 or *Langella* Mendes, 1961. Dorsal interior of the former genus, however, shows a short ridge intercalated at midvalve in the bifurcation of long median ridge which runs from the posterior region of the valve. In *Langella* the short ridge is not developed as is in the case of the Chinese material. These features indicate that the specimens described here should be assigned to the latter genus.

Stratigraphic and geographic range.—The species is very rare in the Muhua Formation. It was found in samples MH1, MH2, M2-8, Mu-42, D2, and D4.

Superfamily Discinoidea Gray, 1840

Family Discinoidea Gray, 1840

Genus *Orbiculoidea* d'Orbigny, 1847

Orbiculoidea sp.

Type species: *Orbicula forbesii* Davidson, 1848; Wenlock, Silurian; West Midlands, England.

Fig. 5O.

Material.—Five very fragmentary dorsal valves, non-silicified.

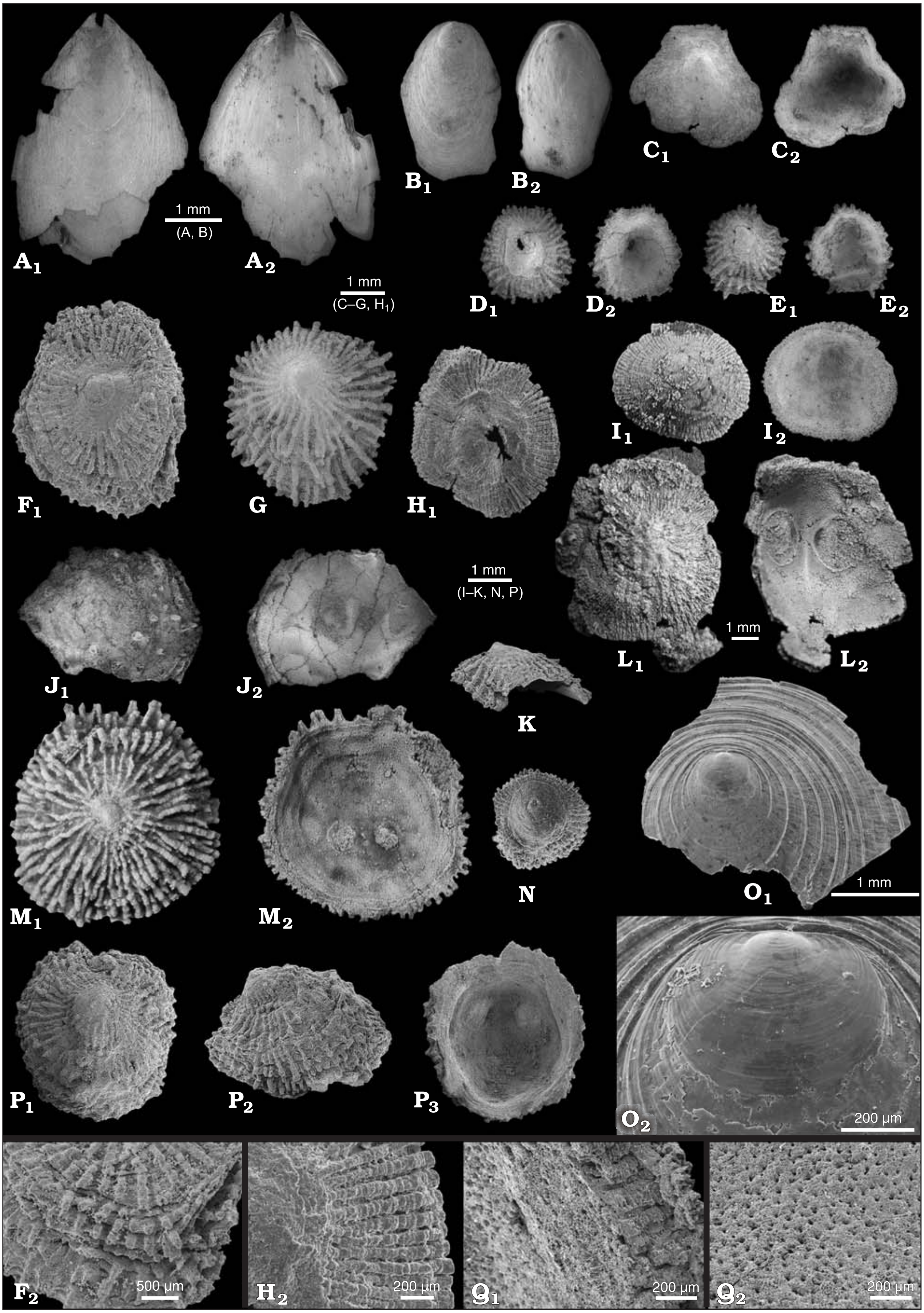
Remarks.—The specimens described here are small fragments of dorsal valves with preserved posterior regions of the valve including subcentral larval shell. The larval shell is subcircular in outline with somewhat flattened posterior margin, with hemiperipheral growth and delicate concentric growth lines, otherwise the valves are smooth. At higher magnification, however, very delicate pitted micro-ornamentation is discernible; the pits attain about 2 μm in diameter on average. Postlarval shell shows holoperipheral growth and distinct, elevated, loosely spaced concentric fila. It seems that the specimens represent the cosmopolitan and stratigraphically long ranging genus *Orbiculoidea* d'Orbigny, 1847.

Stratigraphic and geographic range.—The specimens were found in samples D4 and MH2.

Subphylum Craniiformea Popov, Bassett, Holmer, and Laurie, 1993

Class Craniata Williams, Carlson, Brunton, and Popov, 1996

Order Craniida Waagen, 1885


1 mm
(A, B)
1 mm
(C–G, H1)
1 mm
(I–K, N, P)
1 mm
1 mm
200 µm
500 µm
200 µm
200 µm
200 µm
A1
A2
B1
B2
C1
C2
D1
D2
E1
E2
F1
G
H1
I1
I2
J1
J2
K
L1
L2
M1
M2
N
O1
O2
P1
P2
P3
F2
H2
Q1
Q2

Superfamily Cranioidea Menke, 1828

Family Craniidae Menke, 1828

Genus *Nematocrania* Grant, 1976

Type species: *Nematocrania crassa* Grant, 1976; upper Artinskian, Permian; Ko Muk, Thailand.

Nematocrania pilea sp. nov.

Fig. 5D–G, K, M, P, Q.

?1999 *Acanthocrania* sp.; Baliński 1999: 441, fig. 3A.

Etymology: Latin *pileus*, kind of head cover; referring to the subconical shape of the dorsal valve.

Holotype: Complete dorsal valve PKUM02-0196 illustrated on Fig. 5M.

Type locality: GB site, Muhua section near village of Gedongguan, Changshun County, Guizhou, China.

Type horizon: Upper part of the Muhua Formation, *Siphonodella crenulata* Zone (middle Tournaisian).

Diagnosis.—Small sized, subconical dorsal valve with strong radial ribbing interrupted by growth lamellae and terminating as short spinous projections. From *Nematocrania crassa* Grant, 1976 and *Philhedra trigonalis* (M'Coy, 1884) differs mainly by loosely spaced costellae.

Material.—Seven complete and 10 slightly damaged dorsal valves.

Description.—Shell rather small, attaining up to 4.8 mm in diameter, with subrounded, subelliptical to slightly irregular outline; sometimes with short, flattened posterior margin. Ventral valve unknown; dorsal valve subconical, apex usually slightly posterior to centre, rarely subcentral.

Apical region of ca. 1 mm in diameter rather smooth; rest of valve ornamented with strong radial costellae, 3–5.5 in 1 mm at the valve margins, separated by wide interspaces; costellae added by intercalation, branching not observed; the total number of costellae at the outer margin averages from about 27 (on small specimens) to 57 (on the largest valve); at some distance from the apex they are interrupted by growth lamellae and terminate as protruding tubercles or short spines; usually, on the next growth lamella new costella appears in continuation of the old one. Some costellae appear to be curved. On well preserved specimens the spinous projections of the costellae seem to protrude beyond the valve margins.

Internal features of the dorsal valve poorly preserved; only a pair of large anterior adductor scars can be distinguished. Periphery of the valve interior very lightly flattened to form poorly defined limbus. Shell substance clearly punctate (Fig. 5Q).

Remarks.—The specimens from China are characterized by distinct costellate ornament. The costellae are very strong, rather loosely spaced with wide intertroughs, and terminate at growth lamellae as protruding spinous outgrowths. General character of the ornamentation is reminiscent of that observed in the early Permian *Nematocrania* Grant, 1976 and some Carboniferous craniids attributed to *Philhedra* Koken, 1889. The type species of the former genus *N. crassa* Grant, 1976 was originally described from the late Artinskian (early Permian) of southern Thailand. The specimens described here share with it large dorsal anterior adductor scars and strong external radial costellation of the dorsal valve. In both forms the costellae are interrupted by growth lamellae and as can be seen from some illustrations of the Thailand's species (e.g., Grant 1976: pl. 1: 12, 27), they give rise of short spinous projections. *N. pilea* sp. nov. differs from *N. crassa* mainly in having more loosely spaced costellae.

The specimens studied here are also very similar to *Philhedra trigonalis* (M'Coy, 1884) re-described in detail from the Viséan of County Fermanagh, Northern Ireland by Brunton (1968; see also M'Coy 1844: pl. 20: 2). They differ by the total number of costellae which in the Chinese species is lower. Costellae in *N. pilea* are added by intercalation whereas in specimens from Fermanagh both intercalation and branching have been noted (Brunton 1968: 8). In its costellate ornament *P. trigonalis* differs markedly from the type species of the genus, i.e., *Philhedra baltica* (Koken, 1889) which possesses radially arranged thick hollow spines (Bassett 2000). In this respect, *P. trigonalis* seems to be closer to *Nematocrania*. *Nematocrania pilea* sp. nov. closely resembles *Crania rowleyi* Gurley, 1883 described by Rodriguez and Gutschick (1967: 369, pl. 41: 6–9) from the Sappington Formation (earliest Mississippian) of Western Montana, USA in general character of shell ornamentation. The specimens described here attained smaller shell dimensions and have somewhat less closely spaced costellae.

Nematocrania pilea sp. nov. differs from *Deliella delie* Halamski, 2004 from the Late Eifelian of the Holy Cross Mountains (Poland) in having widely spaced costellae, whereas the latter is characterized by dense parvicostellate ornamentation (see Halamski 2004). A single dorsal valve

← Fig. 5. Linguliform and craniiform brachiopods from the Muhua Formation. **A**, **B**. *Langella* sp. **A**. Incomplete ventral valve, PKUM02-0189, in exterior (A_1) and interior (A_2). **B**. Dorsal valve, PKUM02-0190, in exterior (B_1) and interior (B_2) views. **C**. *Petrocrania*? sp., dorsal valve, PKUM02-0191, in exterior (C_1) and interior (C_2) views. **D**–**G**, **K**, **M**, **P**, **Q**. *Nematocrania pilea* sp. nov. **D**, **E**. Juvenile dorsal valves, PKUM02-0192 (**D**) and PKUM02-0193 (**E**), in exterior (D_1, E_1) and interior (D_2, E_2) views. **F**. Dorsal valve, PKUM02-0194, in exterior view (F_1) and enlargement (F_2) showing well preserved costellae interrupted by growth lamellae and terminating as spinous outgrowths. **G**. Well preserved dorsal valve, PKUM02-0195, in exterior view. **M**. Holotype (dorsal valve), PKUM02-0196, in exterior (M_1) and interior (M_2) views. **P**. Dorsal valve, PKUM02-0197, in exterior (P_1), lateral (P_2), and interior (P_3) views.**Q**. Damaged dorsal valve, PKUM02-0198, showing character of punctation at a fracture surface (Q_1) and from the interior (Q_2). **H**, **I**, **L**, **N**. *Nematocrania* sp. **H**. Dorsal valve, PKUM02-0199, in exterior view (H_1) and enlargement (H_2) showing details of ornamentation. **I**. Dorsal valve, PKUM02-0200, in exterior (I_1) and interior (I_2) views. **L**. Incomplete dorsal valve, PKUM02-0201, in exterior (L_1) and interior (L_2) views, showing large posterior adductor scars. **N**. Juvenile dorsal valve, PKUM02-0202, in exterior view. **J**. *Acanthocrania* sp., incomplete dorsal valve, PKUM02-0203, in exterior (J_1) and interior (J_2) views. **O**. *Orbiculoidea* sp., incomplete dorsal valve, PKUM02-0204, in exterior view (O_1) and enlargement of the larval shell (O_2). Samples MH1 (A), D4 (B), M2/4 (C), GB (D–K, M, Q), GT (P), and MH2 (L, O).

reported as *Acanthocrania* sp. and described from nearby locality at Muhua section (Baliński 1999) may be better assigned to *Nematocrania pilea*. This questionable juvenile specimen, measuring 2 mm in diameter, is poorly preserved but reveals rudiments of weak radial costellae at the valve periphery.

Stratigraphic and geographic range.—This is a rather rare species in samples GB, GT, and D4 collected near the Gedongguan and Daposhang localities. One questionable specimen come from sample Mu-42 from the section near Muhua village (see Baliński 1999).

Nematocrania sp.

Fig. 5H, I, L, N.

Material.—One complete and two fragmentary dorsal valves.

Remarks.—Similar to *N. pilea*, the specimens described here are characterized by having radial costellate ornamentation. However, the costellae of *Nematocrania* sp. are different being closely spaced and separated by very narrow, albeit very deep furrows. The costellae are high and rounded in cross section causing them to seem slightly narrower at the base and wider at the mid-height. Tops of the costellae are transversely crenulated. They increase in number by very rare intercalations and branching, attaining up to 88–92 in total (in *N. pilea* there are 27–57 costellae). There is no evidence of a presence of spinous projections or disruption of the costellae by the growth lamellae in *Nematocrania* sp. Most probably the specimens described here represent new species but the material is inadequate to warrant a full description.

Stratigraphic and geographic range.—All three specimens were found in sample GB which was collected at Gedongguan locality.

Genus *Acanthocrania* Williams, 1943

Type species: *Crania spiculata* Rowley, 1908; Louisiana Limestone, Mississippian; Buffalo Creek, Louisiana, USA.

Acanthocrania sp.

Fig. 5J.

Material.—One fragmentary dorsal valve.

Remarks.—Although the single specimen is poorly preserved, it shows quite satisfactory a characteristic elements of its external ornament. These are sublamellose, slightly irregular growth lines and fairly large, stout hollow spines of various diameters, rather loosely scattered at high angle to the valve surface. Internal surface of the valve is densely punctate. A pair of very large anterior adductor scars is situated near apex.

Because of incompleteness of the material the specimen here described cannot be compared with confidence to any known species. However, the character and distribution of spines is very reminiscent that of *Acanthocrania regularis* Cooper and Grant, 1974 from the Middle Permian (Capitanian) of Texas (see Cooper and Grant 1974: 244–255, pl. 30: 20–24).

Stratigraphic and geographic range.— The single specimen described here comes from sample GB.

Genus *Petrocrania* Raymond, 1911

Type species: *Craniella meduanensis* Oehlert, 1888; Lower Devonian; Ferques, France.

Petrocrania? sp.

Fig. 5C.

Material.—One almost complete dorsal valve.

Remarks.—The valve described here is 3 mm wide and 2.8 mm in long, subconical, subtrapezoidal in outline but slightly deformed anteriorly. Posterior margin is short and straight, lateral margins are indented posteriorly and broadly rounded anteriorly. Beak pointed, located less than one-third of valve length from the posterior margin. The surface seems to be partially worn off but ornamentation is evidently limited to weak concentric growth lines only. The interior shows evident punctation but fails to show details sufficient to determine the adductor scars. Absence of spines, radial ornament or lamellose exterior suggest that the specimen may represent *Petrocrania* but is not specifically definable.

Stratigraphic and geographic range.—This specimen was recovered from sample GB.

Craniidae gen. et sp. indet.

Fig. 6.

Material.—Four almost complete and four fragmentary dorsal valves.

Description.—Dorsal valve subpyramidal, with apex displaced posteriorly to centre, and subrectangular in outline; posterior margin nearly straight, long, almost equal the greatest width of the valve which is located near anterior margin. The valve is weakly sulcate from near the apical region and results in a weak median emargination of the anterior margin. Posterior face of the valve slightly concave, forms large subtriangular, steep area (Fig. $6A_3$). Flanks strongly compressed laterally at one-third of valve length from posterior, resulting in distinct indentation of the lateral margins. Internally, the lateral narrowing forms two symmetric bulges on which a pair of the anterior adductor scars are disposed (Fig. $6A_4$). Posterior adductor scars not discernible, limbus poorly developed.

External ornament dominated by very strong, thick, slightly irregular costellae which are elevated distally forming finger-like extensions at the periphery of the valve (Fig. $6A_4$, B_1, D). Anterolateral costellae are disposed in two bundles which fan out symmetrically on each valve flank (Fig. A_1, C, D_2). Concentric sublamellose ornamentation clearly visible in deep intercostal troughs (Fig. $6A_2$). Shell substance punctate (Fig. $6A_5$, A_6).

Remarks.—The exterior of the specimens is bizarre in their unusually strong external ornamentation (at least on some specimens; see Fig. 6A, D) and strongly indented lateral margins. These features distinguish the Chinese form from all

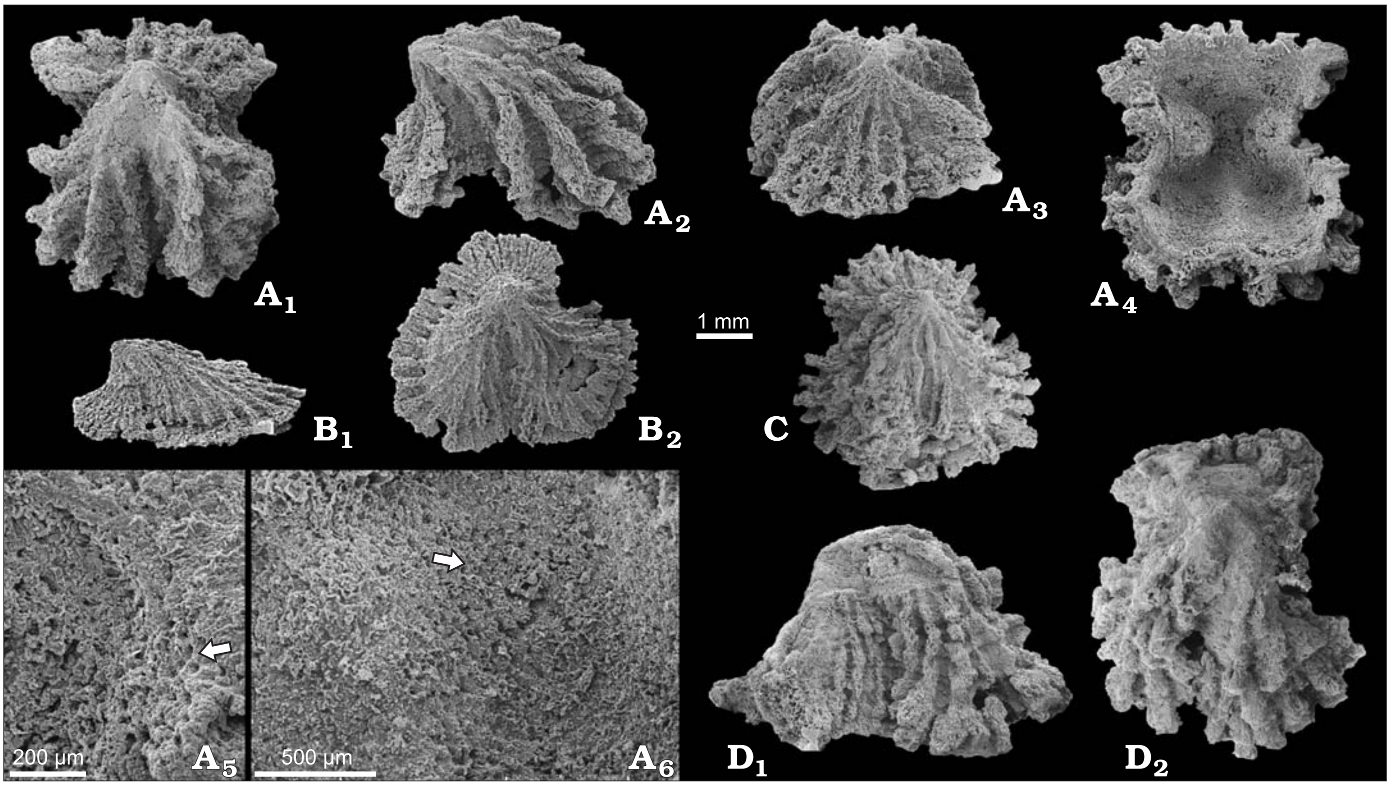


Fig. 6. Craniidae gen. et sp. indet. from the Muhua Formation. **A**. Dorsal valve, PKUM02-0205, in exterior (A_1), lateral (A_2), posterior (A_3), and interior (A_4) views, and enlargements of the internal surface of the same specimen (A_5, A_6) showing poorly preserved shell punctation (arrowed). **B**, **D**. Dorsal valves, PKUM02-0206 (**B**) and PKUM02-0207(**D**), in lateral (B_1, D_1) and dorsal (B_2, D_2) views. **C**. Dorsal valve, PKUM02-0208, in exterior view. Sample MH1.

other craniids known to us. However, the subconical to subpyramidal general aspect, the presence of characteristic muscle scars internally, and punctate shell structure strongly indicates that this is an unknown genus and species of craniid brachiopods. However, insufficient material does not allow for a satisfactory taxonomic diagnosis.

