Post-extinction brachiopod faunas from the Late Permian Wuchiapingian coal series of South China

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This paper describes fourteen brachiopod species in eleven genera from the Late Permian Wuchiapingian Coal Series (Lungtan Formation) of South China. Of these, the shell bed fauna from the basal Lungtan Formation is interpreted to represent the onset of the recovery of shelly faunas in the aftermath of the Guadalupian/Lopingian (G/L) mass extinction in South China. The post-extinction brachiopod faunas in the Wuchiapingian are characterized by the presence of numerous Lazarus taxa, survivors, and newly originating taxa. These elements capable of adapting their life habits were relatively more resistant to the G/L crisis. The post-extinction faunas, including survivors and the elements originating in the recovery period, have no life habit preference, but they were all adapted to a variety of newly vacated niches in the Late Permian oceans. Two new species, *Meekella beipeiensis* and *Niutoushania chongqingensis*, are described, and two Chinese genera, *Niutoushania* and *Chengxianoproductus*, are emended based on re-examination of the type specimens and new topotype materials from the Lungtan Formation.

Key words: Brachiopoda, mass extinction, faunal recovery, Permian, Wuchiapingian, Guadalupian, Lopingian, South China.

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Introduction

Several statistical studies of the Permian marine benthos clearly indicate that the Late Permian extinctions in South China comprised two phases. The first pulse took place in the Guadalupian/Lopingian (G/L) transition and the second at the end-Permian (Jin et al. 1994; Stanley and Yang 1994). Like the end-Permian biotic crisis, the G/L mass extinction also resulted in dramatic declines in diversity and abundance of the marine assemblages. The leading benthos (including sponges, corals, bryozoans, echinoderms, foraminifers, brachiopods, gastropods, bivalves, and ammonoids) all suffered this catastrophe (Jin et al. 1994; Stanley and Yang 1994; Hallam and Wignall 1997; Shi et al. 1999; Wang and Sugiyama 2000; Yang et al. 2000). Nevertheless, in sharp contrast to the well-understood end-Permian extinction and subsequent recovery (e.g., Erwin 1993, 2000, 2001), the G/L mass extinction remains problematic in terms of magnitude, tempo and causes of extinction, and biotic post-extinction recovery has received far less attention. With respect to the Brachiopoda in South China, the G/L extinction saw a change from the extremely abundant and ecologically diverse late Guadalupian faunas to the restricted and impoverished faunas in the early Wuchiapingian followed by the rapid faunal diversification and radiation in the late Wuchiapingian (Shen and Shi 1996). In this paper, we report a brachiopod shell bed from the basal part of the Lungtan Coal Series (early Wuchiapingian) in the Chongqing and eastern Sichuan areas of South China. This collection provides the first record of a biostratigraphically well constrained post G/L extinction recovery faunas from the early Wuchiapingian in South China. The majority of brachiopod genera preserved in the Lungtan shell bed are commonly present in other Wuchiapingian deposits in South China (e.g., Zhan 1979; Liao 1980b; Wang et al. 1982; Zeng 1996). This early Wuchiapingian association is typical of faunas dominated by orthotetid, productid, and spiriferid brachiopod genera whose subsequent diversification marks the post-extinction recovery of Late Permian shelly faunas. The Lungtan fauna therefore signals some information about the composition of shelly faunas from the post-extinction recovery interval of the early repopulation stage (Kauffman and Harries 1996) following the G/L extinction.

In addition, several taxa from slightly higher horizons of the Lungtan Formation are also described here to provide supplementary information for post-extinction recovery and taxonomy of the Wuchiapingian brachiopod faunas. Several related type specimens housed in the Nanjing Institute of Geology and Paleontology, Chinese Academy of Sciences have been examined in this study (by ZQC, in 2000).

