New bizarre micro-spiriferid brachiopod from the Early Carboniferous of China

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The verneuiliid brachiopod *Changshunella yangi* gen. et sp. nov. is described from the Early Carboniferous Muhua Formation of Guizhou, China. This rather unusual form is characterized by having very small shell dimensions (2.6–4 mm in length), a very high flat procline ventral interarea, and by having three prominent plications on both valves that are arranged in opposed folding; the last feature is characteristic for the family Verneuiliidae. We suggest that the family has been derived from an offshoot of the stock that produced the superfamilies Spiriferoidea, Paeckelmanelloidea, and Brachythyridoidea by developing opposed folding and loss of dental plates or dental adminicula as exemplified by *Verneuilia* and *Changshunella* gen. nov.

Key words: Brachiopoda, Verneuiliidae, Early Carboniferous, China.

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Introduction

The family Verneuiliidae is a minor and poorly known group of brachiopods with peculiar external morphology that somewhat resembles some athyridids or zeillerioids, but remains enigmatic. Since the erection of the genus *Verneuilia* Hall and Clarke, 1893, it has been difficult for researchers to establish the systematic relationships of this genus and its allies above the family level due to their rarity and the lack of confident data on their internal structures. Schuchert (1929) was the first who created the subfamily Verneuiliinae within the family Spiriferidae. He placed two genera in the new subfamily, i.e., *Verneuilia* and *Metaplasia* Hall and Clarke, 1893, the latter being since transferred to the Ambocoeliidae. Ivanova (1960: 272) listed the Verneuiliinae separately, but placed *Verneuilia* in association with the plicate ambocoeliid genera *Metaplasia* Hall and Clarke, *Spinoplasia* Boucot, and *Plicoplasia* Boucot. In the old version of the Treatise (Williams et al. 1965) *Verneuilia* was treated as a sole member of the superfamily and family uncertain (Pitrat 1965: H727). In some Chinese works, *Verneuilia* was placed under the family Cyrtinidae Fredericks, 1911 (Wang et al. 1966; Zhang et al. 1983). Brunton (1984) put the family Verneuiliidae into the superfamily Reticulariacea, in which he placed *Verneuilia* and *Minythyra* Brunton, 1984. Blodgett and Johnson (1994) and Carter et al. (1994) attributed this group to the superfamily Ambocoelioidea George, 1931, including three genera *Verneuilia*, *Minythyra*, and *Nuguschella* Tjazheva, 1960. At the same time Gourvennec (1994) listedVerneuiliidae under the superfamily Spiriferacea? King, 1846.

In this paper we report a new genus and species of bizarre micro-spiriferid *Changshunella yangi* recovered by acid dissolution of a limestone lens sample (MH-1) bearing very abundant megafossils from the Lower Carboniferous of South China (Fig. 1). The sample was collected near the base of the Muhua Formation (middle Tournaisian) in the vicinity of the Muhua III Section of Hou et al. (1985: 11), Changshun, Guizhou, Southern China. The GPS coordinates of the sampling site is N 25°47'59'' and E 106°24'11''. Previously, only one genus and species, *Muhuathyris circularis* Sun, Ma, Baliński, and Zhang, 2004, has been described from the same sample (Sun et al. 2004). Baliński (1999) briefly described some brachiopods from a nearby outcrop but from a slightly higher horizon than the current sample. Recently, a new aulostegoid micro-productid was described from samples Mu-42 and M2-8 (Baliński and Sun in press). The silicified shells studied here are rather unusual in having very small size, very high flat procline ventral interarea, which is usually higher than the valve length, and in having opposite folding of radial plicae in a peculiar arrangement (see description below). The new form is generally similar to *Verneuilia* in having a high ventral interarea, opposed folding, and in lacking dental plates but differs in having an additional median plication on both valves.

All the described specimens are housed in the Geological Museum of Peking University (abbreviated as PKUM).