The unusually strong radial costellae arise as rows of fused long extensions formed at valve periphery by radial finger-like appendages of the mantle margin. The costellae are not hollowed but solid and thus strengthened the valve as a probable adaptation to a turbulent environment. Although the specimens studied show a distinct variability in the density of the costellae, they seem to represent one species, as could be ascertained from the same characteristic distribution of the flank costellae, which are grouped in two symmetrical bundles (Fig. 6A_1, B_2, C).

Stratigraphic and geographic range.—This form is known only from sample MH1.

Subphylum Rhynchonelliformea Williams, Carlson, Brunton, and Popov, 1996

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

Order Strophomenida Öpik, 1934

Superfamily Strophomenoidea King, 1846

Family Rafinesquinidae Schuchert, 1893

Subfamily Leptaeninae Hall and Clarke, 1984

Genus *Leptagonia* M'Coy, 1844

Type species: *Producta analoga* Phillips, 1836; Carboniferous Limestone, Viséan, Carboniferous; Yorkshire, England.

Leptagonia cf. *analoga* (Phillips, 1836)

Fig. 7.

cf. 1836 *Producta analoga* Phillips; Phillips 1836: 215, pl. 7: 10.

cf. 1968 *Leptagonia analoga* (Phillips); Brunton 1968: 29–31, pl. 3: 26, 27.

1999 *Leptagonia analoga* (Phillips, 1836); Baliński 1999: 441, fig. 3F, G.

Material.—Over 20 specimens, all are fragmentary single valves.

Remarks.—This is a relatively rare species in the fauna from the Muhua Formation. As in the majority of other forms in the fauna, the species is represented by fragmentary disarticulated valves. Even thick-shelled large individuals are broken indicating high hydrodynamic activity prior to burial.

Externally the visceral region is covered with quite regular concentric rugae and rounded, rather weak radial costae. There are about 6–7 costae in 2 mm measured at 10 mm distance from valve beak. Inside ventral valves there are low dental plates which are continuous with the lateral edges of the wide, circular muscle platform. The platform is clearly elevated above valve floor laterally, but rather low in its

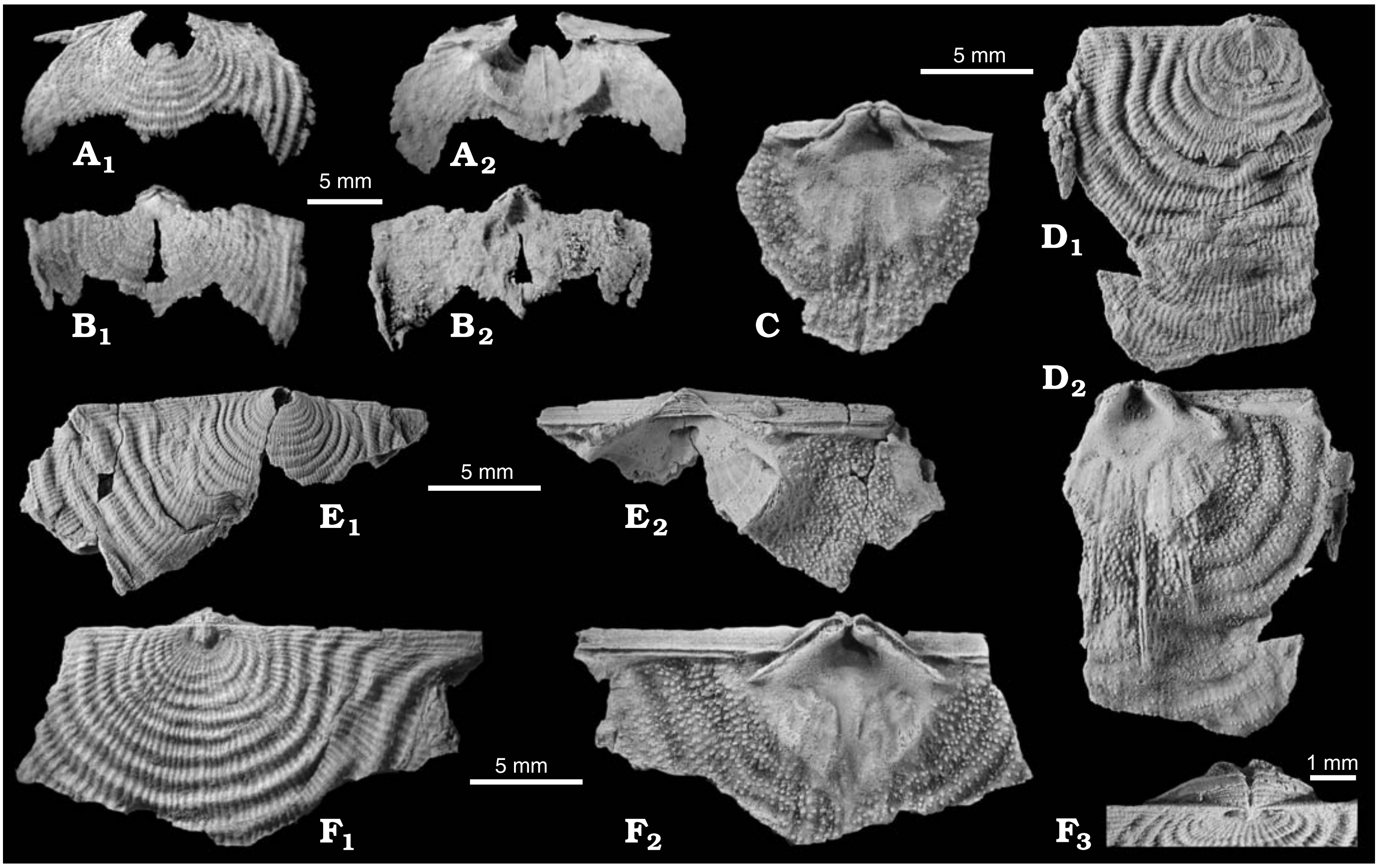


Fig. 7. Strophomenoid brachiopod *Leptagonia* cf. *analoga* (Phillips, 1836) from the Muhua Formation. **A**, **E**. Incomplete ventral valves, PKUM02-0209 (**A**) and PKUM02-0210 (**E**), in exterior (A_1, E_1) and interior (A_2, E_2) views. **B**–**D**. Incomplete dorsal valves, PKUM02-0211 (**B**), PKUM02-0212 (**C**), and ZPAL V. 26/6 (**D**), in exterior (B_1, C_1, D_1) and interior (B_2, D_2) views. **F**. Incomplete dorsal valve, PKUM02-0213, in exterior (F_1), interior (F_2), and enlarged postero-dorsal (F_3) views; notice massive chilidium. Samples MH1 (A, B), GB (E), GT (C, F), and Mu-42 (D; figured in Baliński 1999: fig. 3F, G).

antero-median region. The umbonal region of the ventral valve is pierced by a quite large pedicle foramen, which is clearly seen both internally and externally (Fig. 7E). The interior of the dorsal valve is well seen in three incomplete specimens from samples GT and Mu-42 (Fig. 7C, D, F). Their cardinal process and muscle scars are reminiscent those illustrated by Brunton (1968: pl. 4: 7; text-fig. 9) in juvenile dorsal valve of *Leptagonia analoga* from D zone of County Fermanagh, Northern Ireland. Several specimens of *L. analoga* from Redesdale (Northumberland, England) illustrated by Brunton (1968: pl. 3: 28, pl. 4: 2) were attributed by Brand (1972) to his new species *Leptagonia caledonica* Brand, 1972, which occurs in Britain in the Viséan and basal Namurian. Generally, the specimens from the Muhua Formation resemble *L. analoga* in the shape of valves and external ornamentation as well as in details of the internal structure. The broken material, however, precludes more definite taxonomic identification.

Stratigraphic and geographic range.—This species was found in samples GB, GT, MH1, and Mu-42. According to Brand (1972) *L. analoga* occurs in England, Ireland, and Wales in Tournaisian and early Viséan strata. In China, *L. analoga* was described from Anhui and Jiangsu (Wang et al. 1982), Hunan (Tan 1987), Guangxi (Yang et al. 1977; Xu and Yao 1988), and Sichuan (Tong 1978) provinces. Furthermore, the species was mentioned also in Hubei Province by Xu (1984).

Order Productida Sarytcheva and Skolskaya, 1959
Suborder Chonetidina Muir-Wood, 1955
Superfamily Chonetoidea Bronn, 1862
Family Anopliidae Muir-Wood, 1962
Subfamily Caenanopliinae Archbold, 1980
Genus *Subglobosochonetes* Afanasjeva, 1976

Type species: *Chonetes* (*Rugosochonetes*) *malevkensis* Sokolskaja, 1950; Tournaisian, Carboniferous; Krasnoye, East European Platform, Russia.

Subglobosochonetes gedongguanensis sp. nov.

Fig. 8.

Etymology: Named after the type locality.

Holotype: PKUM02-0218, complete shell illustrated in Fig. 8H.

Type locality: G site, about 20 m west to Gedongguan village, Muhua (Guizhou province, South China).

Type horizon: Middle of the upper part of the Muhua Formation, correlated with the middle Tournaisian, *Siphonodella crenulata* Zone.

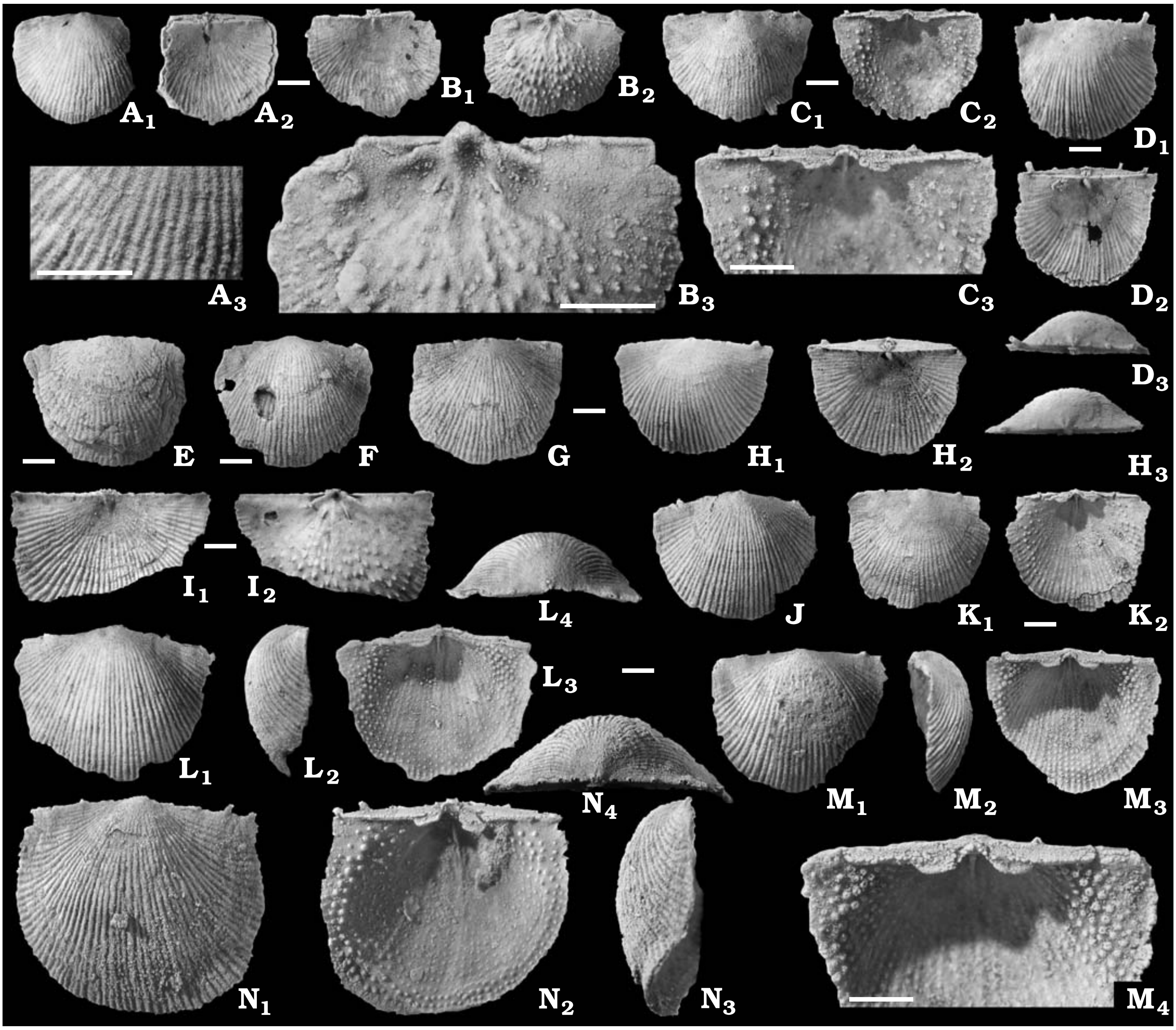


Fig. 8. Chonetoid brachiopod *Subglobosochonetes gedongguanensis* sp. nov. from the Muhua Formation. **A**. Shell, PKUM02-0214, in ventral (A_1) and dorsal (A_2) views. **B**. Dorsal valve, PKUM02-0215, in exterior (B_1), interior (B_2), and enlarged interior (B_3) views. **C**. Ventral valve, PKUM02-0216, in exterior (C_1), interior (C_2), and enlarged interior (C_3) views. **D**, **H**. Shells, PKUM02-0217 (**D**) and PKUM02-0218 (**H**, holotype), in ventral (D_1, H_1), dorsal (D_2, H_2), and posterior (D_3, H_3) views. **E**–**G**, **J**. Shells, PKUM02-0219 (**E**), PKUM02-0220 (**F**), PKUM02-0221 (**G**), and PKUM02-0222 (**J**), in ventral views. **I**. Incomplete dorsal valve, PKUM02-0223, in exterior (I_1) and interior (I_2) views. **K**. Ventral valve, PKUM02-0224, in exterior (K_1) and interior (K_2) views. **L**. Ventral valve, PKUM02-0225, in exterior (L_1), lateral (L_2), interior (L_3), and posterior (L_4) views. **M**. Ventral valve, PKUM02-0226, in exterior (M_1), lateral (M_2), interior (M_3), and enlarged interior (M_4) views. **N**. Ventral valve, PKUM02-0227, in exterior (N_1), interior (N_2), lateral (N_3), and posterior (N_4) views. Samples GB and GT. Scale bars 1 mm.

Diagnosis.—*Subglobosochonetes* with rounded sub-triangular to semicircular shell outline, well differentiated small ears and relatively fine radial ornamentation of six to seven costellae per mm at 3 mm in distance from the beak. Two to four pairs of spines symmetrically arranged and orthomorph oblique at about 75°; anderidia anteriorly divergent at 56–60°.

Material.—Eleven complete to slightly damaged shells, 2 dorsal, and 12 ventral valves.

Description.—Shell small in size, generally attaining 4–6 mm (occasionally over 7 mm) in width and 3.5–7 mm in length, rounded sub-triangular to semicircular in outline, slightly wider than long, with length/width ratio 0.83–0.90, greatest width at the hinge line; cardinal extremities subangular with small, poorly defined and slightly concave ears; concavo-convex in lateral profile; two to four pairs of spines symmetrically arranged and orthomorph oblique at about 75°; shell surface smooth in the posterior region at 1–1.5 mm from the beak, anteriorly with round radial costellae commonly increasing by branching on ventral valve and intercalation on dorsal valve, interspaces narrower than width of costellae, six to seven costellae per mm at 3 mm distance from the beak and 5–6.5 near mid-anterior margin; concentric growth lines very fine, evenly and closely spaced.

Ventral valve strongly and evenly convex in lateral profile, the greatest convexity occurring in the umbonal region; convexity exceeds one-third of the valve length; small elongate protegular pit evident near the beak; ventral interarea flat, apsacline to orthocline, with small apical pseudodeltidium (Fig. $8C_3$, M_4).

Dorsal valve deeply concave posteriorly with gradually decreasing curvature to the anterior and lateral margins; dorsal interarea hypercline with small chilidium; elongate protegular node prominent on the dorsal beak (Fig. $8A_2$, B_1).

Ventral valve interior with short, plate-like teeth, subparallel to hinge line (Fig. $8C_3$, M_4); median septum high, short, posteriorly confined, but commonly extends anteriorly as low ridge for less than one-fourth of the valve length; adductor scars indistinct; endospines radially arranged in rows corresponding to interspaces of costellae, frequently confined to valve marginal area, especially strong on lateral flanks (Fig. $8L_3$).

Interior of dorsal valve with small, bilobate, posteriorly directed cardinal process, anteriorly with deep and large cardinal process pit; inner socket ridges slender, straight, anteriorly divergent at 120–130°; anderidia long, narrow, anteriorly divergent usually at 56–60° (Fig. $8B_3$, I_2); median septum and accessory septa not present; endospines radially arranged, prominent at middle-anterior sector of the valve.

Remarks.— The general external morphology of the new species is very similar to *Globosochonetes* Brunton, 1966, but the dorsal valve interior of the new species is without median septum and accessory septa, and is thus more similar to *Caenanoplia* Carter, 1967 and *Subglobosochonetes* Afanasjeva, 1976. However, *Caenanoplia* has weak rounded costellae while those in our new species are well marked.

The new species differs from the type species of the genus, i.e., *Subglobosochonetes malevkensis* (Sokolskaja, 1950) from Tournaisian of the East European Platform (Russia) by having less transverse shell outline, finer radial ornamentation, larger divergent angle of the anderidia and much shorter ventral median septum (above one-half in *S. malevkensis*; see Sokolskaja 1950, Afanasjeva 1976).

Subglobosochonetes gedongguanensis sp. nov. is similar in shell shape to some adult specimens of *Subglobosochonetes* cf. *malevkensis* (Sokolskaja, 1950) described below. The former, however, is characterized by more rounded and less wide shell outline, while the latter is evidently wider than long, has more rectangular shell outline (especially juveniles), and less concave dorsal valve.

S. gedongguanensis sp. nov. is very similar externally to *S. norquayensis* Carter, 1987 from Tournaisian of Western Alberta, Canada, especially in a general shell outline, dimensions, and its ornamentation (see Carter 1987). It seems, however, that the Canadian species has much shorter ventral interarea and in consequence less angular, nearly straight posterior margin of the ventral valve. The new species is also more elongate and has a shorter ventral median septum and narrowly divergent anderidia in comparison to *S. jerseyensis* Carter, 1988 described from the Glen Park Formation of Missouri (Carter 1988). From *S. acutiliratus* (Girty, 1928) of the Price Formation (Mississippian) of the United States (see Carter and Kammer 1990) the Chinese species is slightly smaller, more elongate, and has fewer costellae. Moreover, the costellae are subangular in the former but rounded in the latter species. Internally, *S. gedongguanensis* sp. nov. differs in lacking accessory septa in the dorsal valve. From *Caenanoplia martinezi* Martinez-Chacon and Winkler Prins, 1977 [= *Caenanoplia* (*Subglobosochonetes*) *martinezi* according to Martinez-Chacon and Winkler Prins 1993] described from the Namurian of Spain (Martinez-Chacon and Winkler Prins 1977) the new species differs in being more strongly concavo-convex, having a longer shell and stronger but finer costellation.

Stratigraphic and geographic range.—This species was found only in samples GB and GT.

Subglobosochonetes cf. *malevkensis* (Sokolskaja, 1950)

Fig. 9.

cf. 1950 *Chonetes* (*Rugosochonetes*) *malevkensis* sp. nov.; Sokolskaja 1950: 23–27, pl. 1: 1–16, figs. 10–11.

cf. 1976 *Subglobosochonetes* cf. *malevkensis* (Sokolskaja); Afanasjeva 1976: 68–69, pl. 5: 4.

Material.—Nine complete to slightly fragmented shells, 29 dorsal and 49 ventral valves.

Description.—Shell small to medium in size for genus, subquadrate in outline, attaining 5–9 mm in width and 4–6.8 mm in length, with length:width ratio 0.72–0.80; greatest width near the hinge line; cardinal extremities subangular with poorly differentiated small ears; concavo-convex in lateral profile, about one-fourth as deep as long; three to four pairs of orthomorph oblique spines symmetrically arranged at an angle varying 48–58° from the hinge line; shell surface smooth for the first 1 to 1.5 mm from the beaks and anteriorly with round radial costellae that increase mainly by bifurcation on ventral valve and intercalation on dorsal valve; there are 5–6 costellae per mm at 3 mm distance from ventral beak and 3.5–5.5 near mid-anterior margin; interspaces narrower than width of costellae; concentric growth lines very fine, evenly and closely spaced.

Ventral valve moderately convex, the greatest convexity in the umbonal region, attaining about one-fourth of valve length; small elongate protegular pit evident near the beak; ventral interarea flat, apsacline, with small pseudodeltidium.

Dorsal valve slightly concave; dorsal interarea hypercline with small chilidium; elongate protegular node prominent on the dorsal beak (Fig. 9A, B, G, H_1).