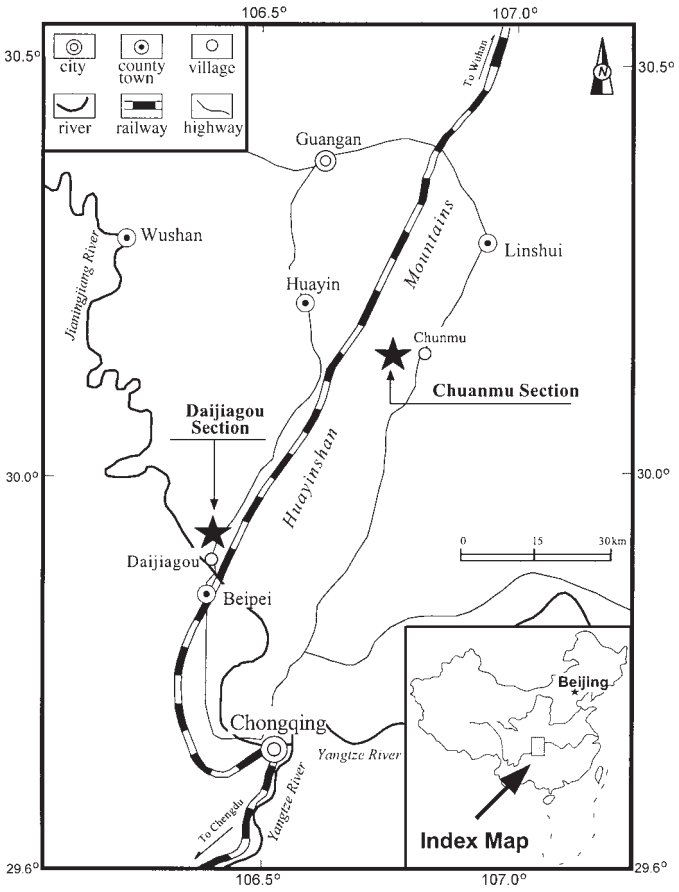


Fig. 1. Generalized map showing the locations of the Daijiagou and Chuanmu sections.

Institutional abbreviations.—NMV P, National Museum of Victoria, Department of Palaeontology, Melbourne, Australia; NIGP, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China.

Stratigraphy of the new material

The described specimens were collected from the Lungtan Formation at two outcrop sections: the Daijiagou section in Beipei, near Chongqing City and the Chuanmu section in Linshui, eastern Sichuan Province (Fig. 1). At Daijiagou, the Lungtan Formation is well exposed and overlies unconformally above the Maokou Formation of the Wordian–Capitanian age, and this formation can be subdivided into five lithologic members (Zeng et al. 1995). Of these, the economically important coal seams are concentrated in the lower three members (Fig. 2). The majority of the described material came from a shell bed in the lower part of the first member (Fig. 2A), which lithologically comprises alternating black mudstone, calcareous sandstone and bioclastic limestone. Eight brachiopod species are identified from the shell bed: *Magniderbyia* sp. indet., *Perigeyerella costellata* Wang, 1955, *Edriosteges poyangensis* (Kayser, 1883), *Chengxianoproductus* cf. *changxingensis* Liao and Meng, 1986, *Spinomarginifera lopingensis* (Kayser, 1883), *Niutoushania chongqingensis* Chen sp. nov., *Permophricodothyris grandis* (Chao, 1929), and *Paraspiriferina* sp. In addition, *Meekella pusilloplicata* Liao, 1980b is preserved in the 3rd member, and *Meekella beipeiensis* Chen sp. nov., *Me. kueichowensis* Huang, 1933, and *Transennatia gratiosa* (Waagen, 1884) appear in the bioclastic limestone of the 4th member (Fig. 2A). *Transennatia gratiosa*, *Peltichia zigzag* (Huang, 1933), and *Spinomarginifera alpha* Huang, 1932 are identified from the 5th member, from which Shi et al. (2002) also described extremely abundant specimens of *Permophricodothyris grandis*.