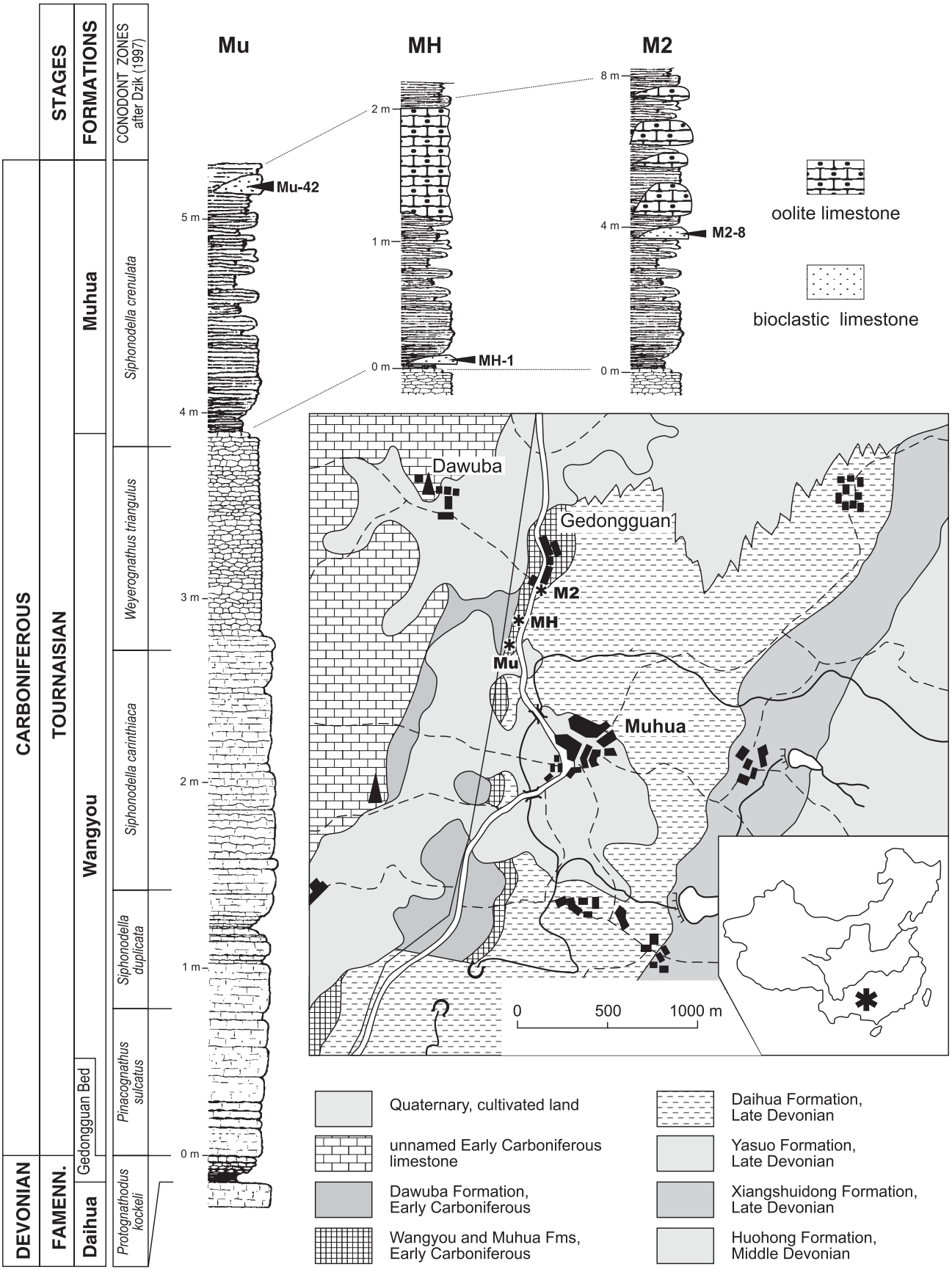

Fig. 1. Lithologic sections of the Late Famennian to Tournaisian sequence and its location at Muhua, Guizhou province, south China; position of samples with silicified brachiopod fauna is marked. Partly after Dzik (1997) and Olempska (1999), modified.

Systematic paleontology

Suborder Spiriferidina Waagen, 1883

[*nom. correct.* Pitrat, 1965: H668 (*pro* suborder Spiriferacea Waagen, 1883: 447)]

[*emend.* Carter, Johnson, and Gourvennec, in Carter et al., 1994: 330]

Family Verneuiliidae Schuchert, 1929

[*nom. transl.* Brunton, 1984: 101 (*ex* Verneuiliinae Schuchert, in Schuchert and LeVene, 1929: 21)]

Type genus: *Verneuilia* Hall and Clarke, 1893.

Emended diagnosis.—Transverse to subcircular, biconvex, with opposed folding forming lobate to metacarinate anterior margins; ventral interarea narrow to full width of valves, apsacline to procline, with open delthyrium or restricted by the apical pseudodeltidium; hinge line commonly denticulate; growth lines without capillae; dental plates or dental adminicula absent.

Discussion.—Four genera are assigned to this family: *Verneuilia* Hall and Clarke, 1893, *Minythyra* Brunton, 1984, *Nuguschella* Tjazheva, 1960, and the new genus *Changshunella* described herein. Previously, some researchers placed verneuiliids under a different family or superfamilies, such as Cyrtinidae Frederiks, 1911 (Wang et al. 1966: 590; Zhang et al. 1983: 374), Reticulariacea Waagen, 1883 (Brunton 1984), Ambocoelioidea George, 1931 (Blodgett and Johnson 1994; Carter et al. 1994), and Spiriferacea? King, 1846 (Gourvennec 1994).