Ventral valve interior with short, plate-like teeth that are subparallel to hinge line; median septum high, posteriorly confined but commonly extended anteriorly as low ridge for about one-fifth of valve length; adductor scars indistinct; endospines confined to marginal sector of the valve, the

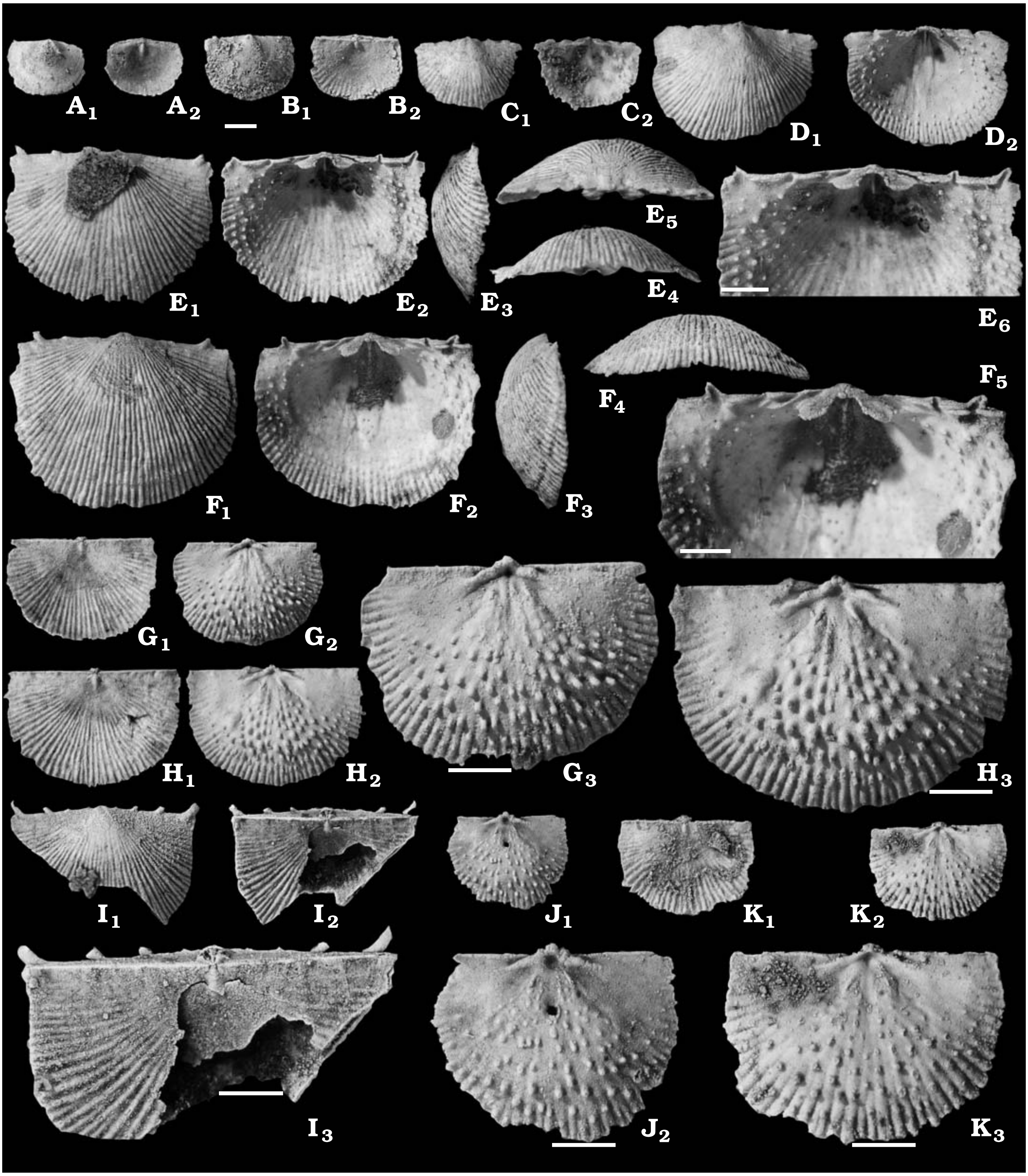


Fig. 9. Chonetoid brachiopod *Subglobosochonetes* cf. *malevkensis* (Sokolskaja, 1950) from the Muhua Formation. **A**, **B**. Shells, PKUM02-0228 (**A**) and PKUM02--0229 (**B**) in ventral (A_1, B_1) and dorsal (A_2, B_2) views. **C**, **D**. Ventral valves, PKUM02-0230 (**C**) and PKUM02-0231 (**D**), in exterior (C_1, D_1) and interior (C_2, D_2) views. **E**. Ventral valve, PKUM02-0232, in exterior (E_1), interior (E_2), lateral (E_3), anterior (E_4), posterior (E_5), and enlarged interior (E_6) views. **F**. Ventral valve, PKUM02-0233, in exterior (F_1), interior (F_2), lateral (F_3), anterior (F_4), and enlarged interior (E_5) views. **G**, **H**, **K**. Dorsal valves, PKUM02-0234 (**G**), PKUM02-0235 (**H**), and PKUM02-0236 (**K**), in exterior (G_1, H_1, K_1), interior (G_2, H_2, K_2), and enlarged interior (G_3, H_3, K_3) views. **I**. Incomplete shell, PKUM02-0237, in ventral (I_1), dorsal (I_2), and enlarged dorsal (I_3) views. **J**. Dorsal valve, PKUM02-0238, in interior view (J_1) and enlargement (J_2). Samples M2/2 and M2/4 (A–H), M2-8 (I), M2/3 (J, K). Scale bars 1 mm.

strongest near ears, arranged in radial rows corresponding to interspaces of costellae.

Dorsal interior with small, bilobate, posteriorly directed cardinal process, which bears anteriorly a deep and large pit; inner socket ridges slender, straight, or slightly curved, anteriorly divergent at 118–130°; anderidia long, narrow, anteriorly divergent at 50–54°; median septum and accessory septa absent; endospines radially arranged, prominent in middle and anterior sectors of valve (Fig. 9G_3, H_3).

Remarks.—The studied specimens are similar to *Subglobosochonetes malevkensis* in shell outline and ornamentation. There are small differences in the length/width ratio and the angle of divergence of the anderidia, which is slightly greater in the Chinese specimens. *S. malevkensis* differs also in possessing a more inflated posterior region of the ventral valve. See *Subglobosochonetes gedongguanensis* sp. nov. for comparison with that species.

Although the external outline and ornamentation of the Chinese specimens are very similar to those of most species of *Rugosochonetes*, the lack of median septum in the dorsal valve may exclude the possibility that the species is a rugosochonetid.

Subglobosochonetes cf. *malevkensis* is similar in general outline of the shell to *S. acutiliratus* (Girty, 1928) described from the Price Formation by Carter and Kammer (1990). The species from the Muhua Formation can be differentiated by its smaller size, more closely spaced and rounded costellae, and absence of dorsal accessory septa. It also differs from *S. jerseyensis* Carter, 1988 in having more regular shell costellation and in lacking accessory septa and brachial ridges (see Carter 1988).

Stratigraphic and geographic range.—The species has been recovered from sample MH1, M2-8, M2/2, M2/3, M2/4, and D4. *Subglobosochonetes malevkensis* is known from the Tournaisian of the East European Platform, Russia (Sokolskaja 1950; Afanasjeva 1976).

Genus *Globosochonetes* Brunton, 1968

Type species: *Globosochonetes perseptus* Brunton, 1968; Viséan, Carboniferous; Fermanagh, Northern Ireland.

Globosochonetes gracilis sp. nov.

Fig. 10.

Etymology: From the Latin *gracile*, meaning "slender" or "lean"; referring to the fine costellation of the shell.

Holotype: PKUM02-0240, an almost complete shell illustrated in Fig. 10B.

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

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

Diagnosis.—*Globosochonetes* with semicircular shell outline, ventral umbo not prominent, and fine radial ornamentation with density of 8–10 costellae per mm near mid-anterior margin; two to four pairs of orthomorph oblique spines inclined at 53–80° to hinge line. Anderidia divergent at 61–78°.

Material.—Twenty-five complete or fragmented shells, 18 dorsal and 35 ventral valves.

Description.—Shell small in size, attaining 4–5.7 mm in width and 3.5–5 mm in length, semicircular in outline, slightly wider than long, with length/width ratio 0.82–0.90, greatest width at the hinge line; ears small and poorly defined; concavo-convex in lateral profile; two to four pairs of orthomorph oblique spines usually asymmetrically arranged, but on some rare specimens they seem to be more or less symmetrical (compare Brunton 1968: figs. 36–39); spines extend at 53–80° to hinge line; shell surface with fine radial costellae which increase by branching on ventral and intercalation on dorsal valve; eight to ten costellae per mm near mid-anterior margin.

Ventral valve strongly and evenly convex in lateral profile, the greatest convexity in the umbonal region, attaining a depth of over one-third of valve length; small elongate protegular pit evident near the beak; ventral interarea flat, orthocline to anacline with small pseudodeltidium.

Dorsal valve deeply concave posteriorly with gradually decreasing curvature to the anterior and lateral margins; dorsal interarea hypercline, with small chilidium; elongate protegular node prominent on the dorsal beak.

Ventral valve interior with short, plate-like teeth, subparallel to hinge line; median septum high, confined to umbonal region, usually continues anteriorly as low ridge for less than one-fourth of valve length; adductor scars indistinct; endospines confined to periphery of valve area, arranged in radial rows corresponding to intercostal spaces.

Dorsal interior with small, bilobate cardinal process, posteriorly directed, anteriorly with deep but small alveolus; inner socket ridges slender and straight or slightly curved, divergent anteriorly at 141–160°; median septum absent; endospines radially arranged, strongest in central region lateral to the accessory septa; accessory septa divergent anteriorly at 21–30°, formed by two rows of enlarged endospines increasing in size anteriorly; anderidia long, narrow, divergent anteriorly at 60–78° (Fig. 10I).

Remarks.—The new species is similar to the type species of the genus, i.e., *Globosochonetes parseptus* Brunton, 1968 in size and shape of the shell (see Brunton 1968). The former differs mainly in having much finer radial costellae and less inflated ventral umbo. Furthermore, the anderidia of the new species diverge from each other at 60–78°, while in *G. parseptus* they are divergent at 90°. It is also noteworthy that short dorsal median septum (breviseptum) reported in gerontic specimens of *G. parseptus* (Brunton 1968: 49) is not observed in specimens from Muhua.

Previously, only one species, *G. zhongnanensis* Yang, 1984, was reported from South China (Yang 1984). Its dorsal accessory septa are plate-like, and diverge anteriorly at 6–20° while in the new species here described the dorsal accessory septa are ridge like and diverge at 27–30°. The former attains larger shell size and more transverse outline.

Stratigraphic and geographic range.—*Globosochonetes gracilis* sp. nov. was found in samples GB and GT.

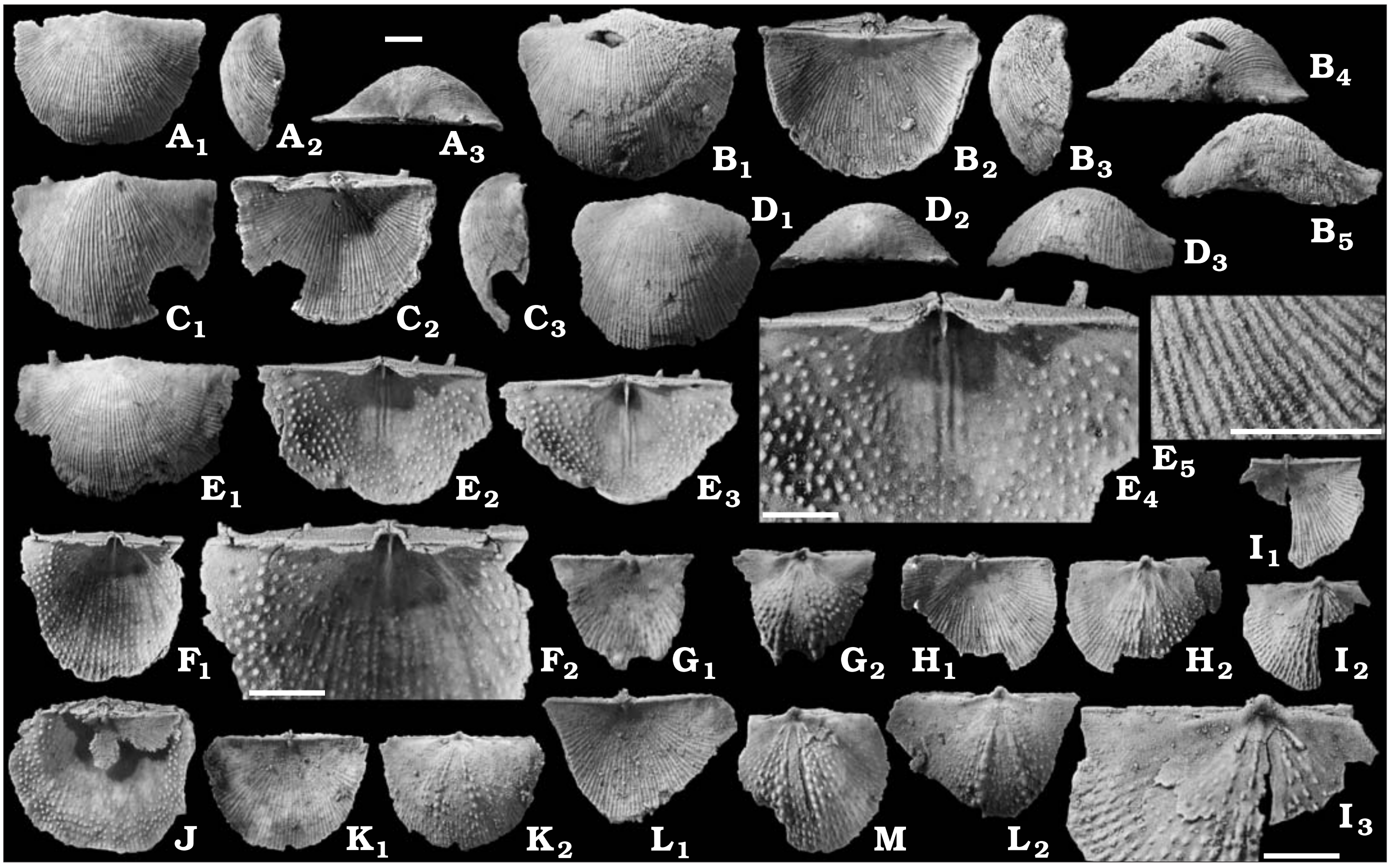


Fig. 10. Chonetoid brachiopod *Globosochonetes gracilis* sp. nov. from the Muhua Formation. **A**. Ventral valve, PKUM02-0239, in exterior (A_1), lateral (A_2), and posterior (A_3) views. **B**. Holotype, PKUM02-0240, in ventral (B_1), dorsal (B_2), lateral (B_3), posterior (B_4), and anterior (B_5) views. **C**. Shell, PKUM02-0241, in ventral (C_1), dorsal (C_2), and lateral (C_3) views. **D**. Shell, PKUM02-0242, in ventral (D_1), posterior (D_2), and anterior (D_3) views. **E**. Ventral valve, PKUM02-0243, in exterior (E_1), interior (E_2), anterodorsal (E_3), and enlarged interior (E_4) views, and enlargement showing external ornamentation (E_5). **F**. Ventral valve, PKUM02-0244, in interior view (F_1) and enlargement (F_2). **G**, **H**, **K**, **L**. Dorsal valves, PKUM02-0245 (**G**), PKUM02-0246 (**H**), PKUM02-0247 (**K**), and PKUM02-0248 (**L**), in exterior (G_1, H_1, K_1, L_1) and interior (G_2, H_2, K_2, L_2) views. **I**. Dorsal valve, PKUM02-0249, in exterior (I_1), interior (I_2), and enlarged interior (I_3) views. **J**. Shell with almost removed dorsal valve, PKUM02-0250, in dorsal view. **M**. Dorsal valve, PKUM02-0251, in interior view. Samples GB and GT. Scale bars 1 mm.

Globosochonetes sp.

Fig. 11.

Material.—One almost complete shell, 1 incomplete dorsal valve and 3 slightly broken ventral valves.

Description.—Small to medium in size, attaining 4–9.7 mm in width and 3.5–7.7 mm in length, semicircular in outline, slightly wider than long, with length:width ratio 0.73–0.80, greatest width near the hinge line; ears small and poorly developed; concavo-convex in lateral profile. Traces of three pairs of spines can be observed in one ventral valve, symmetrically arranged at an angle probably of less than 30° to hinge line. Shell surface with faint and fine radial costellae which increase by branching on ventral and intercalation on dorsal valve; seven costellae per mm at 3 mm distance from the ventral beak and 5.5–7 near mid-anterior margin.

Ventral valve moderately and evenly convex in lateral profile, the greatest convexity at one-third of valve length from the ventral beak; ventral interarea narrow, apsacline to orthocline with small pseudodeltidium.

Dorsal valve slightly concave posteriorly with gradually decreasing curvature to the anterior and lateral margins; dorsal interarea linear, hypercline; elongate protegular node prominent on the dorsal beak.

Teeth in the ventral valve not observed due to the preservation; short, probably high posteriorly ventral median septum is observed in one specimen; adductor scars indistinct; endospines very small and indistinct, confined to periphery of valve, arranged in radial rows corresponding to intercostal spaces.

Dorsal interior with small, bilobate trifid cardinal process, posteriorly directed, anteriorly with weak pit; inner socket ridges relatively weakly developed with only slight curvature and divergent anteriorly at 125–130°; anderidia not clear; median septum absent; a pair of accessory septa long and plate-like, divergent anteriorly at about 15°; endospines fine, evident in region lateral to the accessory septa.

Remarks.—The specimens here described are characterized by a weakly costellate external ornamentation with 7 costellae per mm at 3 mm distance from ventral beak, less concave lat-

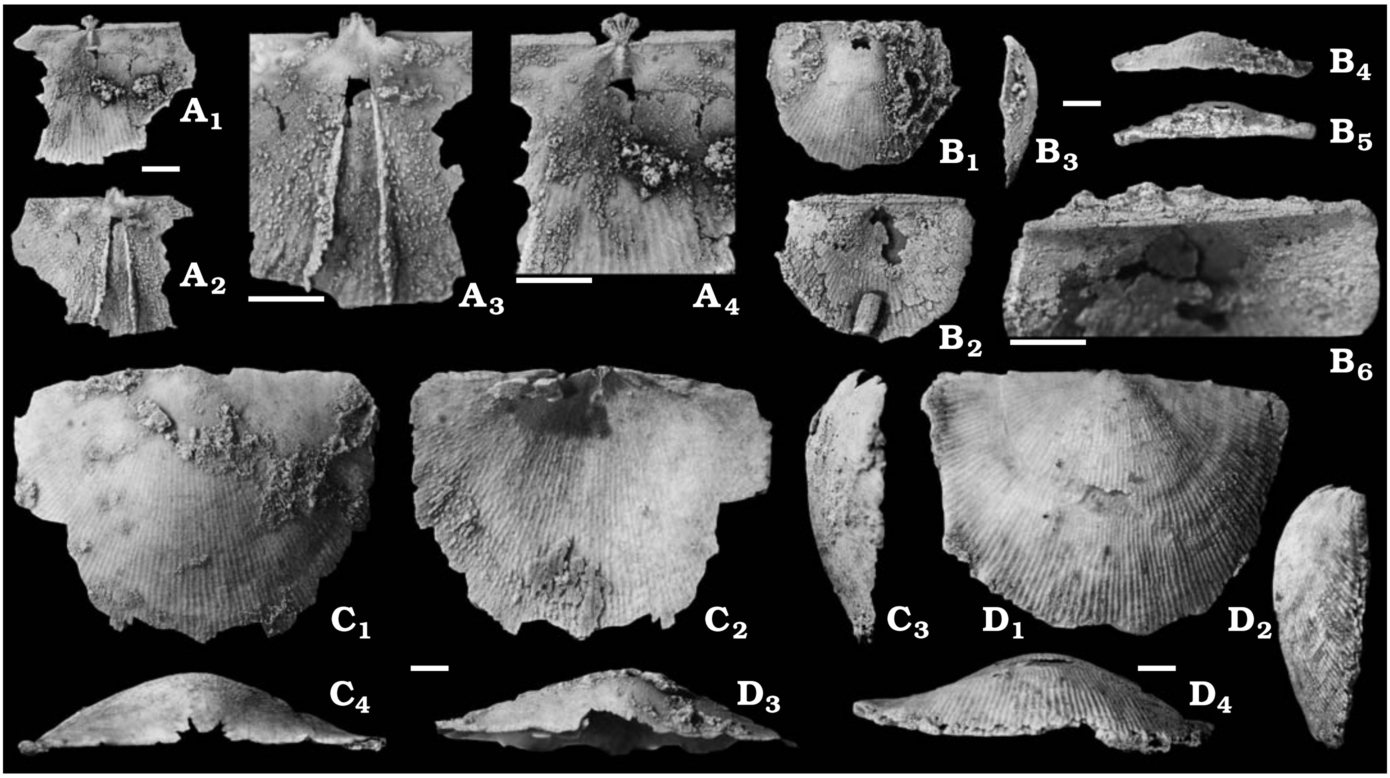


Fig. 11. Chonetoid brachiopod *Globosochonetes* sp. from the Muhua Formation. **A**. Incomplete dorsal valve, PKUM02-0252, in exterior (A_1), interior (A_2), enlarged interior (A_3), and enlarged exterior (A_4) views. **B**. Shell, PKUM02-0253, in ventral (B_1), dorsal (B_2), lateral (B_3), anterior (B_4), posterior (B_5), and enlarged dorsal (B_6) views. **C**. Incomplete ventral valve, PKUM02-0254, in exterior (C_1), interior (C_2), lateral (C_3), and posterior (C_4) views. **D**. Ventral valve, PKUM02-0255, in exterior (D_1), lateral (D_2), posterior (D_3), and anterior (D_4) views. Sample MH1. Scale bars 1 mm.

eral profile, relatively large shell size, large cardinal process without or with very weak pit, and a pair of long and high, plate-like accessory septa. The assignment of this material to the genus *Globsochonetes* is based mainly on shell outline and internal structures of the dorsal valve. It differs, however, from *Globosochonetes gracilis* sp. nov. described above, as well as from other species of the genus by having relatively faint radial costellae and by the absence of well developed cardinal process pit, as well as large shell size and less convex lateral profile. The current material may represent a new form of the genus but more material is needed to describe it satisfactory.