At the Chuanmu section numerous specimens of *Peltichia zigzag*, *Spinomarginifera alpha*, *Transennatia gratiosa*, *Edriosteges poyangensis*, and *Permophricodothyris grandis* were obtained from the upper Lungtan Formation (Fig. 2B). Of these, *P. grandis* is extremely abundant in the field. At Chuanmu, the upper Lungtan Formation comprises the basal coal seams with overlying calcareous sandstones, which are overlain by the dark limestone of the Changhsing Formation. The lithology, faunas and stratigraphic position (just below the Changhsingian limestone) indicate that the upper Lungtan Formation at Chuanmu can be correlated with the 5th member of the formation at Daijiagou (Fig. 2A, B).

Faunal correlations and age

Although most species persist throughout the whole Lungtan Formation, the brachiopod species from the basal Lungtan Formation at Daijiagou are characterized by abundant specimens of *Edriosteges poyangensis* and *Spinomarginifera lopingensis* and the presence of *Niutoushania chongqingensis* Chen sp. nov. and *Chengxianoproductus* cf. *changxingensis*. Of these, *E. poyangensis* is the most characteristic species of the lower Lungtan Formation in South China (Huang 1932; Zhan 1979; Liao 1980b; Zeng et al. 1995), reflected by its nomination as a zonal species by Liao (1980b). In addition, Hu (1989) created the *Niutoushania niutoushanensis* Assemblage to include the brachiopods from the lower Lungtan Formation; this zone was regarded as the first assemblage of the Wuchiapingian, and is slightly older than the *Edriosteges poyangensis* Assemblage of Liao (1980b). The brachiopods from the lower Lungtan Formation from eastern Sichuan and Chongqing areas have also been collectively referred to the *Edriosteges poyangensis–Spinomarginifera lopingensis* Assemblage by Zeng et al. (1995). Many species of the described fauna are also characteristic of the Zeng et al. assemblage, but the latter includes the taxa mainly from the upper part of the 1st member and 2nd member of the formation. Other elements, all being characteristic of the Lungtan Coal Series in South China, were also assigned to the *Edriosteges poyangensis* Assemblage by Liao (1980b). Liao's assemblage is, however, composed mainly of species from the 2nd member of the Lungtan Formation.