Although some members of the verneuiliids possess a cyrtiniform shell reminiscent of the Cyrtinidae, none of the verneuiliids is known with a punctate shell structure. According to Carter et al. (1994), the impunctate and punctate spiriferid brachiopods are placed in different orders. The presence of a denticulate hinge line in both *Verneuilia* (Brunton 1984; Gourvennec 1994) and the new genus *Changshunella* strongly suggests that the verneuiliids neither belong to the Reticulariacea nor Ambocoelioidea; they may have close affinity with spiriferids having a denticulate hinge line. According to the recently revised classification of the spiriferid brachiopods (Carter et al. 1994), all denticulate spiriferids are grouped into the three superfamilies, Spiriferoidea King, 1846, Paeckelmanelloidea Ivanova, 1972, and Brachythyridoidea Frederiks, 1924. Gourvennec (1994) considered assigning Verneuiliidae to the superfamily Spiriferacea (= Spiriferoidea proposed in Carter et al. 1994), however, the lack of dental plates or dental adminicula in verneuiliids does not support this viewpoint, although the condition exceptionally can also be observed in spiriferoids. Internally the verneuiliids might fit into the Brachythyridoidea but the latter generally have a narrow hinge line and rounded cardinal extremities. Furthermore, none of spiriferoids, paeckelmanelloids or brachythyridoids is known to have opposite folding. In the current paper we maintain verneuiliids as a separate family of the suborder Spiriferidina and are reluctant to assign them to any of the three superfamilies characterized by denticulation unless they are regrouped in one superfamily. Alternatively, verneuiliids could have their own superfamily, namely Verneuilioidea, derived from an offshoot of the same stock that produced the superfamilies of Spiriferoidea, Paeckelmanelloidea and Brachythyridoidea by developing opposite folding and loss of dental plates or dental adminicula.

Genus *Changshunella* nov.

Type species by monotypy: *Changshunella yangi* gen. et sp. nov.

Etymology: From Changshun, the county of the type locality.

Diagnosis.—Small sized, transverse, ventribiconvex verneuiliids with very high and flat, procline ventral interarea. Delthyrium narrowly elongate triangular, covered by convex pseudodeltidum. Hinge line denticulate. Ventral valve with three prominent round to medially grooved compound plications. Dorsal valve with three simple plications. Flanks smooth. Ornament of growth lamellae only. Ventral interior with dental ridges. Dorsal interior with well-developed bilobate and striated cardinal process (ctenophoridium), lack of crural plates.

Occurrence.—Lower Carboniferous, Tournaisian. Muhua, Changshun County, Guizhou, China.

Changshunella yangi gen. et sp. nov.

Figs. 2–6.

Holotype: Dorsal valve PKUM02-0035 illustrated on Fig. 3C. Other materials examined: 18 ventral valves and 30 dorsal valves.

Type locality and horizon: Muhua III section, Muhua, Changshun County, Guizhou, China (Fig. 1; see also Hou et al. 1987: 11, fig. 3). The GPS coordinator is N 25°47'59'' and E 106°24'11''. About 0.2 m above the base of the Muhua Formation, conodont *crenulata* Zone (middle Tournaisian).

Etymology: This species is named for the late Professor Shifu Yang, of the Chinese Geological University at Beijing, in recognition of his contributions to the study of the Carboniferous brachiopods of Southern China.

Diagnosis.—Shell small, transverse and ventribiconvex with denticulate hinge line; maximum width at hinge line. Ventral valve hemipyramidal with a very high and flat, procline, triangular ventral interarea. Delthyrium narrowly elongate triangular, at least apically covered by convex pseudodeltidum. Dorsal valve gently convex, transverse triangular to trapezoidal in outline. Both valves medially plicate, with three prominent round to medially grooved plications on dorsal valve and three compound plications on ventral valve. Flanks generally smooth. Ornament of growth lamellae only. Ventral interior with dental ridges. A short median ridge may be present apically. Dorsal interior with well-developed ctenophoridium; crural plates or dorsal adminicula and median septum lacking.

Description.—The shell is small in size, generally 2.6–4 mm in length and 5–8 mm in width, transverse and ventribiconvex. Ventral valve is broadly triangular in outline (Fig. $2A_3$, B_2, B_3, H_1) with a very high, vertically striated ventral interarea that is moderately to strongly procline (Fig. $2A_1$,