Stratigraphic and geographic range.—It was found in sample MH1 taken at the base of the Muhua Formation.

Family Rugosochonetidae Muir-Wood, 1962

Genus *Rugosochonetes* Sokolskaja, 1950

Type species: *Orthis hardrensis* Phillips, 1841; Viséan, Carboniferous; Yorkshire, England.

Rugosochonetes cf. *celticus* Muir-Wood, 1962

Figs. 12, 13E.

cf. 1962 *Rugosochonetes celticus* sp. nov.; Muir-Wood 1962: 68–70 (partim); pl. 7: 3–5, 7, 8; text-fig. 24; [pl. 6: 8, 9; pl. 7: 6, 10–14 = *R. speciosus* (Cope, 1938)].

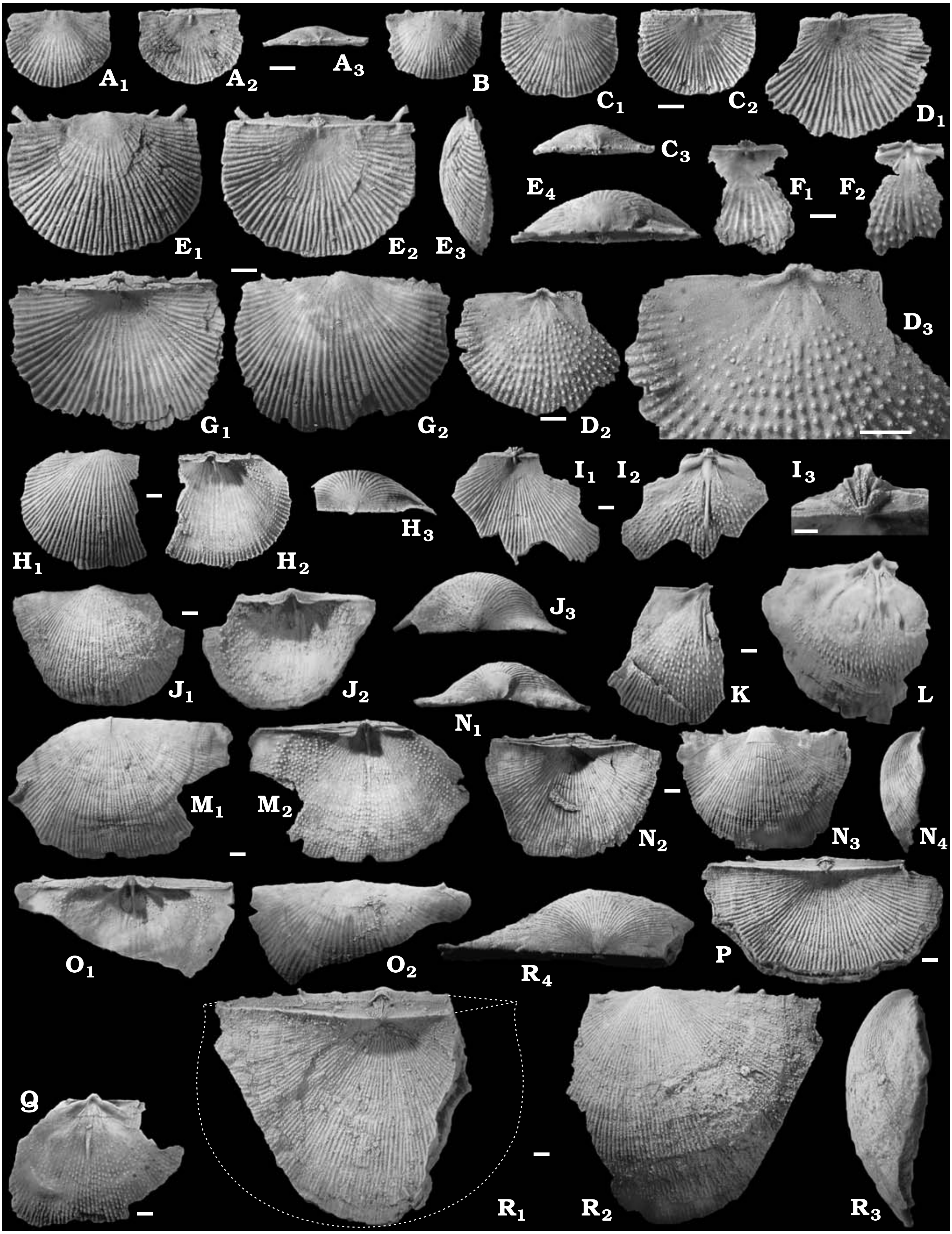
cf. 1968 *Rugosochonetes celticus* Muir-Wood; Brunton 1968: pl. 7: 28–30; pl. 8: 1–9.

cf. 1970 *Rugosochonetes celticus* Muir-Wood; Brand 1970: 108–111; pl. 10: 12–20; pl. 13: 5, 6, 9.

Material.—Thirty-seven complete and damaged shells, 32 broken dorsal and 67 broken ventral valves.

Description.—Shell medium to large in size for the genus; the estimated width and length of the largest broken specimen is about 25 mm and 16 mm, respectively; subelliptical to

Fig. 12. Chonetoid brachiopod *Rugosochonetes* cf. *celticus* Muir-Wood, 1962 from the Muhua Formation. **A**, **C**. Juvenile shells, PKUM02-0256 (**A**) and PKUM02-0257 (**C**), in ventral (A_1, C_1), dorsal (A_2, C_2), and posterior (A_3, C_3) views. **B**. Juvenile shell, PKUM02-0258, in ventral view. **D**. Incomplete dorsal valve, PKUM02-0259, in exterior (D_1), interior (D_2), and enlarged interior (D_3) views. **E**. Shell, PKUM02-0260, in ventral (E_1), dorsal (E_2), lateral (E_3), and posterior (E_4) views. **F**. Incomplete dorsal valve, PKUM02-0261, in exterior (F_1) and interior (F_2) views. **G**. Shell, PKUM02-0262, in dorsal (G_1) and ventral (G_2) views . **H**, **J**. Ventral valves PKUM02-0263 (**H**) and PKUM02-0264 (**J**), in exterior (H_1, J_1), interior (H_2, J_2), and posterior (H_3, J_3) views. **I**. Incomplete dorsal valve, PKUM02-0265, in exterior (I_1), interior (I_2) views, and enlarged posterior view of cardinalia (I_3). **K**, **L**, **Q**. Incomplete dorsal valves, PKUM02-0266 (**K**), PKUM02-0267 (**L**), and PKUM02-0268 (**Q**), in interior views. **M**. Ventral valve, PKUM02-0269, in exterior (M_1) and interior (M_2) views. **N**. Shell, PKUM02-0270, in posterior (N_1), dorsal (N_2), ventral (N_3), and lateral (N_4) views. **O**. Incomplete ventral valve, PKUM02-0271, in interior (O_1) and exterior (O_2) views. **P**. Slightly damaged shell, PKUM02-0272, in dorsal view. **R**. Incomplete large shell, PKUM02-0273, in dorsal (R_1), ventral (R_2), lateral (R_3), and posterior (R_4) views. All from sample GB and GT. Scale bars 1 mm. →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subquadrate in outline with the greatest width near the hinge line in subquadrate forms and near the mid-length of the shell in subelliptical forms, and length:width ratio 0.67–0.76; cardinal extremities rounded to subangular, with poorly demarcated, small ears; concavo-convex in lateral profile, about one-fourth as deep as long; three to five pairs of orthomorph oblique, symmetrically arranged spines, inclined at 32–50° to the hinge line. Shell surface smooth over the first 1 to 2 mm of the beaks and anteriorly with round radial capillae that increase anteriorly mainly by bifurcation on ventral and by intercalation on dorsal valve; interspaces narrower than capillae, 3.5 to 5 capillae per mm at 3 mm distance from ventral beak and 3–5 (on one specimen exceptionally 6.5) near mid-anterior margin.

Ventral valve moderately to strongly convex with the greatest convexity occurring at about one-third of valve length from the beak, with depth about one-fifth to one-third of valve width; ventral interarea flat and orthocline, with small pseudodeltidium. Dorsal valve generally slightly concave to strongly concave; dorsal interarea hypercline with small chilidium; elongate protegular node prominent on the dorsal beak.

Ventral valve interior with short and plate-like teeth, subparallel to hinge line (Fig. 12M); median septum high, posteriorly confined but commonly extended anteriorly as low ridge for about one-fifth of valve length (Figs. 12M, 13E); adductor scars large and subovate; endospines confined to antero-lateral marginal area, radially arranged and correspond to intercapillary spaces.

Dorsal interior with bilobate, posteriorly directed, and externally narrowly confined quadrifid cardinal process (Fig. $12I_3$). Some specimens show a large and deep cardinal process pit; inner socket ridges straight or slightly curved (Figs. 12H, I, 13E), anteriorly divergent at 140–160°; anderidia long, narrow, anteriorly divergent at 57–65° (Fig. 13E); median septum ridge like, variable, becoming strong late in ontogeny; accessory septa absent; endospines radially and evenly arranged, prominent at central region of the visceral disc (Figs. 12D, 13E).

Remarks.—The specimens from the Muhua Formation seem to be closest to *Rugosochonetes celticus* described from the Carboniferous (Late Viséan to Early Namurian) of England, Scotland, and Ireland (Muir-Wood 1962: 69; Brunton 1968: pl. 8: 1–9; Brand 1970). As Muir-Wood (1962: 69) and Brunton (1968: 54–55) remarked, the species is quite variable as far as radial ribbing is concerned. The studied specimens are intermediate between fine- and coarse capillate morphotypes described by these authors. The only important difference between specimens described by Muir-Wood (1962) and those from China is the inclination of ventral spines which in the former attain 20–30° whereas in the latter the angle reaches 32–50° to the hinge line. On the other hand Brand (1970: 109) noted that on larger specimens of *R. celticus* examined by him the spine inclination varies from about 80° near the umbo to about 45° near the cardinal extremities (see also Brunton 1968: 56–57). It seems that specimens from China possesses more elongated teeth in comparison to triangular in *R. celticus* examined by Brand (1970: 108), but this difference is poorly discernible on the illustrated Scottish specimens.

The Chinese specimens can be distinguished readily from Tournaisian *R. distinctus* Afanasjeva, 1976, *R. sargensis* (Nalivkin, 1979), and Viséan *R. annae* Afanasjeva, 1976 of the East European Platform and the Urals by having coarser capillate shell ornament (see Sokolskaja 1950; Afanasjeva 1976; Nalivkin 1979). The specimens described here are similar externally to *Rugosochonetes chesterensis* (Weller, 1914) described from the Paint Creek Formation (Mississippian) of Illinois, USA (Weller 1914), but differ from the latter mainly in having less developed ears and coarser radial ornament.

The young specimens of this species are very similar to *Subglobosochonetes* cf. *malevkensis* described above in shell outline and ornamentation. However, the latter does not show any trace of the dorsal median septum and has relatively higher length/width ratio. Furthermore, the endospines in the dorsal valve seem to be more evenly and regularly disposed in *Rugosochonetes* cf. *celticus* than in *S.* cf. *malevkensis*.

Stratigraphic and geographic range.—*R. celticus* was described from Late Viséan–Early Namurian of North Wales, England, Scotland, and Ireland (Muir-Wood 1962). The form under consideration was found in the Muhua Formation in Samples GB, GT, M2/1, and Mu-42.

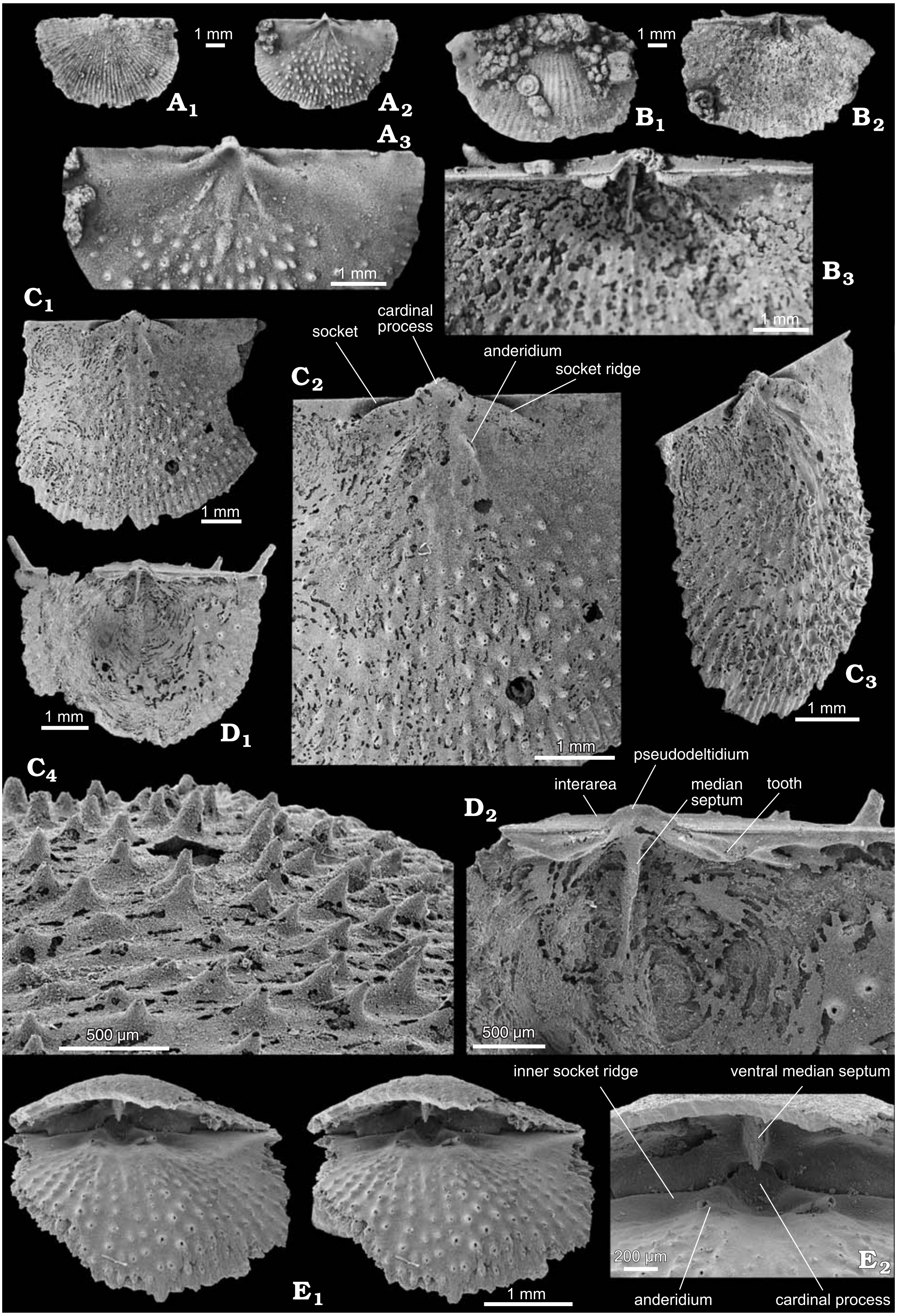
Rugosochonetes sp.

Fig. 13A, C, D.

Material.—One complete dorsal valve.

Remarks.—This single dorsal valve from sample M2-8 (Fig. 13A) is 7.4 mm wide and 5 mm long with subquadrate outline. It is flat to slightly concave anteriorly, and covered with radial capillae. There are 6 capillae per mm at 3 mm distance from dorsal beak. Internally the inner socket ridges are relatively short, anteriorly divergent from the hinge line at angle about 30°. Anderidia divergent anteriorly at about 65°. A rudimentary median septum can be seen slightly anterior to the anderidia. Prominent endospines are concentrated on the anterior median portion. It differs from *R.* cf.

Fig. 13. Chonetoids from the Muhua Formation. **A**. *Rugosochonetes* sp., dorsal valve from sample M2-8, PKUM02-0274, in exterior (A_1), interior (A_2), and enlarged interior (A_3) views. **B**. *Plicochonetes* sp., ventral valve from sample M2-8, PKUM02-0275, in exterior (B_1), interior (B_2), and enlarged interior (B_3) views. **C**, **D**. *Rugosochonetes* sp. from sample MH1. **C**. Slightly damaged dorsal valve, PKUM02-0276, in interior (C_1), enlarged interior showing cardinalia (C_2), and oblique lateral (C_3) views, and enlargement of the internal surface showing disposition of endospines (C_4). **D**. Interior of ventral valve, PKUM02-0277, in general (D_1) and enlarged (D_2) views showing details of main internal features. **E**. *Rugosochonetes* cf. *celticus* Muir-Wood, 1962 from sample GT, incomplete shell showing cardinalia, ZPAL V. 26/58, in anterior (E_1, stereomicrographs) and enlarged anterior (E_2) views. →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D2
E1
E2
1 mm
500 µm
200 µm
socket
cardinal process
anderidium
socket ridge
pseudodeltidium
interarea
median septum
tooth
inner socket ridge
ventral median septum
anderidium
cardinal process

celticus described above in having a dorsal valve with flat lateral profile, a slightly finer radial ornament, more anteriorly directed inner socket ridges, more posteriorly located rudimentary median septum, and more strongly developed endospines.

A few incomplete specimens found in sample MH1 also represent *Rugosochonetes* (see Fig. 13C, D) but differ from *R*. cf. *celticus* described above in having slightly finer radial capillae.

Stratigraphic and geographic range.—The single specimen referred here to the genus *Rugosochonetes* was recovered from M2-8, about 3.5 m above base of the Muhua Formation. Another form representing the genus was found in sample MH1.

Subfamily *Plicochonetinae* Sokolskaja, 1960

Genus *Plicochonetes* Paeckelmann, 1930

Type species: *Chonetes buchianus* de Koninck, 1843; Namurian, Carboniferous; Yorkshire, England.

Plicochonetes sp.

Fig. 13B.

Material.—One incomplete ventral valve.

Remarks.—The single specimen has a semicircular to subquadrate outline, medium convexity, flat orthocline ventral interarea preserving small traces of the pseudodeltidium along the edges of the triangular delthyrium. Externally there is rather coarse radial ornamentation with a density of 2 costae per mm at 3 mm distance from the ventral beak. Internally the teeth are transverse, plate-like, and subparallel to the hinge line. The ventral median septum is short. The specimens are here attributed to *Plicochonetes* mainly because of the rather coarse radial costae.

Stratigraphic and geographic range.—It was recovered from M2-8, about 3.5 m above base of the Muhua Formation.

Suborder Productidina Waagen, 1883

Superfamily Productoidea Gray, 1840

Family Productellidae Schuchert, 1929

Subfamily Productellinae Schuchert, 1929

Genus *Argentiproductus* Cooper and Muir-Wood, 1951

Type species: *Producta margaritacea* Phillips, 1836; Asbian, Carboniferous; northern Wales.

Argentiproductus margaritaceus (Phillips, 1836)

Figs. 14–16.

1836 *Producta margaritacea* Ph.; Phillips 1836: 215, pl. 8: 8.

1861 *Productus margaritacea* Phillips; Davidson 1861: 159, pl. 44: 5–8.

1960 *Argentiproductus margaritacea* (Phillips), Muir-Wood and Cooper 1960: 182, pl. 123: 11–16 (not 17, 17a).

1966 *Productina margaritacea* (Phillips); Brunton 1966: 209–213, pl. 8: 1–19; pl. 15: 1–8.

1971 *Productina margaritacea* (Phillips); Roberts 1971: 94–96, pl. 17: 11–28; text-fig. 22.

1993 *Argentiproductus margaritaceus* (Phillips, 1836); Brunton et al. 1993: 103–104, figs. 3–15.

1999 *Argentiproductus* sp.; Baliński 1999: 441, fig. 3J.

1999 Productoid gen et sp. indet. 1; Baliński 1999: 441–442, fig. 3I–L.

Material.—Two shells, 19 ventral and 7 dorsal valves; in addition about 20 juvenile specimens most likely representing this species.

Remarks.—Specimens from the Muhua Formation are virtually identical with *Argentiproductus margaritaceus* described from the Late Viséan of northern Wales and Northern Ireland by Muir-Wood and Cooper (1960), Brunton (1966), and Brunton et al. (1993). The species has been reported also from the early Carboniferous of Europe (e.g., de Koninck 1847; Żakowa 1985), Russia (e.g., Bublichenko 1976), Kazakhstan (Litvinovich et al. 1969), Algeria (Pareyn 1962), and Australia (Roberts 1971) (see also Brunton et al. 1993).

Among the material from Muhua there are several juvenile specimens found in samples Mu-42, MH1, and M2-8. They reveal perfectly preserved juvenile shell, probably formed immediately after settlement of a larva. The ventral part of the shell shows a median swelling which protrudes posteriorly beyond the hinge margin. This swelling possesses a median, posteriorly directed, and more or less cylindrical structure, which was mentioned or described as "pedicle sheath" in productoids by Brunton (1965, 1966), Brunton and Cocks (1996), and Baliński (1999) (see also Bassett et al. 2008). On the ventral exterior the median swelling bears a deep longitudinal groove (Fig. 15A, D) which was interpreted by Brunton (1966: 181–182) as an impression left by the anchoring object or as a result of differential growth rate reflecting a juvenile development of the muscles. The position and structure of the groove observed on the studied specimens from Muhua suggest, however, that at the moment of settlement it functioned as an open slit through which the pedicle epithelium was probably attached to the substrate (Fig. 16A). Later during growth the slit was filled by shell material (Fig. $15A_4$).

After settlement of a larva and its attachment to substrate by the pedicle epithelium the anchoring of a shell was almost immediately aided by a pair of symmetrically disposed clasping spines (Figs. 15A, D, 16A). The shape and extent of the spines were adjusted to the object which served as a substrate or attachment site (Fig. 15A–D). This mode of the attachment of *Argentiproductus margaritaceus* larvae seems to be more functionally reasonable and advantageous than the attachment by the tip of cylindrical, thread-like pedicle (Fig. 16B) which is most common among pediculate living, as well as fossil, brachiopods. Latter during growth the pedicle atrophied and the slit in the ventral umbo was filled by the shell material (Fig. 15A, D). Eventually, when the shell became big and heavy the clasping spines were not able to hold the shell above the substrate, they broke away and the shell settled on the sea floor (Muir-Wood and Cooper 1960).

Stratigraphic and geographic range.—The species was re-

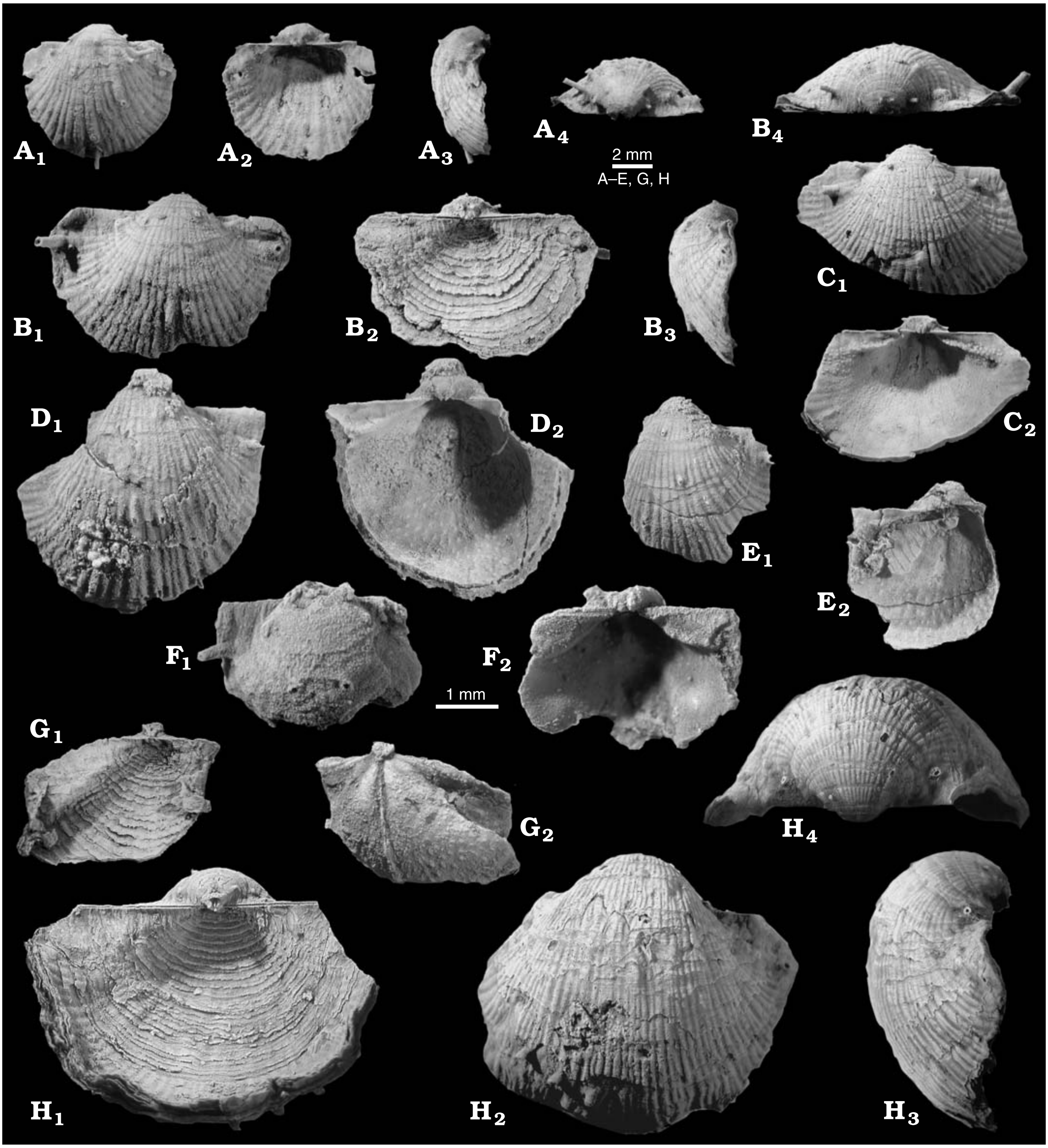
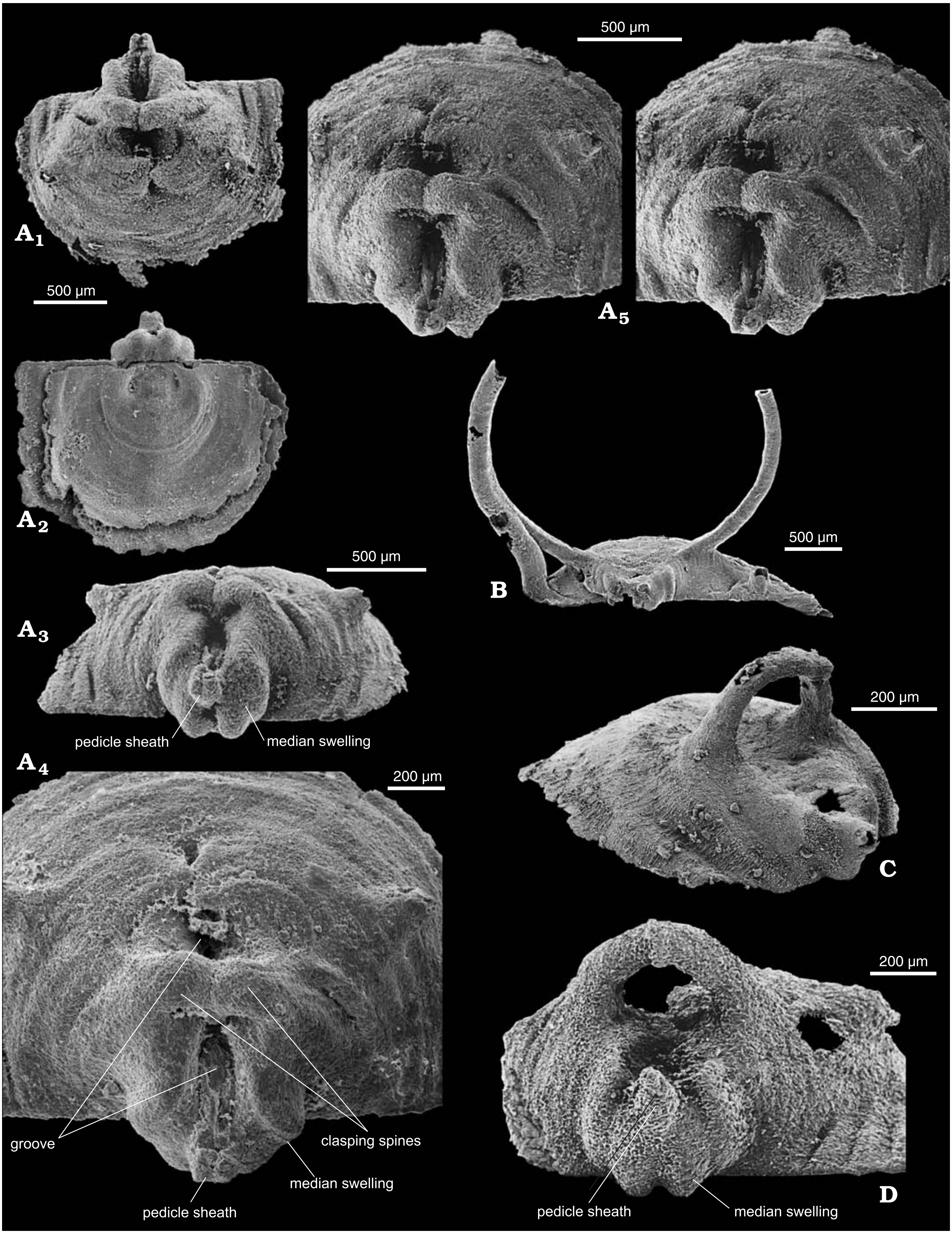


Fig. 14. Productoid brachiopod *Argentiproductus margaritaceus* (Phillips, 1836) from the Muhua Formation. **A**. Small ventral valve, PKUM02-0278, in exterior (A_1), interior (A_2), lateral (A_3), and posterior (A_4) views. **B**. Shell, PKUM02-0279, in ventral (B_1), dorsal (B_2), lateral (B_3), posterior (B_4) views. **C**–**F**. Incomplete ventral valves, PKUM02-0280 (**C**), PKUM02-0281 (**D**), PKUM02-0282 (**E**), and PKUM02-0283 (**F**), in exterior (C_1, D_1, E_1, F_1) and interior (C_2, D_2, E_2, F_2) views showing well developed ear baffles. **G**. Incomplete dorsal valve, PKUM02-0284, in exterior (G_1) and interior (G_2) views. **H**. Large, almost complete shell, PKUM02-0285, in dorsal (H_1), ventral (H_2), lateral (H_3), and posterior (H_4) views; the ribbing in the middle of the ventral valve resembles ornamentation of *Productina*. Samples GB–GT.

vealed in samples GB, GT, MH1, M2-8, and Mu-42. Outside the study area it is known from the Viséan of Europe (Belgium, Poland), Kirghizia, Algerian Sahara, and northwest Australia (see Brunton et al. 1993).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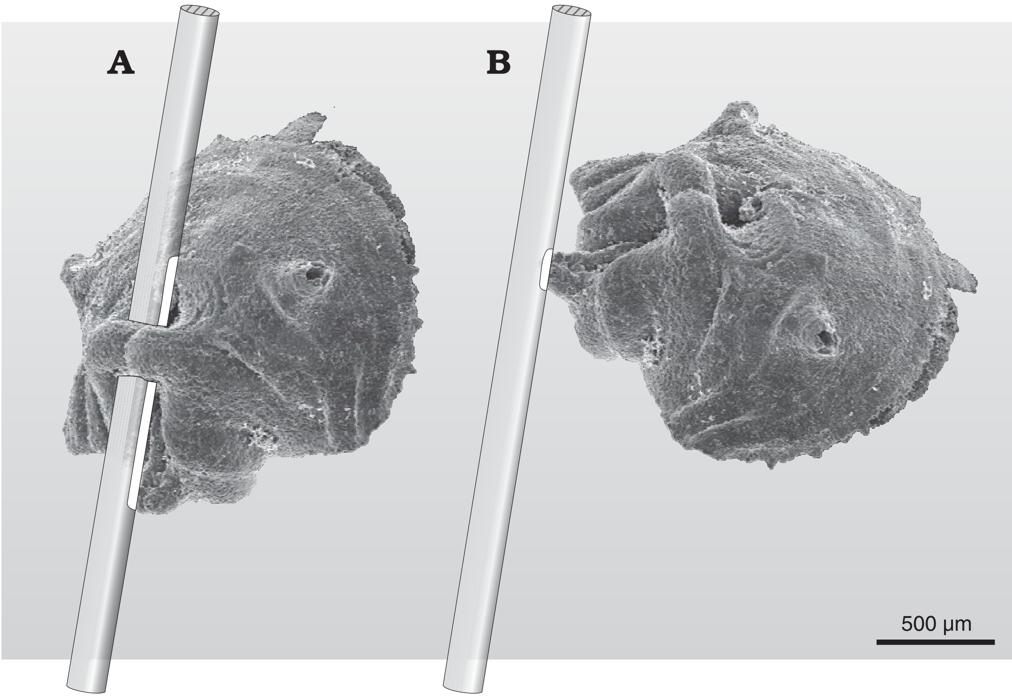

Fig. 16. **A**, **B**. Two hypothetical mode of attachment of juvenile *Argentiproductus margaritaceus* (Phillips, 1836). The extent of attachment (here marked with white areas) by the epithelium emerging through longitudinal median slit in the umbonal region of the ventral valve (**A**) seems more probable and functionally efficient than the attachment by the tip of a cylindrical pedicle (**B**). Note also that the function of clasping spines in A is clear whereas in B reminds unresolved.

Suborder Strophalosiidina Schuchert, 1913
Superfamily Strophalosioidea Schuchert, 1913
Family Strophalosiidae Schuchert, 1913
Subfamily Strophalosiinae Schuchert, 1913
Subfamily Dasyalosiinae Brunton, 1966
Genus *Dasyalosia* Muir-Wood and Cooper, 1960

Type species: *Spondylus goldfussi* von Münster, 1839; Upper Permian; Gera, Germany.

Dasyalosia cf. *panicula* Brunton, 1966

Fig. 17.

cf. 1966 *Dasyalosia panicula* sp. n.; Brunton 1966: 193–194; pl. 2:1–17; pl. 3: 1–5.

Material.—One complete shell, one fragmentary ventral and one dorsal valve.

Description.—A single articulated shell is 3.3 mm in length and 4.0 mm in width, is subcircular in outline, nearly plano- to weakly concavoconvex in profile, with a cicatrix on the ventral valve measuring about 1.2 mm in diameter; a straight hinge line, one-half of the maximum width. Ventral valve with distinct, triangular but rather short interarea; delthyrium narrow, covered by a slightly convex pseudodeltidium; teeth are distinct and strong (Fig. 17A). Dorsal interior with elongate, postero-ventrally directed, narrow trifid cardinal process, with an elongate internal median groove at its base (Fig. 17B); sockets well developed, although with short, curved inner socket ridges; median septum highest at mid-length, posteriorly not reaching the base of cardinal process; adductor scars slightly elevated, elongate and suboval.

Both valves sublamellose, densely covered with recumbent and erect spines.

Remarks.—Genus *Dasyalosia* was established by Muir-Wood and Copper (1960) with *D. goldfussi* (Münster, 1839) from Permian of Germany as a type species. Brunton (1966) described two other species of the genus, namely *D. panicula* and *D. lamnula*, both from Viséan of County Fermanagh, Northern Ireland. Thus, these two species expanded markedly the stratigraphic range of *Dasyalosia*. The lower stratigraphic range of the genus is extended further to the middle Tournaisian thanks to the material here described. Waterhouse (2001) recently regarded both Viséan species of *Dasyalosia* mentioned above as representing his new genus *Bruntonaria*

← Fig. 15. Productoid brachiopod *Argentiproductus margaritaceus* (Phillips, 1836) from the Muhua Formation. **A**. Juvenile shell, ZPAL V. 26/9, in ventral (A_1), dorsal (A_2), posterior (A_3), more detailed postero-ventral (A_4) views, and stereopair (A_5), showing details of exceptionally well preserved pedicle sheath, clogged attachment slit (groove), and clasping spines (see also Baliński 1999: fig. 3K, L). **B**. Ventral valve, PKUM02-0286, in posterior view, showing long ring-like clasping spines. **C**. Slightly damaged ventral valve, ZPAL V. 26/60, in oblique lateral view showing ring of clasping spines. **D**. Incomplete shell, ZPAL V. 26/61, in posterior view, showing well preserved pedicle sheath and a pair of clasping spines. All SEM micrographs. Samples Mu-42 (A, D), MH1 (B), and M2-8 (C).

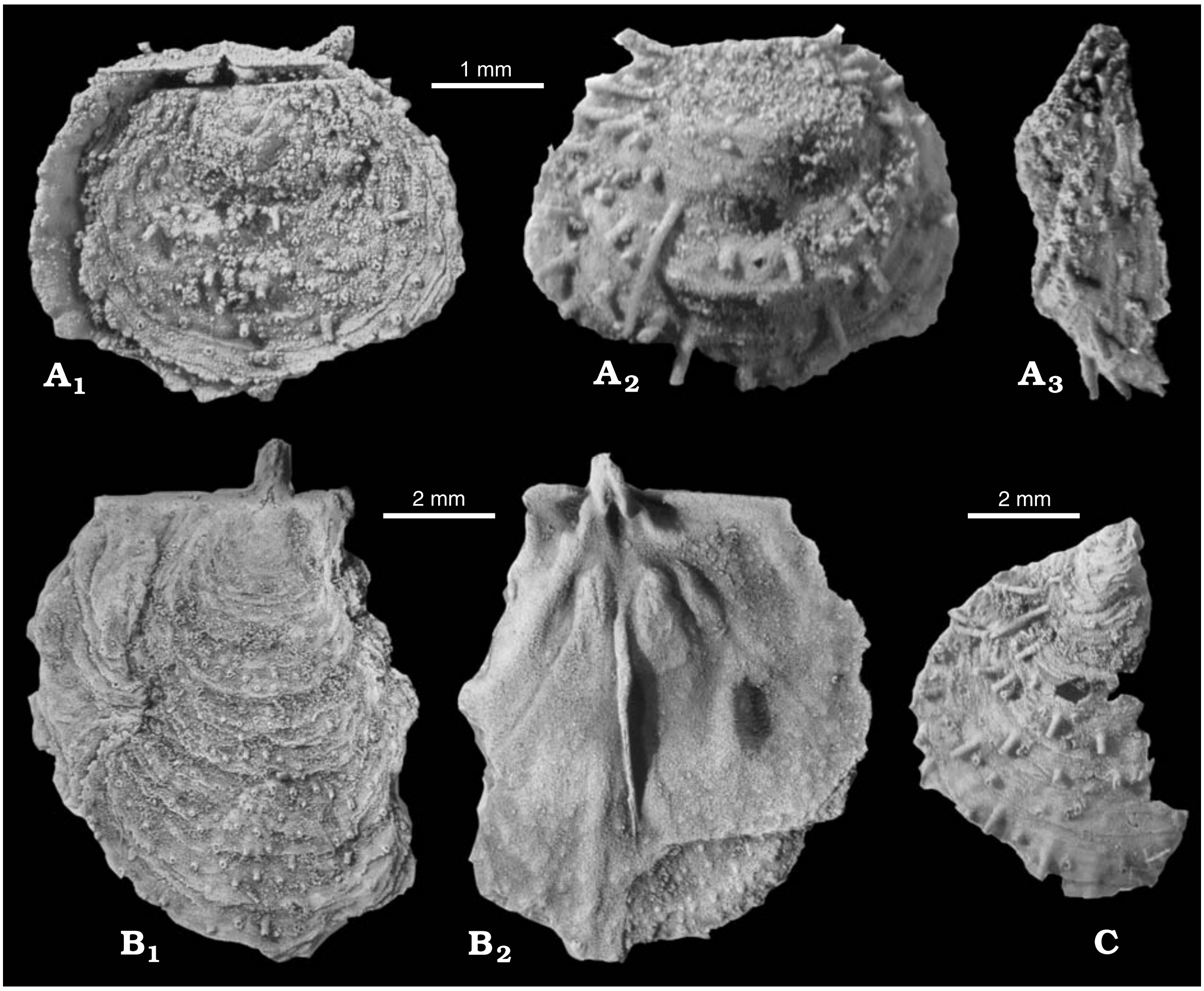

Fig. 17. Strophalosioid brachiopod *Dasyalosia* cf. *panicula* Brunton, 1966 from the Muhua Formation. **A**. Shell, PKUM02-0287, in dorsal (A_1), ventral (A_2), and lateral (A_3) views. **B**. Incomplete dorsal valve, PKUM02-0288, in exterior (B_1) and interior (B_2) views. **C**. Incomplete ventral valve, PKUM02-0289, in exterior view. Sample GB.

Waterhouse, 2001 with *D. panicula* as a type species. However, Brunton (2007) regarded *Bruntonaria* as congeneric with *Dasyalosia*.

Dasyalosia cf. *panicula* from Muhua differs evidently from *D. lamnula* in having much wider ventral interarea and less lamellose ventral valve. From *D. panicula* the Chinese form differs in having slightly wider shell and less abundant spine cover of both valves. Besides these differences both forms seem to be quite closely related. It is highly possible that the studied form represents a new species, but scarcity of material does not allow for a satisfactory specific diagnosis.

Stratigraphic and geographic range.—The species is known from the Viséan of County Fermanagh, Northern Ireland. In Muhua it is very rare occurring in sample GB only.

Superfamily Aulostegoidea Muir-Wood and Cooper, 1960

Family Cooperinidae Pajaud, 1968

Subfamily Muhuarininae Baliński and Sun, 2005

Genus *Muhuarina* Baliński and Sun, 2005

Type species: *Muhuarina haeretica* Baliński and Sun, 2005; Muhua Formation, Tournaisian, Carboniferous; Muhua, Guizhou, China.

Muhuarina haeretica Baliński and Sun, 2005

Fig. 18.

1999 Productoid gen. et sp. indet. 2; Baliński 1999: 442; fig. 4P, S.

2005 *Muhuarina haeretica* gen. et sp. nov.; Baliński and Sun 2005: 450–453, text-figs. 1A, B, 2, 3.

2008 *Muhuarina haeretica* Baliński and Sun, 2005; Baliński and Sun 2008: 106–107, fig. 1.

Material.—Seven almost complete and one fragmentary shell, nine ventral and nine dorsal valves.