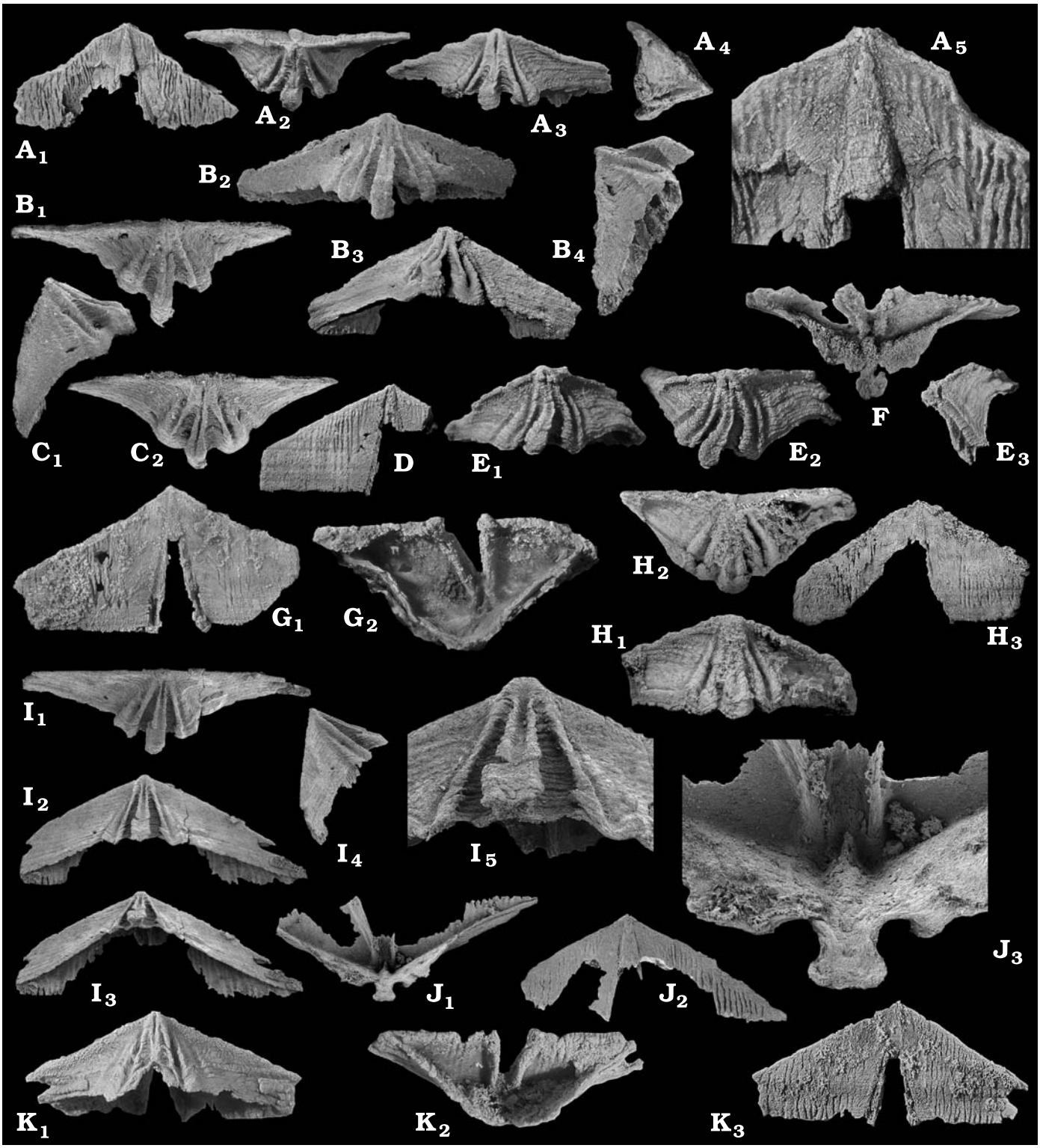

Fig. 2. Ventral valves of *Changshunella yangi* gen. et sp. nov. Muhua III section, Muhua, Changshun County, Guizhou, China. **A**. PKUM02-0023, in posterior (A_1), ventral (A_2), anterior (A_3), and lateral (A_4, anterior to left) views, and enlargement of part of ventral interarea showing the pseudodeltdium (A_5). **B**. PKUM02-0024, in ventral (B_1), anterior (B_2),), inclined anterior (B_3), and oblique lateral (B_4) views. **C**. PKUM02-0025, in oblique lateral (C_1) and ventral (C_2) views. **D**, PKUM02-0026 in posterior view. **E**. PKUM02-0027, in anterior (E_1), ventral (E_2), and lateral (E_3) views. **F**. PKUM02-0028, in internal view. **G**. PKUM02-0029, in posterior (G_1) and internal (G_2) views. **H**. PKUM02-0030, in anterior (H_1), ventral (H_2), and posterior (H_3) views. **I**. PKUM02-0031, in ventral (I_1), inclined anterior (I_2), more inclined anterior (I_3), and oblique lateral (I_4) views, and enlargement of part of the valve in inclined anterior view (I_5). **J**. PKUM02-0032, in internal (J_1), posterior (J_2), and enlarged internal view (J_3). **K**. PKUM02-0042, in anterior (K_1), internal (K_2) and posterior (K_3) views. B, C, I, and J are SEM images. All × 6 except A_5, I_5, and J_3 × 20.

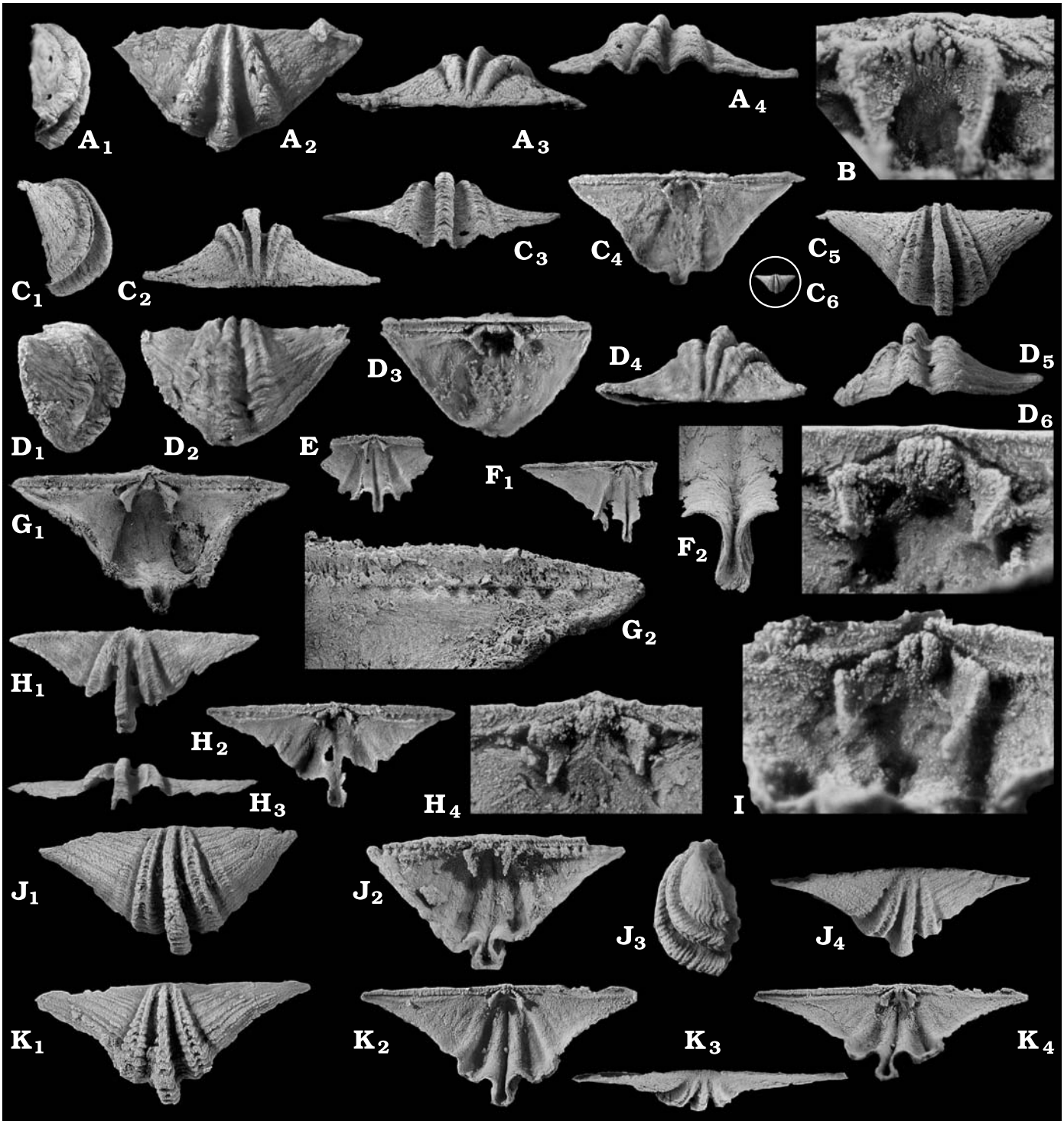

Fig. 3. Dorsal valves of *Changshunella yangi* gen. et sp. nov. Muhua III section, Muhua, Changshun County, Guizhou, China. **A**. PKUM02-0033, in lateral (A_1), dorsal (A_2), posterior (A_3) and anterior (A_4) views. **B**. PKUM02-0034, cardinalia in ventral view showing the striated cardinal process. **C**. PKUM02-0035, holotype in lateral (C_1), posterior (C_2), anterior (C_3), internal (C_4), and dorsal (C_5 and C_6) views. **D**. PKUM02-0036, in lateral (D_1), dorsal (D_2), internal (D_3), posterior (D_4), and anterior (D_5) views, and cardinalia in ventral view showing the striated cardinal process (D_6). **E**. PKUM02-0037, internal view showing the trough-like median furrow corresponding to the external median plication. **F**. PKUM02-0038, interior of an incomplete valve showing the trough-like median furrow corresponding to the external median plication in general (F_1) and more detailed (F_2) views. **G**. PKUM02-0039, internal view (G_1) and enlargement of lateral hinge area showing a row of accessory sockets (G_2). **H**. PKUM02-0040, in dorsal (H_1), internal (H_2) and anterior (H_3) views, and cardinalia in ventral view (H_4) showing the cardinal process developed from secondary shell between apical inner socket ridges and crural bases. **I**. PKUM02-0041, cardinalia in ventral view showing the bilobate cardinal process. **J**. PKUM02-0043, in external (J_1),internal (J_2), lateral (J_3) and posterior (B_4) views. **K**. PKUM02-0044, in external (K_1), internal (K_2), posterior (K_3) views, and interior in anterior view (K_4). C_1–C_3, C_5, C_6, E–G are SEM images. All × 6 except C_6 × 1, B, D_6, F_2, G_2, H_4, and I × 20.