Remarks.—This micromorphic aulostegoid productid was recently described in details (Baliński and Sun 2005, 2008). As it was suggested by the authors *Muhuarina haeretica* seems to be the oldest and most primitive representative of a highly specialized Permian family Cooperinidae. The Permian members of the family are characterized by an evolutionary trend to complicate a structure of the lophophore support

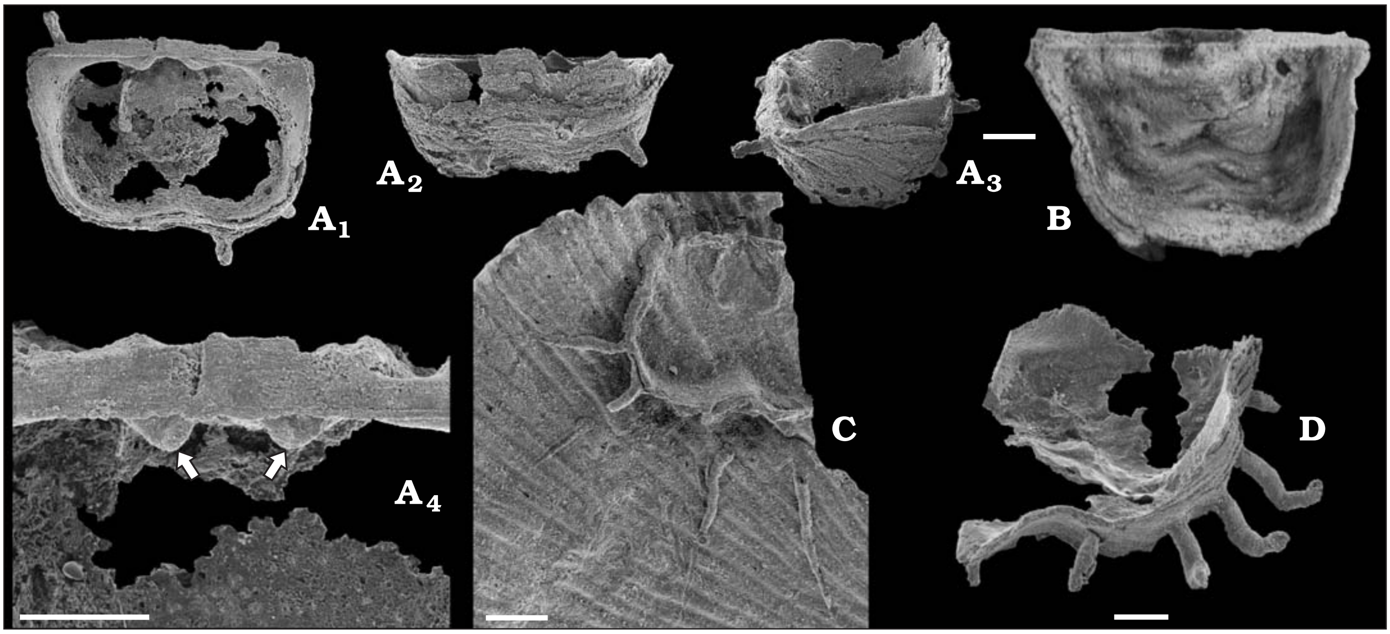

Fig. 18. Aulostegoid brachiopod *Muhuarina haeretica* Baliński and Sun, 2005 from the Muhua Formation. **A**. Slightly damaged ventral valve, PKUM02-0290, in interior (A_1), anterior (A_2), lateral (A_3, posterior to the left), and enlarged interior (A_4) views; notice well preserved teeth (arrowed) and interarea. **B**. Shell, PKUM02-0046, in dorsal view. **C**. Incomplete juvenile ventral valve, PKUM02-0080, (posterior to top) cemented to the chonetoid shell; notice well preserved rhizoid spines and muscle platform (after Baliński and Sun 2008: fig. 1E). **D**. Incompletely preserved ventral valve, PKUM02-0047, in lateral view (posterior to the left) showing rhizoid spines (after Baliński and Sun 2008: fig. 1D). Sample M2-8 (A) and GB (B–D). Scale bars 0.5 mm.

and in consequence, as it can be deduced, to modify the lophophore itself. The subperipheral ridge of the middle Tournaisian *Muhuarina* may indicate the possession of a simple trocholophe type of the lophophore (Baliński and Sun 2005). The Late Permian *Falafer* Grant, 1972 and *Ceocypea* Grant, 1972 have highly folded subperipheral ridges or platforms suggesting a very complex multilobate lophophore, termed a falafer by Grant (1972).

The recently recovered specimens of *M. haeretica* show that the brachiopod used its numerous rhizoid spines to cement to some hard substrate (mainly to brachiopod shells; Fig. 18C, D; see also Baliński and Sun 2008) in the same way as the Permian *Cooperina* Termier, Termier, and Pajaud, 1966 from West Texas (Cooper and Grant 1975).

Stratigraphic and geographic range.— The species has been recovered from samples Mu-42, M2/2, M2/3, M2-8, GB, GT taken from the Muhua Formation.

Productidina gen. et sp. indet.

Fig. 19.

Remarks.—As was mentioned in the general section of this paper the most characteristic feature of the studied material is the disarticulation and fragmentation of skeletal material, especially when larger specimens are involved. As a result, there are several dozens of fragments of large valves of productoids, echinoconchoids, and linoproductoids in the collection which are not possible to determine taxonomically with confidence. A few of them are presented herein (Fig. 19) in order to illustrate more adequately the high taxonomic variability of the fauna from Muhua. The following forms could be represented:

- Semicostellini gen. et sp. indet. (Fig. 19A–F). There are several fragments of dorsal and ventral valves in the collection coming from sample M2-8. Spines are developed only on ventral valve. Low cardinal process and distinct lateral ridges are developed in dorsal valve interior.
- Strophalosiidina gen. et sp. indet. (Fig. 19G). A single fragmentary ventral valve was found in sample M2-8. The valve is thin-shelled, flat, and has well marked wide interarea and convex pseudodeltidium. Rudimentary teeth are also present (Fig. 19F_4).
- Productininae gen. et sp. indet. (Fig. 19R). Morphological features of a very fragmentary material are suggestive of *Avonia* Thomas, 1914 or *Overtonia* Thomas, 1914.
- *Orbinaria*? sp. (Fig. 19L). The illustrated fragment of the productellid dorsal valve is similar to *Orbinaria* Muir-Wood and Cooper, 1960.
- *Spinocarinifera*? sp. (Fig. 19K, M). These leioproductine specimens show cardinalia and shell ornamentation similar to *Spinocarinifera* Roberts, 1971.
- *Acanthocosta* sp. (Fig. 19H–J). Internal structure of the dorsal valve and external shell ornamentation agree with those of *Acanthocosta* Roberts, 1971.
- Echinoconchoidea gen. et sp. indet. (Fig. 19O, P). Several small fragments in the collection do not preserve cardinalia but show characteristic shell ornamentation.
- Auriculispininae gen. et sp. indet. (Fig. 19N). This rather incomplete ventral valve is very suggestive of *Undaria* Muir-Wood and Cooper, 1960. Similar form was reported

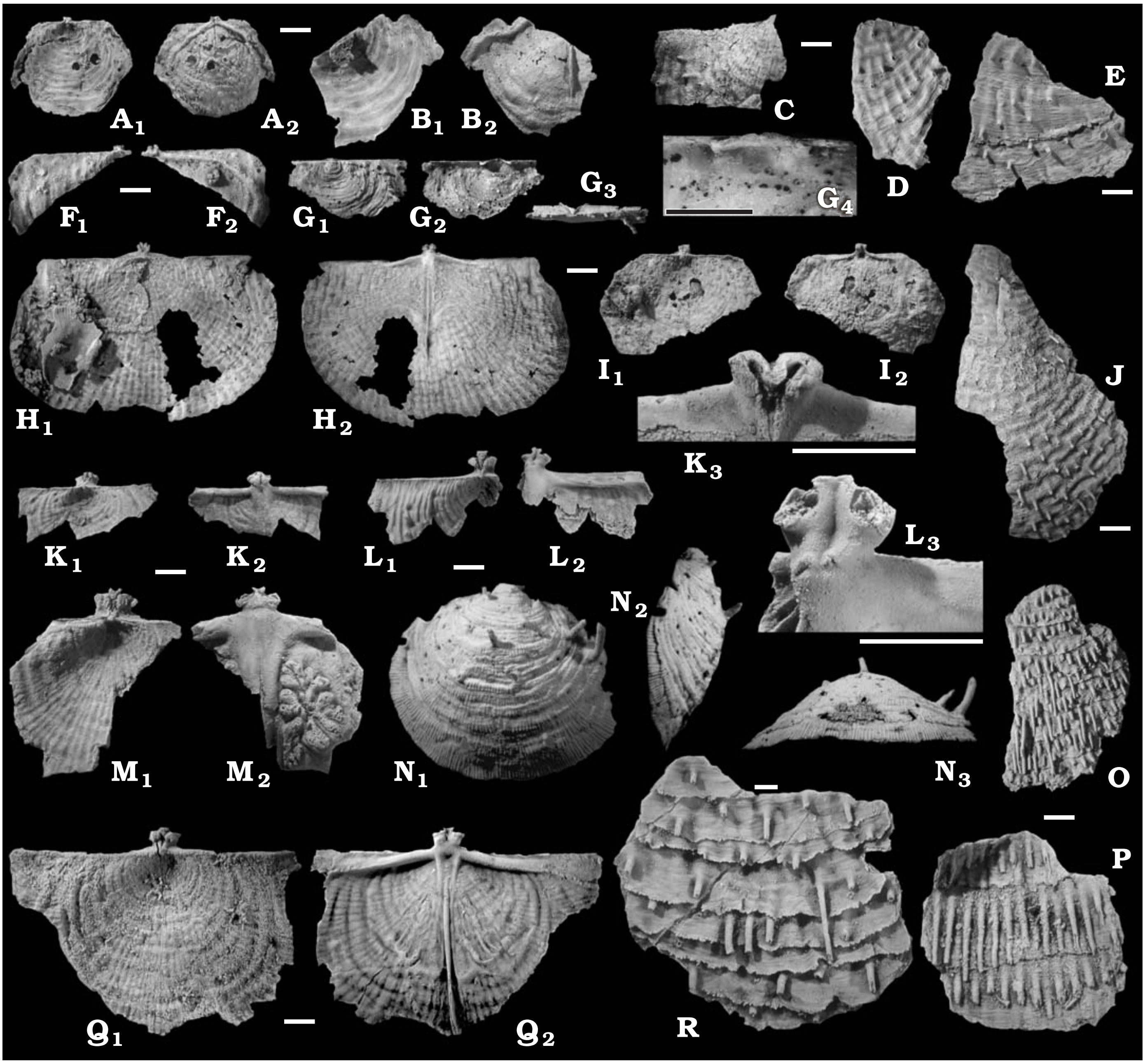

Fig. 19. Productidines from the Muhua Formation. **A**–**F**. Semicostellini gen. et sp. indet. **A**, **B**, **F**. Incomplete dorsal valves, PKUM02-0291 (**A**), PKUM02-0292 (**B**), and PKUM02-293 (**F**), in exterior (A_1, B_1, F_1) and interior (A_2, B_2, F_2,) views. **C**–**E**. Fragments of ventral valves, PKUM02-0294 (**C**), PKUM02-0295 (**D**), and PKUM02-0296 (**E**), in exterior view. **G**. Strophalosiidina gen. et sp. indet., incomplete ventral valve, PKUM02-0297, in exterior (G_1), interior (G_2), and posterior (G_3) views, and SEM enlargement of G_2 showing rudimentary teeth (G_3). **H**–**J**. *Acanthocosta* sp. **H**, **I**. Incomplete dorsal valves, PKUM02-0298 (**H**) and PKUM02-0299 (**I**), in exterior (H_1, I_1) and interior (H_2, I_2) views. **C**. Fragment of ventral valve, PKUM02-0300, showing external ornamentation. **K**, **M**. *Spinocarinifera*? sp.; incomplete dorsal valves, PKUM02-0301 (**K**) and PKUM02-0302(**M**), in exterior (K_1, M_1), interior (K_2, M_2), and enlarged posterior (K_3) views. **L**. *Orbinaria*? sp.; fragmented dorsal valve, PKUM02-0303, in exterior (L_1), interior (L_2), and enlarged interior (L_3) views. **N**. Auriculispininae gen. et sp. indet., probably belonging to *Undaria* Muir-Wood and Cooper, 1960; ventral valve, PKUM02-0304, in exterior (N_1), lateral (N_2), and anterior (N_3) views. **O**, **P**. Echinoconchoidea gen. et sp. indet.; fragments of ventral valve, PKUM02-0305 (**O**) and dorsal valve, PKUM02-0306 (**P**) , showing external ornamentation. **Q**. Juresaniinae gen. et sp. indet., incomplete dorsal valve, PKUM02-0307, in exterior (Q_1) and interior (Q_2) views. **R**. Productininae gen. et sp. indet.; fragment of dorsal valve, PKUM02-0308, probably representing *Avonia* Thomas, 1914 or *Overtonia* Thomas, 1914. Samples M2-8 (A–J), GB-GT (K–M, O–R), and MH1 (N). Scale bars 2 mm.

as monticuliferid gen. et sp. indet. by Wang et al. (2006: 545, fig. 4.10–4.11) from the Tournaisian of northern Guangxi, South China.

– Juresaniinae gen. et sp. indet. (Fig. 19Q). Interior of the illustrated dorsal valve reminds that of some juresaniines, e.g., *Parajuresania* Lazarev, 1982. The genus, however, occurs in upper Carboniferous (Pennsylvanian), so our specimen represents most probably another form.

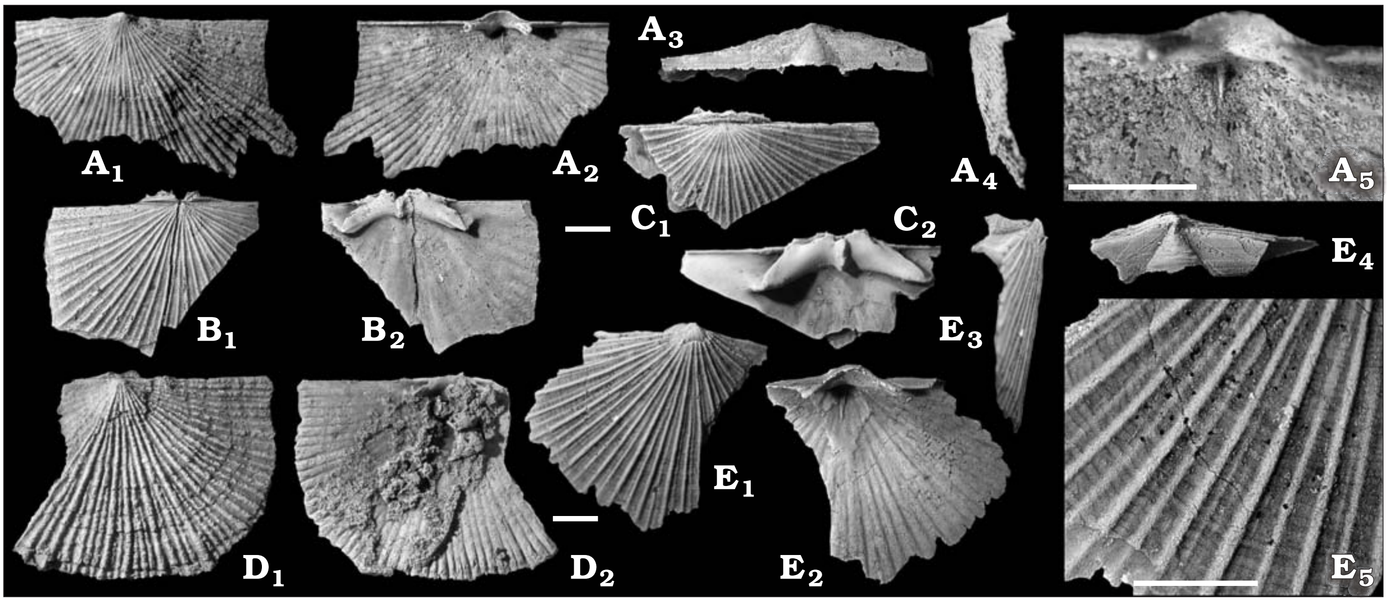

Fig. 20. Orthotetoid brachiopod *Brochocariina*? sp. from the Muhua Formation. **A**. Incomplete ventral valve, PKUM02-0309, in exterior (A_1), interior (A_2), posterior (A_3), lateral (A_4), and enlarged interior (A_5) views. **B**–**D**. Incomplete dorsal valves, PKUM02-0310 (**B**), PKUM02-0311 (**C**), and PKUM02-0312 (**D**), in exterior (B_1, C_1, D_1) and interior (B_2, C_2, D_2) views. **E**. Incomplete ventral valve, PKUM02-0313, in exterior (E_1), interior (E_2), lateral (E_3), posterior (E_4), and enlarged exterior (E_5) views. Samples M2-8 (A, D) and GB (B, C, E). Scale bars 2 mm.

Order Orthotetida Waagen, 1884
Suborder Orthotetidina Waagen, 1884
Superfamily Orthotetoidea Waagen, 1884
Family Orthotetidae Waagen, 1884
Genus *Brochocarina* Brunton, 1968

Type species: *Schuchertella wexfordensis* Smyth, 1930; Asbian, Carboniferous; Fermanagh, Northern Ireland.

Brochocarina? sp.

Fig. 20.

Material.—Two ventral and 9 dorsal valves mostly fragmentary but with well preserved internal structure.

Remarks.—The material is very fragmentary but reveals internal structures of the ventral and dorsal valves which seem to be characteristic for the family Orthotetidae. The most characteristic are low, discrete cardinal process lobes and recurved socket ridges which diverge at 20–24° from hinge line (Fig. 20B). Between the lobes there is a wide median ridge terminating antero-ventrally as a node of variable extent. Inside the ventral valve there is a short median septum which is confined to the most posterior region of the valve (Fig. 20A_2, A_5, C_2). Ornamentation of the valves is parvicostellate with fine radial costellae showing two kinds of distribution. In most specimens from sample M2-8 they are fine and closely spaced (Fig. 20A, D). On the other hand on specimens from sample GB and a few from sample M2-8 the costellae are separated by wider interspaces (Fig. 20B, C) suggesting that they may be not conspecific with the former. Unfortunately, the present material does not allow to establish whether this variability is intra- or interspecific.

The studied specimens are tentatively referred to *Brochocarina* on the basis of their costellate pattern which involves intercalation rather than branching.

Stratigraphic and geographic range.—The species was revealed in samples M2-8 and GB.

Family Pulsiidae Cooper and Grant, 1974
Genus *Schellwienella* Thomas, 1910

Type species: *Spirifera crenistria* Phillips, 1836; Viséan, Carboniferous; Lancashire, England.

Schellwienella sp.

Fig. 21.

Material.—Two fragmentary ventral valves, one complete and five fragmentary dorsal valves.

Description.—Single complete dorsal valve is transversely semi-oval in outline and nearly two-thirds as long as wide; hinge line straight, almost equal the greatest valve width; interarea short but distinct, triangular, and apsacline; chilidium thick, rather small. Cardinal process generally high, ventrally directed when valve is deep, or almost posteriorly directed in weakly convex valves (Fig. 21C, D); lobes well separated by deep sulcus and bear deep, divergent myophore slits. Socket ridges rather short, recurved, and ankylosed to the cardinal process. Dorsal adductor scars well marked in one thick-shelled valve (Fig. 21D_2), laterally bounded by curved ridge and divided anteriorly by short and low median myophragm. Interior of ventral valve with short dental plates.

Ornamentation finely parvicostellate by intercalation.

Remarks.—Lack of more complete ventral valves in the studied material, which could be attributed to the same spe-

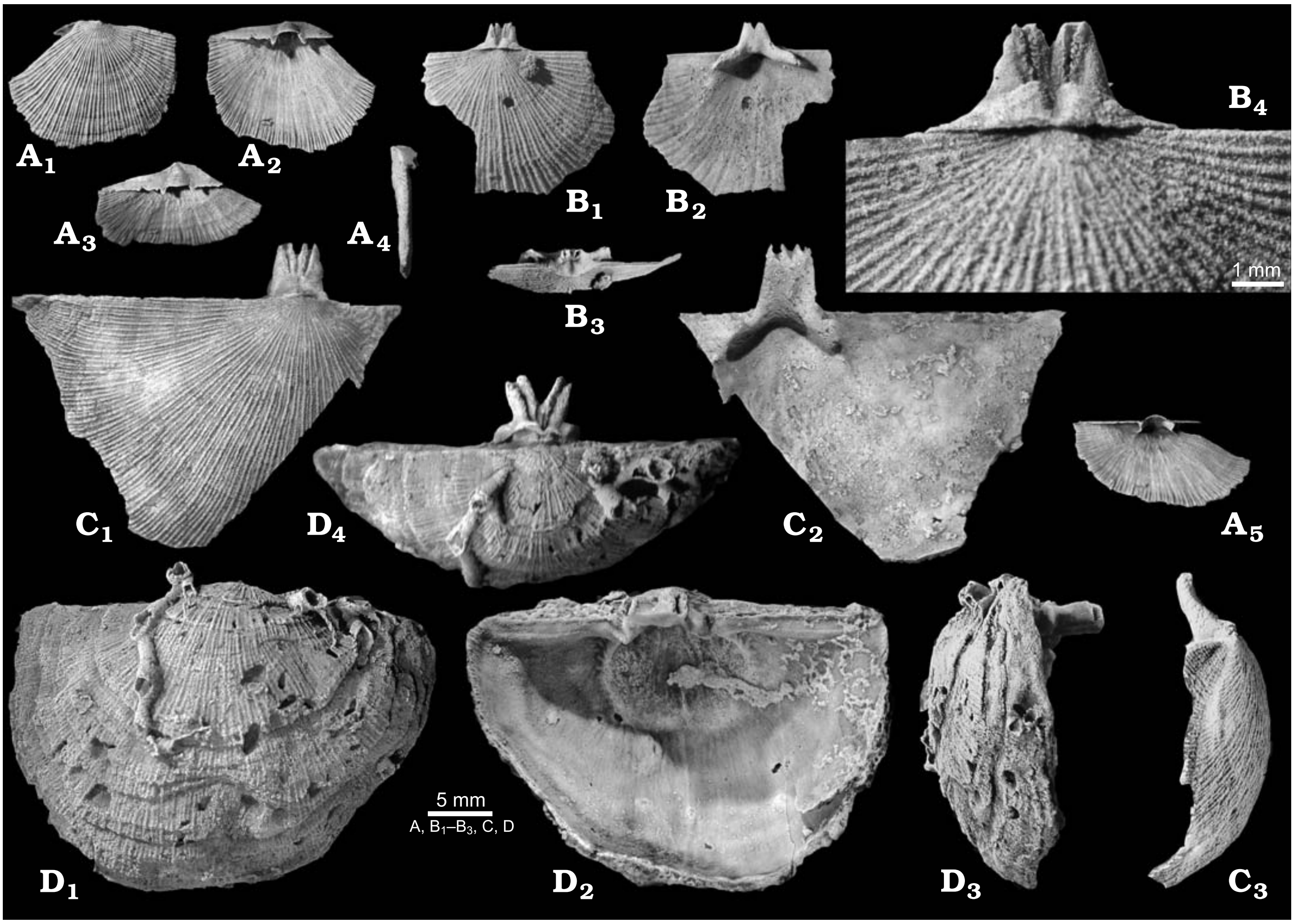

Fig. 21. Orthotetoid brachiopod *Schellwienella* sp. from the Muhua Formation. **A**. Slightly incomplete ventral valve, PKUM02-0314, in exterior (A_1), interior (A_2), posterior (A_3), lateral (A_4), and anterodorsal (A_5) views. **B**. Slightly damaged dorsal valve, PKUM02-0315, in exterior (B_1), interior (B_2), posterior (B_3), and enlarged dorsal (B_4) views. **C**. Incomplete dorsal valve, PKUM02-0316, in exterior (C_1), interior (C_2), and lateral (C_3) views. **D**. Dorsal valve, PKUM02-0317, in exterior (D_1), interior (D_2), posterior (D_3), and lateral (D_4) views. Samples M2/4 (A), M2-8 (B), and MH2 (C, D).

cies as the four dorsal valves here described, precludes more precise identification. The single complete dorsal valve attains 32 mm in width and is quite deep, possibly representing gerontic stage. The cardinal process of the specimen is ventrally directed (Fig. D_3), as compared to other valves in the collection in which it is posteriorly directed (Fig. C_3). It seems that this feature depends on curvature of the valve: specimens with strongly convex posterior region of the valve have the cardinal process turned more ventrally. A single dorsal valve also shows several strong concentric growth lines which might have been induced by damage to the mantle epithelium by boring organisms (Fig. 21D).