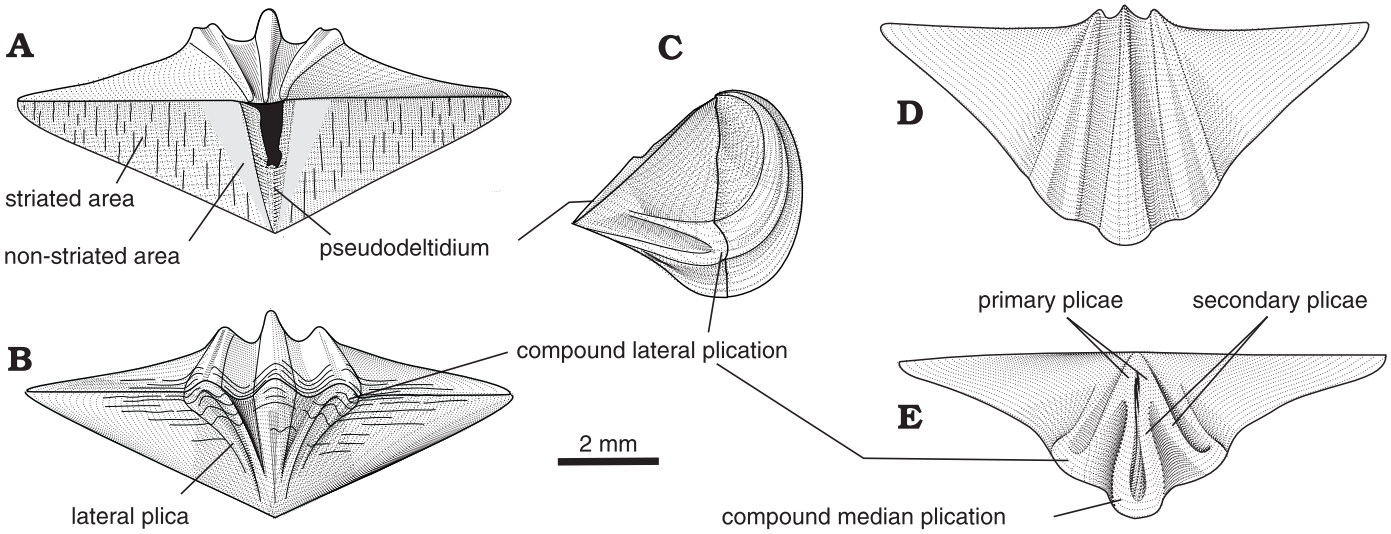

Fig. 4. Reconstruction of conjunct shell of *Changshunella yangi* gen. et sp. nov. in posterior (**A**), anterior (**B**), lateral (**C**), dorsal (**D**), and ventral (**E**) views.

A_4, D, G_1, H_3, J_2, K_3). The ventral interarea is strikingly flat, transverse triangular, with height generally larger than the length of the valve; beak is minute. Most part of the ventral interarea bears vertical striation except the triangular areas lateral to the delthyrium (Figs. $2A_5$, D, 4A). The cardinal angles are acute. Slopes of the ventral valve are slightly concave to make the valve hemipyramidal in form (Fig. $2A_4$, K_1). In lateral profile the valve is usually slightly concave (Fig. $2A_4$, C_1, I_4). In some specimens the posterolateral slopes merge with lateral edges of the ventral interarea to form cavity-free, thin-bladed extensions (Fig. $2B_2$, F). The delthyrium is narrowly elongate triangular with an apical angle about 18–21°. Although a convex pseudodeltidum is observed in all ventral valves only to cover two-fifth to half of the delthyrium apically, it is possible that it may, in fact, fully cover the delthyrium because in several specimens remnants of the plate can be traced along the edges of the delthyrium (Fig. $2A_1$, G_1).

Dorsal valve is gently convex, transverse triangular to trapezoidal in outline. Dorsal interarea is narrowly rectangular, flat or curved, orthocline in less convex specimens (Fig. 3E–G, H_2) and apsacline in gently convex specimens (Fig. $3C_4$, D_3), with width/height ratio of 23–28. Both valves are medially plicate.

The general development of plications on the ventral valve is very peculiar. The valve bears three round major plicae each composed of a pair of subordinary plicae (Figs. 4B, E, 5A). The medial four subordinary plicae originate by bifurcation from two wide and flat primary plicae separated by a very narrow but deep interspace in the umbonal region (Fig. $2A_3$, B_1, C_2, I_5, K_1). There are also two lateral plicae, one on each flank of the valve, that are intercalated slightly later than the bifurcations of the primary plicae (Fig. 5A). The inner branch of each primary plica runs anteriorly very close to the other to form a single and high compound median plication (Fig. $2A_3$, B_1, C_2); the interspace between the primary plicae continues anteriorly as a longitudinal groove on the top of the compound median plication. On the other hand, the outer branch of each primary plica extends forward divergently and adheres to the nearby simple intercalated lateral plica to form a medially grooved compound lateral plication. The interspaces between the lateral and median compound plications are rather profound and wide. Besides the lateral compound plication, flanks of the ventral valve are generally smooth but occasionally a weak and simple additional plication is developed (Fig. $2B_2$). Several ventral valves show evidence of growth deformation of external features (Fig. 2E).

The dorsal valve is covered medially with three prominent plications. Compared to the ventral plications, these on dorsal valve are developed from dorsal beak region independently (Figs. $3A_3$, C_2, D_4, J_1, K_1, 5B). The median plication is very high, relatively narrow and carinate posteriorly, becoming wider and round anteriorly, occasionally with a shallow median furrow (Fig. $3C_5$). On some specimens the median plica attains great height anteriorly (Fig. $3C_1$, C_2, H_1) being slightly constricted at its base; it must have been produced by distinct outward plication of the mantle (Fig. 3E, F,

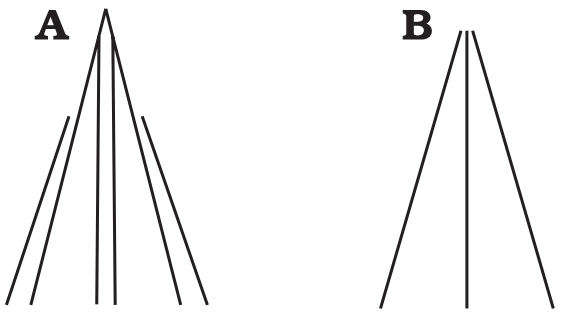

Fig. 5. Plication patterns of ventral (**A**) and dorsal (**B**) valves of *Changshunella yangi* gen. et sp. nov.

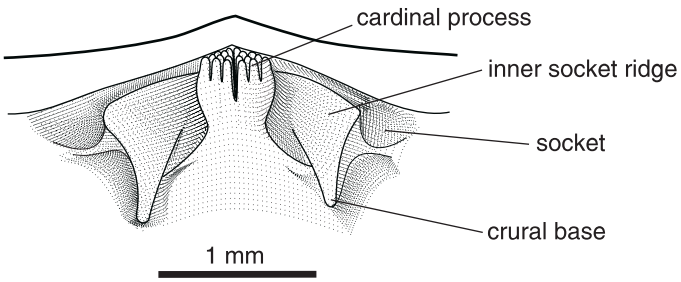

Fig. 6. Reconstruction of the cardinalia of *Changshunella yangi* gen. et sp. nov.

J_2) which later during the growth was withdrawn during simultaneous infilling of the emptied space with secondary shell material (Figs. 3E, F, G_1). The lateral plicae are usually medially grooved with a weak and shallow median furrow on them (Fig. $3C_2$, C_5, D_2, D_4, H_1, J_1, K_1). In our collection, only two dorsal valves have none of the plications medially grooved and two specimens have all plications medially grooved. The interspaces between the lateral and median plications are very deeply concave. Lateral slopes of the dorsal valve are smooth. Although all the specimens are preserved as disarticulated valves, judging from the width of the plications and interspaces at the anterior margin it seems obvious that the dorsal plications are arranged in opposed folding with their counterparts on ventral valve, forming a trilobate anterior margin (Fig. 4B, D). The presence of a median furrow or sulcus in the apical region of the ventral valve (i.e., in early juvenile stage) would suggest that this opposed folding may be derived from a bilobate stage. Surfaces of both valves are covered with growth lamellae.