Stratigraphic and geographic range.—This is rather rare species in the Muhua Formation. The studied specimens were found in samples D2(?), D4, MH2, M2/4, M2-8, and GB.

Family Schuchertellidae Williams, 1953

Subfamily Schuchertellinae Williams, 1953

Genus *Schuchertella* Girty, 1904

Type species: *Streptorhynchus lens* White, 1862; upper Famennian, Devonian; Missouri, USA.

Schuchertella sp.

Fig. 22.

Material.—A few mostly fragmented dorsal and ventral valves.

Remarks.—Although the studied material is invariably very fragmented the external ornamentation as well as dorsal cardinalia and asymmetrical ventral umbo lacking dental plates suggest that the specimens represent a species of *Schuchertella*.

Stratigraphic and geographic range.—The species is uncommon in samples GB and MH1.

Genus *Serratocrista* Brunton, 1968

Type species: *Serratocrista fistulosa* Brunton, 1968; Asbian, Carboniferous; Fermanagh, Northern Ireland.

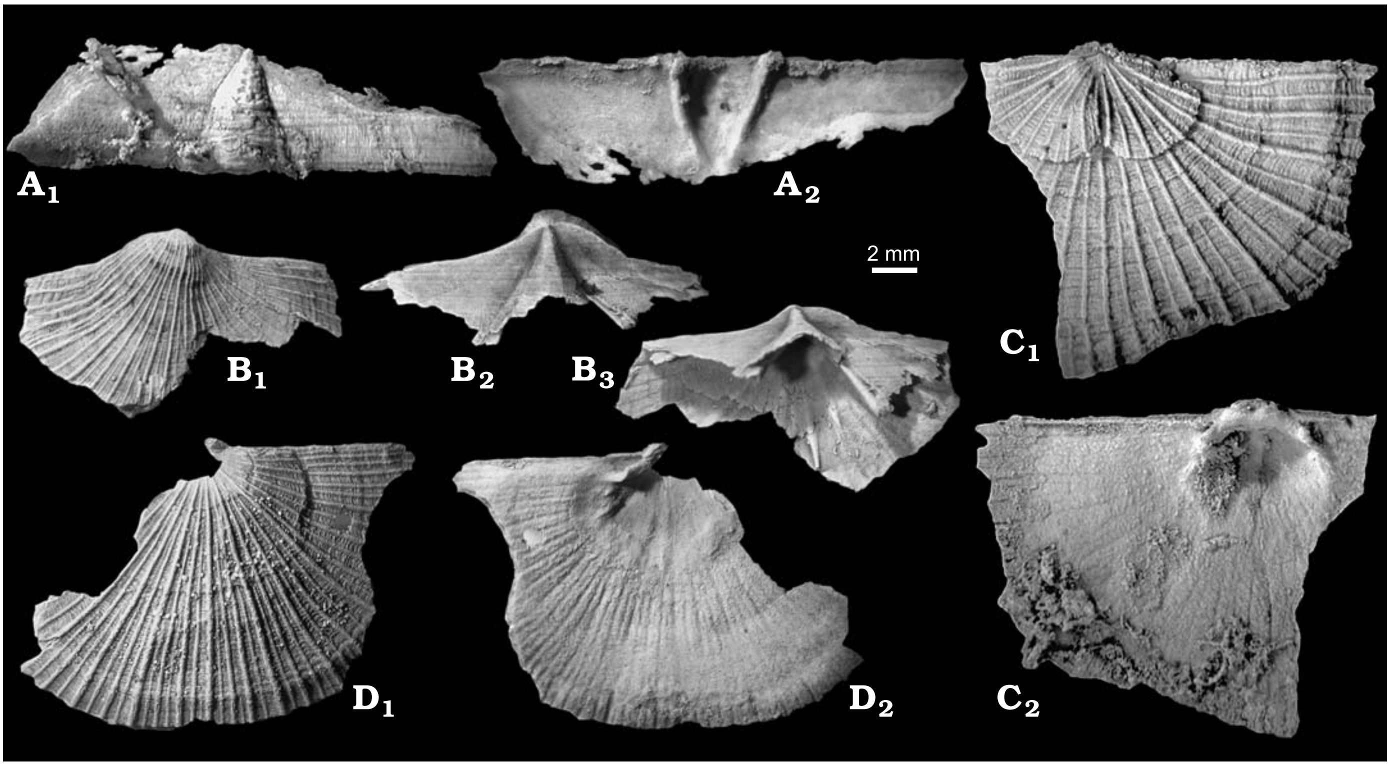

Fig. 22. Orthotetoid brachiopod *Schuchertella* sp. from the Muhua Formation. **A**. Posteriormost fragment of the ventral valve, PKUM02-0318, in external (A_1) and internal (A_2) views showing interarea, pseudodeltidium and dental ridges. **B**. Incomplete ventral valve, PKUM02-0319, in exterior (B_1), dorsal (B_2), and anterodorsal (B_3) views. **C**. Incomplete dorsal valve, PKUM02-0320, in exterior (C_1) and interior (C_2) views; note abnormal development of juvenile shell. **D**. Incomplete dorsal valve, PKUM02-0321, in exterior (D_1) and interior (D_2) views. Samples D4 (A) and MH1 (B–D).

Serratocrista sp.

Fig. 23.

1999 Orthotetidine gen. et sp. indet.; Baliński 1999: 441, fig. 3R, S.

Material.—Five fragmentary dorsal valves, one ventral valve, and three indeterminable fragments.

Remarks.—The specimens reveal characteristic cardinalia, parvicostellate ornamentation by intercalation, and arrays of short, spinous projections along the crest of costellae. Cardinal process is low, bilobed, with a very weakly marked median boss. Socket ridges are slightly recurved, diverging from hinge at about 22°.

The specimens from the Muhua Formation are comparable to *Serratocrista* in having similar external ornamentation and dorsal interior structure but their fragmentary preservation is insufficient to permit a specific assignment.

Stratigraphic and geographic range.—This is a rare species in samples D4, GB, MH1, M2/3, and M2/4.

Genus *Lamellispina* nov.

Type species: *Lamellispina spinosa* gen. et sp. nov., by monotypy.

Etymology: From the characteristic ornamentation of the shell of concentric lamellae and radial spinous projections.

Diagnosis.—Small to medium sized orthotetoid cemented (at least at the earlier ontogenetic stages) at its asymmetrical ventral umbo; ventral valve subconical with high interarea

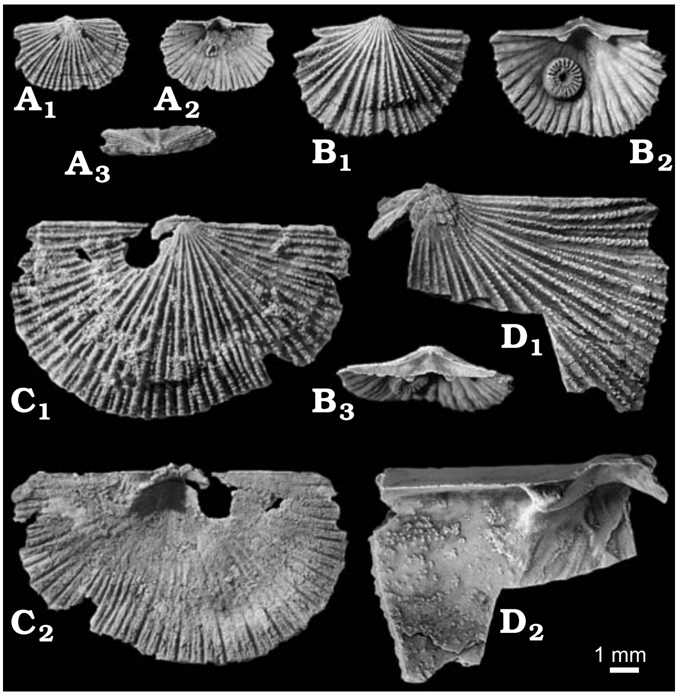

Fig. 23. Orthotetoid brachiopod *Serratocrista* sp. from the Muhua Formation. **A**, **B**. Young ventral valves, PKUM02-0322 (**A**) and PKUM02-0323 (**B**), in exterior (A_1, B_1), interior (A_2, B_2), and posterior (A_3, B_3) views. **C**. Slightly damaged dorsal valve, PKUM02-0324, in exterior (C_1) and interior (C_2) views. **D**. Incomplete ventral valve, PKUM02-0325, in exterior (D_1) and interior (D_2) views. Sample D4 (A, C) and GB (B, D).

and strongly convex pseudodeltidium, without perideltidium or monticulus; dorsal interarea low, but wide to linear, chilidium convex with median groove. Dental ridges unsupported by dental plates, not developed umbonally; median septum absent; cardinal process low, bilobed; socket ridges divergent, partially ankylosed to cardinal process. Ornamentation lamellose and strongly costellate by intercalation; costellae extend at periphery of concentric lamellae as spinous projections inclined at low angle away from the valve surface. The genus differs from the majority of schuchertellids in its lamellose-costellate ornamentation with a tendency to produce spinous projections. From *Goniarina* Cooper and Grant, 1969, *Bothrostegium* Cooper and Grant, 1974, and *Chelonomia* Cooper and Grant, 1974 it differs by less conical ventral valve. From *Streptorhynchus* King, 1850 it differs mainly in the absence of monticulus and having low cardinal process.

Remarks.—The most important shell features defining the new genus are: the subconical ventral valve, asymmetrical ventral umbo with a cicatrix, absence of a perideltidium, monticulus, and dental plates, and divergent socket plates ankylosed to the bilobed cardinal process. These characteristics strongly suggest that *Lamellispina* belongs to the family Schuchertellidae Williams, 1953. Subfamily affiliation is more difficult, but the presence of low cardinal process lobes and absence of a perideltidium and monticulus in *Lamellispina* gen. nov. precludes its attribution to Streptorhynchinae Stehli, 1954 and is more in agreement with characteristics of the Schuchertellinae Williams, 1953.

One of the most characteristic features of the genus, however, is its shell ornamentation combining concentric lamellose structure and strong radial costellae which form long, half-tube projections at the periphery of concentric lamellae. The combination of the above features helps to discriminate this newly proposed genus from all known orthotetoids, and, particularly, schuchertellids. By having distinct lamellose-costellate ornamentation *Lamellispina* resembles *Goniarina*, *Bothrostegium*, *Chelononia*, and *Streptorhynchus*. The first three genera, however, are much younger stratigraphically, coming from the Early Permian of Texas (Cooper and Grant 1969, 1974) and they all have more conical ventral valve. The new genus differs from *Goniarina* also by having divergent, not recurved, socket ridges. From *Bothrostegium* it is distinguished also by the absence of a perideltidium and shorter cardinal process lobes, and from *Chelononia* it differs by having wider hinge margin, shorter cardinal process, and lacking a monticulus. The last two features separate the new genus also from the Carboniferous–Permian genus *Streptorhynchus*.

Although the presence of distinct spine-like, half-tube outgrowths in *Lamellispina* is a very important distinguishing feature, we do not overemphasize it when comparing the new genus with other orthotetoids because the recognition of such delicate structures may depend importantly on taphonomic characteristics of the material.

Stratigraphic and geographic range.—The genus is known only from its type locality and type horizon.

Lamellispina spinosa sp. nov.

Figs. 24, 25.

1999 *Schuchertella* sp.; Baliński 1999: 441, fig. 3H.

Etymology: After the presence of spinous projections on the shell exterior.

Holotype: Dorsal valve PKUM02-0327 figured in Fig. 24B.

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

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

Diagnosis.—Shell biconvex, wider than long, with long, straight hinge line developing short ears; ventral valve with asymmetrical umbo, and subtriangular, frequently irregular in outline, apsacline interarea; delthyrium covered by pseudodeltidium; dorsal valve weakly convex with linear to low-triangular interarea; chilidium semicircular with median groove; shell ornamentation costellate to parvicostellate, costellae very strong, extending marginally from concentric growth lamellae as semi-tubular projections.

Material.—More than 120 loose valves, predominantly juvenile; almost three-quarters of them are dorsal valves.

Description.—Shell biconvex, rounded-rectangular to rounded-quadrate in outline, hinge line straight equals or slightly less the greatest width of the shell, postero-laterally developing short pointed ears. Ventral valve subconical, variable in lateral profile, generally convex to slightly concave, especially in its posterior region; interarea apsacline, subtriangular, frequently irregular in outline, nearly flat to slightly convex or concave; umbo asymmetrical and deformed by attachment cicatrix; delthyrium completely covered by strongly convex pseudodeltidium which in large specimens is massive and thick and frequently bears clearly marked, imbricate growth lamellae; perideltidium and monticulus absent. Dorsal valve is usually weakly convex, but some gerontic specimens might be very deep; small umbo is well marked, slightly swollen and protruding a little behind hinge margin (Fig. 25B), but partly shadowed by overhanging chilidium; interarea linear to low-triangular; chilidium well developed, semicircular, thickened, with median groove.

Interior of the ventral valve with strong teeth and dental ridges, the later being well developed only distally, while proximally they are buried under a shell thickening; no dental plates; muscle scars poorly differentiated, presumably occupying a large surface in the posterior region of the valve, possibly including the whole umbonal cavity; in the most posterior part of the umbonal cavity a low and very short median ridge or thickening may be observed infrequently in some thick-shelled specimens. Dorsal valve interiors have divergent socket ridges at about 90° (total range: 65–114°), in some they are expanded antero-ventrally to form distinct plates or brachiophore bases (Fig. 25C, D); when well pre-

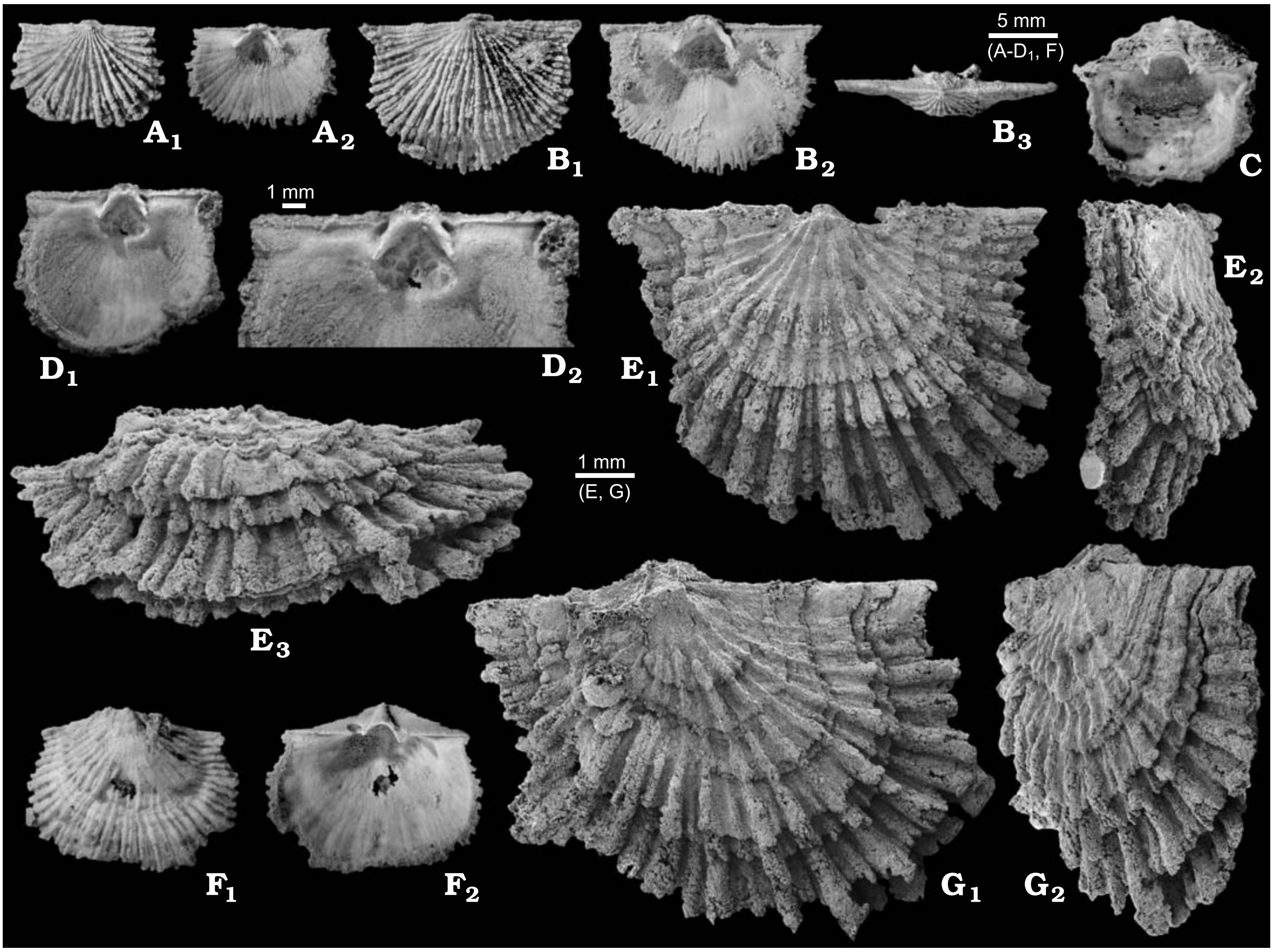

Fig. 24. *Lamellispina spinosa* gen. et sp. nov. from the Muhua Formation. **A**. Small dorsal valve, PKUM02-0326, in exterior (A_1) and interior (A_2) views. **B**. Dorsal valve, PKUM02-0327 (holotype), in exterior (B_1), interior (B_2), and posterior (B_3) views. **C**. Ventral valve, PKUM02-0328, in interior view. **D**. Dorsal valve, PKUM02-0329, in interior view (D_1) and enlarged view showing cardinalia and dendritic adductor scars (D_2). **E**, **G**. SEM micrographs of exterior of dorsal valves, PKUM02-0330 (**E**) and PKUM02-0331 (**G**), in dorsal (E_1, G_1), oblique lateral (E_2, G_2), and anterior (E_3) views. **F**. Ventral valve, PKUM02-0332, in exterior (F_1) and interior (F_2) views. All from sample MH1.

served the ridges are ankylosed to the cardinal process but commonly damage to the thin proximal ends of the inner socket ridges results in gaps between them and the cardinal process; cardinal process low but wide, bilobed, without an internal median node; myophore grooves posteriorly directed; adductor scars more clearly impressed that the scars in the ventral valve, located between and anterior to the socket ridges, mostly flabellate but occasionally with clear dendroid pattern (Fig. 24D), bordered laterally and anteriorly by a low thickened ridge, divided by a low median myophragm which is highest anteriorly.

Shell ornamentation is dominated by very distinct, imbricate concentric lamellae and costellate to parvicostellate ribbing. Costellae are very strong, high, with rounded crests, separated by deep interspaces of varying width; increasing by intercalation and extending marginally from lamellose growth lines as spinous, semi-tubular projections. These projections are inclined at a low angle away from the valve surface, and being concave on their inner surfaces to overlap onto the rib anteriorly, thus forming the continuous costellate appearance (Figs. 24E, G; 25D). On well preserved specimens the concentric lamellae show a clear tendency to form short frilly extensions (Fig. 24E, G).

Remarks.—The main characteristic of this new orthotetoid and its comparison with other representatives of the group have been discussed in details in generic description above.

The shape of the socket ridges and their relationship to the cardinal process merits some additional comments. In the majority of dorsal valves the ridges are not ankylosed to the cardinal process but this condition seems to be caused by partial damage of the very thin proximal (i.e., adaxial) walls of the sockets. In some rare well preserved specimens these ridges are more completely preserved and ankylosed to the cardinal process (Fig. 25E). This type of breakage may have

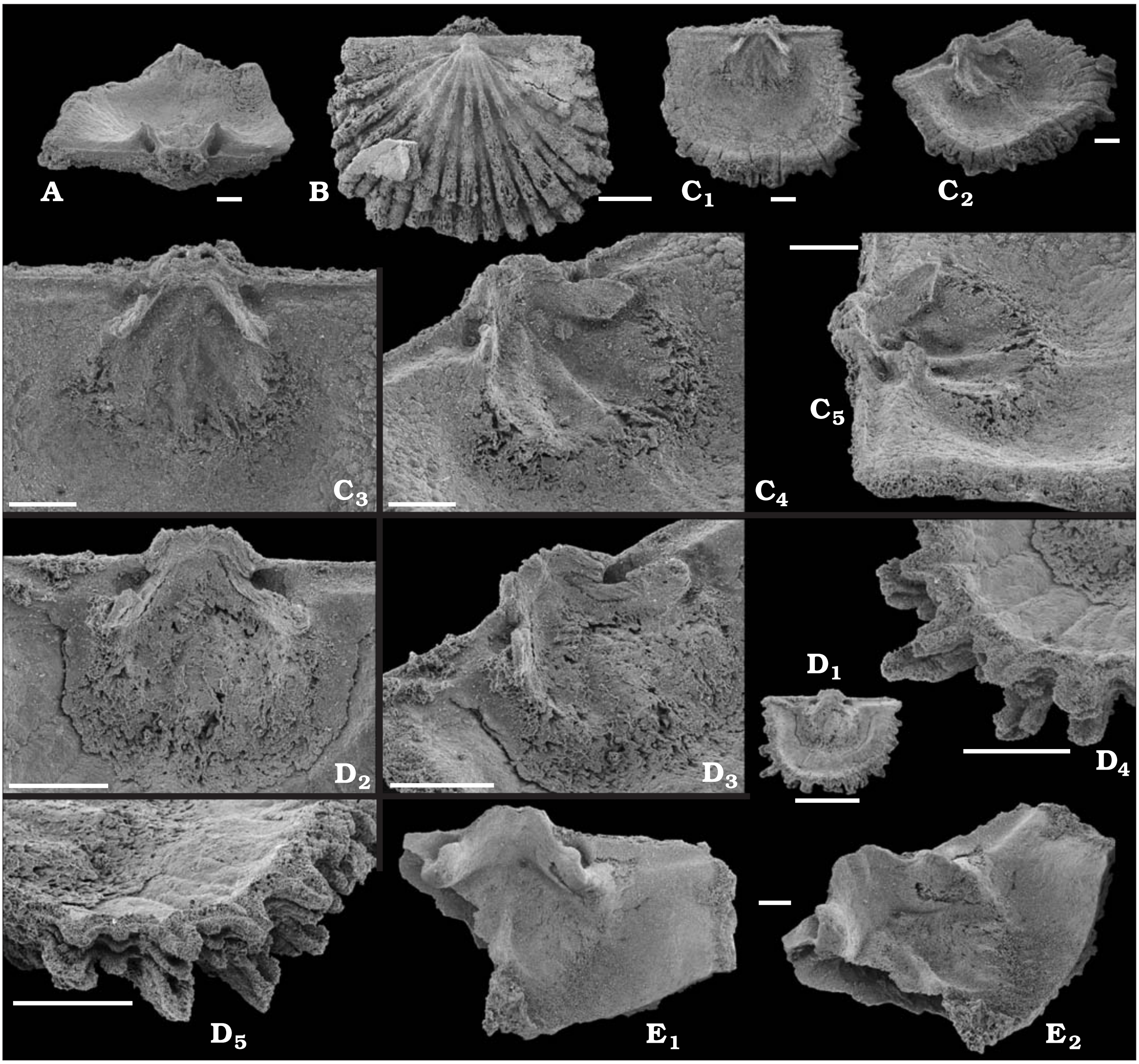

Fig. 25. Orthotetoid brachiopod of *Lamellispina spinosa* gen. et sp. nov. from the Muhua Formation, sample MH1. **A**. Dorsal valve, PKUM02-0333, in posterior view showing cardinalia. **B**. Juvenile dorsal valve, PKUM02-0334, in exterior view. **C**. Interior of dorsal valve, PKUM02-0335, in ventral (C_1), oblique lateral (C_2), enlarged ventral (C_3), enlarged oblique (C_4), and ventrolateral (C_5) views illustrating disposition of socket ridges, cardinal process and adductor scars. **D**. Dorsal valve, PKUM02-0336, in interior (D_1), enlarged interior (D_2; notice slightly damaged socket ridges), ventrolateral (D_3), oblique anterior (D_4, D_5; notice spinous, half-tube-like projections at the valve margin) views. **E**. Fragment of a large dorsal valve, PKUM02-0337, showing well preserved cardinalia. All SEM micrographs. Scale bars 1 mm.

resulted from post-mortem disarticulation. Similar damage to the sockets can be observed in some disarticulated Recent brachiopods (C. Howard C. Brunton, personal communication 2007).

Stratigraphic and geographic range.—This is one of the most common brachiopod species in the fauna of Muhua. It was found mostly in sample MH1, but a few specimens come also from samples D2, D4, M2/3, M2/4, DPS2, and Mu-42.

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

Order Orthida Schuchert and Cooper, 1932

Suborder Dalmanellidina Moore, 1952

Superfamily Dalmanelloidea Schuchert, 1913

Family Rhipidomellidae Schuchert, 1913

Subfamily Rhipidomellinae Schuchert, 1913

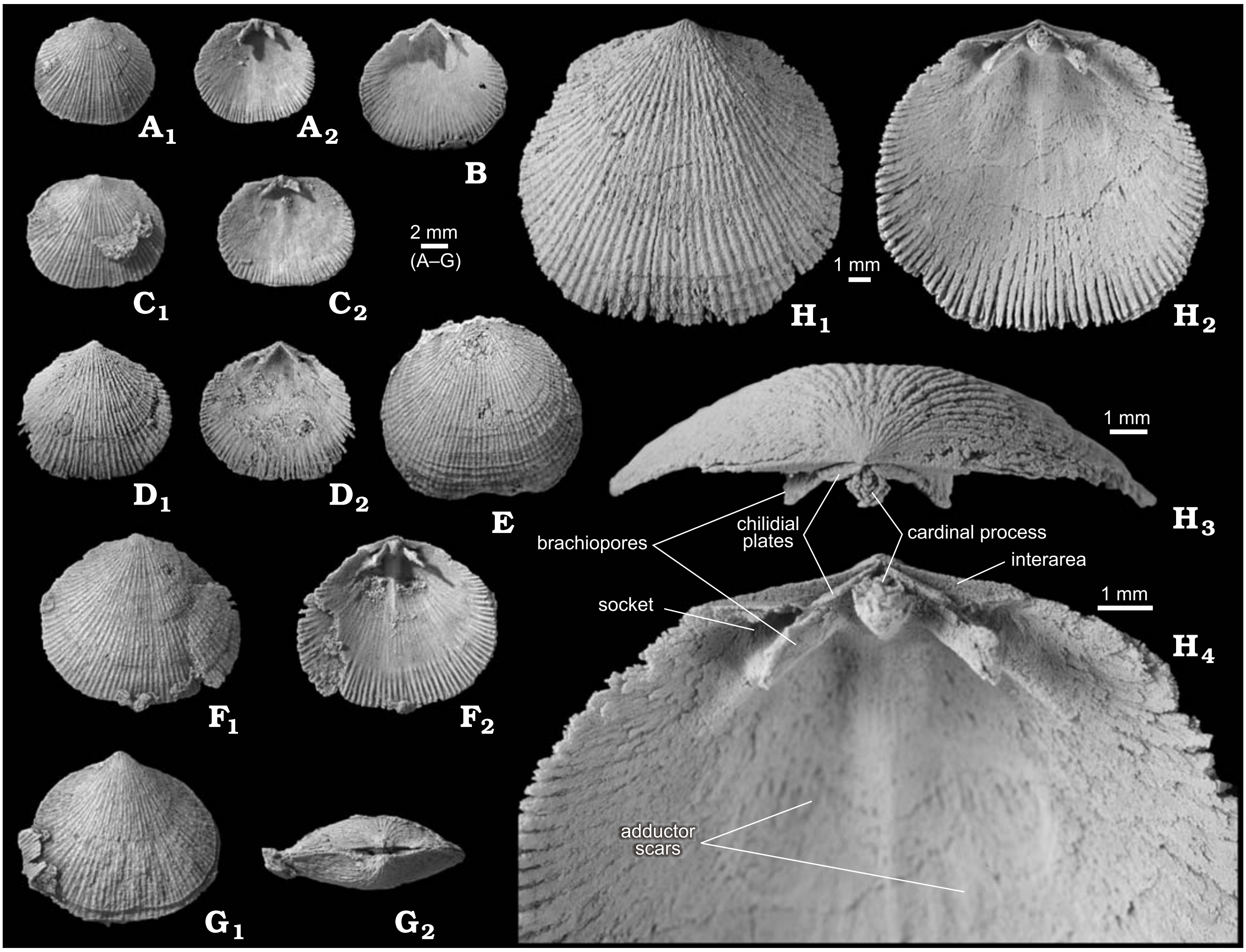

Fig. 26. Dalmanelloid brachiopod *Rhipidomella michelini* (Léveillé, 1835) from the Muhua Formation. **A**, **C**, **F**. Dorsal valves, PKUM02-0338 (**A**), PKUM02-0339 (**C**), and PKUM02-0340 (**F**), in exterior (A_1, C_1, F_1) and interior (A_2, C_2, F_2) views. **B**. Ventral valve, PKUM02-0341, in interior view. **D**. Ventral valve, PKUM02-0342, in exterior (D_1) and interior (D_2) views. **E**. Dorsal valve, PKUM02-0343, in exterior view. **G**. Shell, PKUM02-0344, in ventral (G_1) and posterior (G_2) views. **H**. Dorsal valve, ZPAL V. 26/59, in exterior (H_1), interior (H_2), posterior (H_3), and enlarged interior (H_4) views with labelled morphology. Samples MH1 (A–G) and D1 (H).

Genus *Rhipidomella* Oehlert, 1890

Type species: *Terebratula michelini* Léveillé, 1835; Viséan, Carboniferous; Belgium–France (exact horizon and locality unknown).

Rhipidomella michelini (Léveillé, 1835)

Fig. 26.

1835 *Terebratula Michelini*; Léveillé 1835: 39, pl. 2:14–17.

1968 *Rhipidomella michelini* (L'Eveillé) 1835; Brunton 1968: 17–21, pl. 3: 1–25, text-fig. 5.

cf. 1971 *Rhipidomella michelini*? (Léveillé); Roberts 1971: 41–42; pl. 1: 1–5; pl. 2: 1–5.

2006 *Rhipidomella michelini* (Léveillé, 1835); Bassett and Bryant 2006: 502–504; pl. 1: 1–4; pl. 6: 11–17.

Material.—140 complete shells and more than three hundred well preserved isolated dorsal and ventral valves representing wide range of growth stages.

Description.—Shell medium sized, gently dorsibiconvex, rounded in outline, slightly wider than long, very weakly unisulcate, with straight and narrow hinge line. Ventral valve with apsacline, concave interarea and wide, open delthyrium with apical angle of about 89°. Dorsal interarea lower than ventral, concave, notothyrium closed.

Interior of the ventral valve with strong teeth supported by sub-vertical dental plates; small triangular pedicle callist developed apically; slightly elongate suboval diductor scars weakly impressed, bounded laterally with low ridges running from bases of dental plates. Dorsal valve interior with prominent cardinal process; chilidial plates very short, enclosing cardinal process postero-laterally (Fig. 26H); brachiophores widely divergent at about 116°, supported by more or less vertical plates; adductor scars poorly differentiated but in some specimens a low median ridge extends from near cardinal pro-

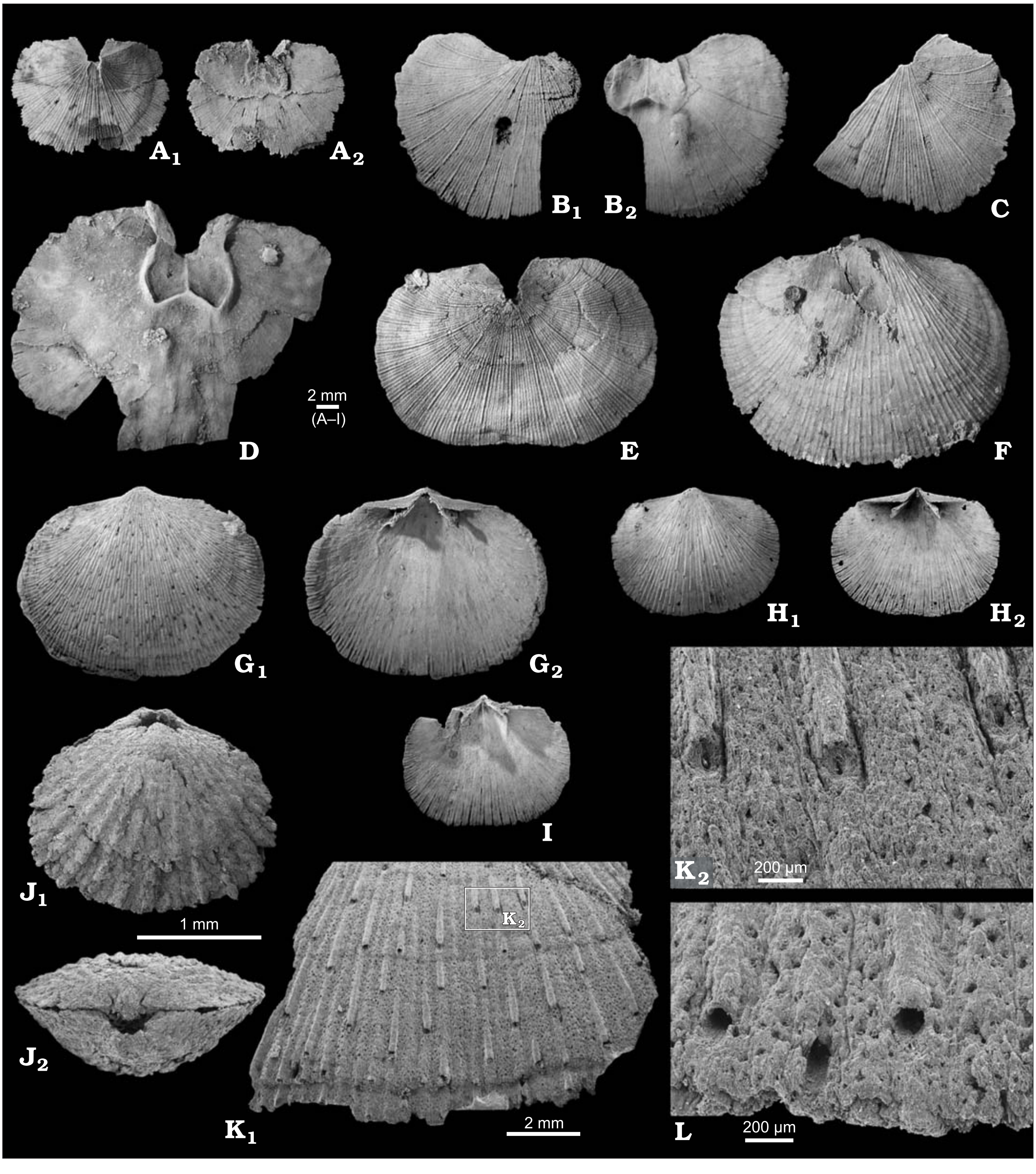

Fig. 27. Schizophoriid brachiopods from the Muhua Formation, sample MH1. **A**–**E**. *Schizophoria* sp. **A**, **B**. Incomplete ventral valves, PKUM02-0345 (**A**) and PKUM02-0346 (**B**), in exterior (A_1, B_1) and interior (A_2, B_2) views. **C**. Incomplete ventral valve, PKUM02-0347, in exterior view. **D**. Incomplete ventral valve, PKUM02-0349, in interior view. **E**. Ventral valve, PKUM02-0348, in exterior view. **F**–**L**. *Schizophoria* (*Schizophoria*) *resupinata* (Martin, 1809). **F**. Ventral valve, PKUM02-0350, in exterior view. **G**, **H**. Dorsal valves, PKUM02-0351 (**G**) and PKUM02-0352 (**H**), in exterior (G_1, H_1) and interior (G_2, H_2) views. **I**. Ventral valve, PKUM02-0353, in interior view. **J**. SEM micrograph of juvenile shell, PKUM02-0354, in dorsal (J_1) and posterior (J_2) views. **K**. SEM micrographs of incomplete valve, PKUM02-0355, showing external costellae, nearly filled with shell substance openings of aditicules, and shell punctation; specimen in general (K_1) and enlarged (K_2) views. **L**. SEM micrograph, PKUM02-0356, showing external ornamentation, large openings of aditicules, and shell punctation.

cess to about one-third of the valve length (Fig. 26F, H). Anterior internal surface of both valves bears long radial grooves which are the deepest at the anterior margin (Figs. 26A_2, B, C_2, D_2, F_2, H_2; see also discussion in Brunton 1968: 18–19).

Shell ornamentation costellate with 18–22 costellae in 5 mm at 5 mm distance from valve apex, increasing by bifurcation; rib apertures at variable frequency, usually every 0.7–1.3 mm of the rib length.

Remarks.—Morphological characteristic of the species from the Muhua Formation suggests close relationship with *Rhipidomella michelini*. In comparison with the specimens of the species described from Ireland and Belgium by Brunton (1968) the Chinese specimens differ in having slightly larger apical angle of delthyrium. However, this difference is rather minor and general external aspect of both valves and details of shell ornamentation are the same.

Stratigraphic and geographic range.—This is rather common Mississippian species in Europe, but was also reported from China and Australia. The present material was found in samples D1, MH1, MH2, and Mu-42.

Superfamily Enteletoidea Waagen, 1884

Family Schizophoriidae Schuchert and LeVene, 1929

Genus *Schizophoria* King, 1850

Type species: *Conchyliolithus (Anomites) resupinatus* Martin, 1809; Viséan, Carboniferous; Derbyshire, England.

Subgenus *Schizophoria* (*Schizophoria*) King, 1850

Schizophoria (*Schizophoria*) *resupinata* (Martin, 1809)

Fig. 27F–L.

1809 *Conchyliolithus Anomites* (*resupinatus*); Martin 1809: 49, figs. 13, 14.

1968 *Schizophoria resupinata* (Martin) 1809; Pocock 1968: 80–86, pl. 18: 7; text-figs. 13–15.

1968 *Schizophoria resupinata* (Martin); Brunton 1968: pl. 2: 1–6.

1989 *Schizophoria* (*S.*) *resupinata* (Martin, 1809); Żakowa 1989: 103–106, pl. 1: 1–5; pl. 2: 1–5; pl. 3: 1–4; text-figs. 2–10.

2006 *Schizophoria resupinata* (Martin, 1809); Bassett and Bryant 2006: 504–508; pl. 6: 1–10; pl. 7: 1–16; text-figs. 5–7.

Material.—70 complete shells and more than thousand isolated dorsal and ventral valves, several very small shells usually not exceeding 2 mm in width are also present.

Remarks.—The specimens from China are characterized by elliptical shell outline, width exceeding length, with rather gently rounded lateral and anterior margins. The shell is ornamented with more or less uniform costellae, but those with aditicules are slightly and gradually higher just prior to the termination with the aditicules' apex (Fig. 27K, L). Those of aditicules which are filled with shell substance terminate with a small opening, in diameter similar to that of puncta, about 25μm (Fig. 27K_2; see also Jin et al. 2007). In some specimens the openings of aditicule, especially those near the anterior margin, remain quite large attaining 120 μm in diameter (Fig. 27L).

Schizophoria (*Schizophoria*) *resupinata* is divided by some authors (e.g., Demanet 1934; Bond 1942; Pocock 1968) into several varieties which are regarded by some other as subspecies. Although the material from Muhua is numerous and well preserved, it is represented generally by disarticulated immature valves. This causes some difficulties in identifying it with any of these varieties or subspecies. Moreover, as Bassett and Bryant (2006) noted, some shell features are quite variable and their range should be studied carefully before separating stocks.

Stratigraphic and geographic range.—The species is one of the commonest form in sample MH1. It was revealed also in samples DPS-3, GB, Mu-42, and MH2. *Schizophoria (Schizophoria) resupinata* is a widely recognizable species ranging from the Late Devonian till the late Carboniferous (Pennsylvanian; K–D zones according to Pocock 1968).

Schizophoria sp.

Fig. 27A–E.

Material.—30 fragmentary single valves.

Remarks.— Although the described material is fragmentary it likely represents the genus *Schizophoria* based on the characteristic ventral muscle platform. This form, however, cannot be assigned to the species described above because it is distinguished by having a clearly parvicostellate shell ornamentation. There are usually about 8–9 stronger costae which appear near the beak and continue to the anterior margin of valves. Some additional stronger costellae may appear later during growth. At 5 mm from beak there are 4–8 weaker costellae between each pair of stronger ones. Aditicules are very rare or not observed. Valves are thin-shelled and densely punctate. In lateral profile the ventral valves are weakly convex posteriorly but concave in the middle region. Most probably this form represents a new species but it is not possible to define it more precisely due to insufficient material.

Stratigraphic and geographic range.—This species occurs in sample GB, MH1, and D2.

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