Ventral valve interior reveals well-developed dental ridges (Fig. 2F, G_2, J_1, J_3, K_2), but no dental plates or dental adminicula. Some specimens show a short median ridge at the posterior of the valve floor (Fig. $2J_3$) and others do not have this feature.

Dorsal valve interior reveals triangular to subcircular conical sockets. Inner socket ridges are high forming with crural bases subtriangular plate-like structures. The crural bases are antero-ventrally directed. The spiralium is not preserved. The cardinal process is relatively large and developed as an outgrowth of the secondary shell apically between the inner socket ridges (Fig. $3D_6$, H_4, I). In some specimens the cardinal process is bilobate (Fig. 3I) or knoblike while in others it is striated (Fig. 3B, D_6); this is probably a result of preservation. It is likely that the cardinal process of the new genus and species is both bilobate and striated (Fig. 6). There are neither crural plates nor median septum. In most specimens the reflection of the negative relief of plications and interspaces on the internal surface of the valve is generally indistinct, at least not as obvious as that of external surface except in the most anterior portion of the median plication (Fig. $3C_4$, D_3, G_1, H_2). Only in three dorsal valves we observed a prominent trough-like median furrow corresponding to the external median plication (Fig. 3E, F, K).

Discussion

At first glance, the external morphological features of the ventral valve of the new genus and species give the impression of a hypoplastic young of some kind of paeckelmanelloid spiriferids because of the growth form, high and procline ventral interarea and denticulate hinge line reminiscent of some paeckelmanelloids. We have considered the possibility that the new genus and species represents young specimens of co-occurring *Voiseyella* sp. sharing with the latter some morphological features, such as transverse outline, high and procline ventral interarea, denticulate hinge line, etc. However, *Voiseyella* sp. differs from the new genus and species externally in having an extremely transverse outline, distinct ventral sulcus and medially deep-furrowed dorsal fold, and internally in having dental plates. Furthermore, the growth pattern of plications on the ventral valves of the new genus and species differs markedly from that of *Voiseyella* sp. In the latter all ventral plications are simple whereas in the Chinese form they are of a compound nature. Further, *Changshunella yangi* gen. et sp. nov. has the delthyrium covered by a well-developed pseudodeltidum. Instead of the pseudodeltidum a deltidial plate is attached apically beneath the delthyrium in *Voiseyella* sp. The fully differentiated internal structures of the dorsal valves of *C. yangi* suggest strongly that they are mature specimens. Finally, it is noteworthy that opposed folding is not known in *Voiseyella* or other paeckelmanelloids. Thus, it is unlikely that *Changshunella yangi* comprises immature specimens of *Voiseyella* or other paeckelmanelloids.

Morphologically, the new genus is similar to the verneuiliid genera *Verneuilia* and *Nuguschella*. All of them have opposed shell folding and lack dental plates and median septum. To our knowledge the family Verneuiliidae is the unique group among spiriferids with opposed shell folding. This is why we put the new genus within this family. Besides the opposed folding, the new genus shares also many other features with *Verneuilia*, e.g. high ventral interarea, well-developed pseudodeltidium, denticulate hinge line, smooth and concave lateral slopes, lack of dental plates or dental adminicula, etc. The new genus differs from *Verneuilia* in having one median plication and a pair of rounded to medial-grooved lateral plications on each valve, whereas the latter has only one pair of carinate to rounded plications on each valve. The ventral interarea is procline in the new genus while in *Verneuilia* it is catacline to apsacline. Gourvennec (1994) observed a striated cardinal process in a specimen of *Verneuilia oceani* that is located on an elevated cardinal platform prolonged anteriorly by a narrow median shaft. This cardinal process is basically similar to the one of the new genus except for the median shaft, which is not observed in *Changshunella*. Although Gourvennec (1994) considered the median shaft in front of the cardinal process as a possible area for attachment of the anterior adductor muscle, it seems to be a pathological feature because this specimen does not

have well-defined hinge plates as can be presumed from Gourvennec's (1994) description and figures. The internal features described by Gourvennec (1994) are different from those in *Verneuilia langenstrasseni* recorded by Blodgett and Johnson (1994) from Alaska as well as in the new genus. According to Blodgett and Johnson (1994) *Verneuilia langenstrasseni* has short crural plates which merge with well-defined triangular hinge plates. Although the cardinal process differs in appearance in *V. oceani* and *V. langenstrasseni*, as in the new genus, this is probably only the result of preservation and cannot be treated as a constant character. However, the Alaskan species differs from *V. oceani* and *Changshunella* gen. nov. in having crural plates and one to two plications on the lateral flanks. It is thus more likely that *Verneuilia langenstrasseni* can be assigned to *Nuguschella*, although the former differs in having carinate plications. *Changshunella* gen. nov. differs from *Nuguschella* in having a procline ventral interarea, median plication on both valve, and in lacking crural plates and plications on lateral flanks.

Acknowledgments

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