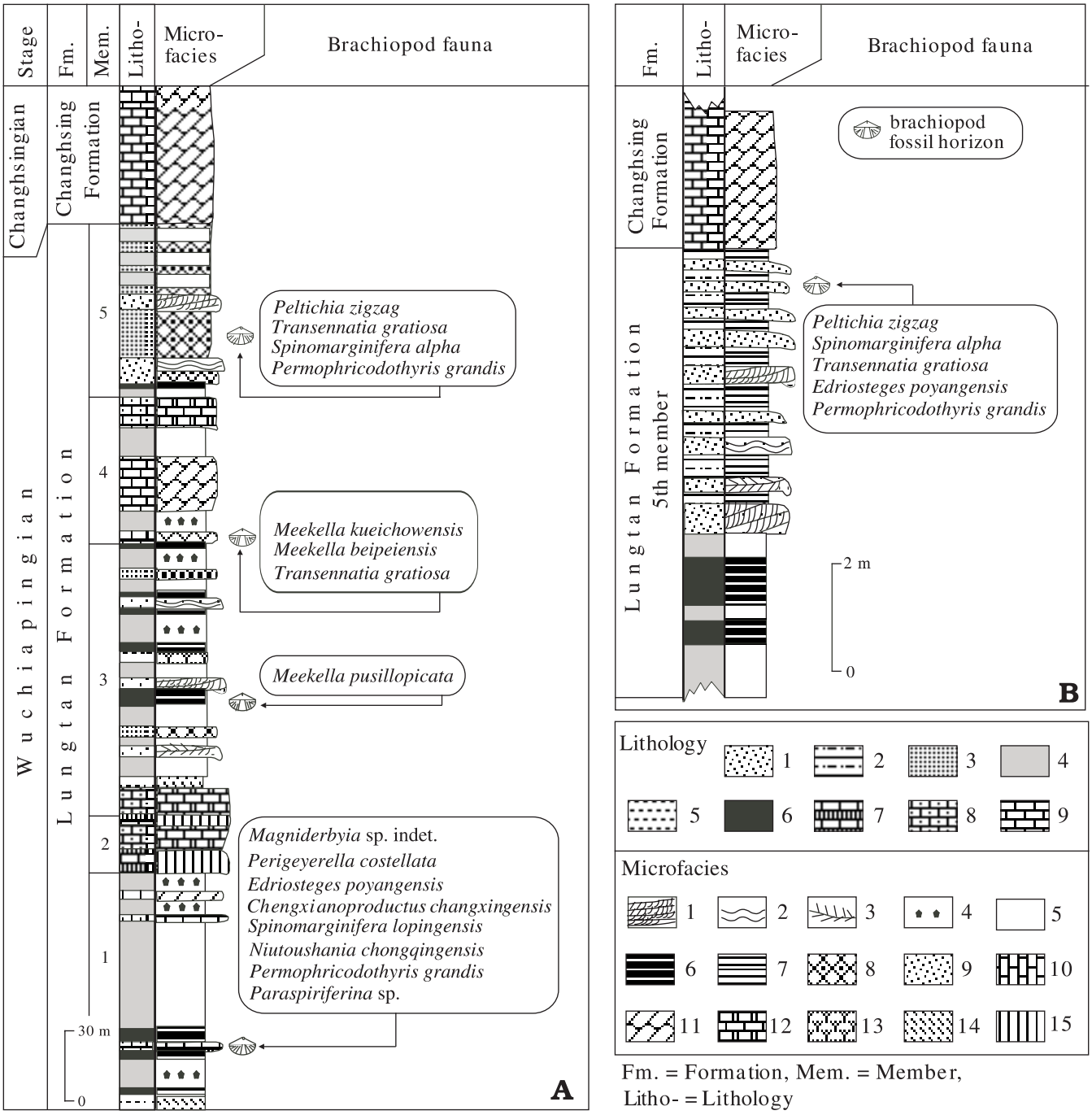


Fig. 2. Composite stratigraphy of the Lungtan Formation at the Daijiagou and Chuanmu sections, showing lithology, microfacies and fossil horizons. **A**. Daijiagou section. **B**. Chuanmu section. Lithology: 1, coarse sandstone; 2, alternating mudstone and sandstone; 3, siltstone; 4, fine sandstone; 5, clay; 6, coal seam; 7, cherty limestone; 8, bioclastic limestone; 9, limestone. Microfacies: 1, low-angle cross bedding; 2, wavy bedding; 3, bimodal cross bedding; 4, brackish water ironstone concretions; 5, black shale; 6, coal seam; 7, sandy mudstone; 8, siltstone; 9, quartz sandstone; 10, alternating siliceous shale and cherty limestone; 11, sparite; 12, grainstone-packstone; 13, roots (coal seats); 14, weathered clay; 15, cherty limestone.

Alternatively, in Chongqing *Edriosteges poyangensis* and other elements occur at the basal Lungtan Formation (1st member). *Spinomarginifera lopingensis* has also been reported from the upper Lungtan Formation in Guizhou (Liao 1980b) and Jiangxi (Wang et al. 1982). As such, we considered that the present fauna is slightly older than the above assemblages (Fig. 3), although it is also of early Wuchiapingian in age. In addition, the ammonoid *Roadoceras* sp. has also been found in the basal Lungtan Formation of the Huayinshan region (Sheng and Jin 1994), suggestive of an early Wuchiapingian age. The coal-bearing strata of the Lungtan Formation in South China are usually subdivided into five lithological members; each of which is easily correlated basinwide. These five stratigraphic units form two and

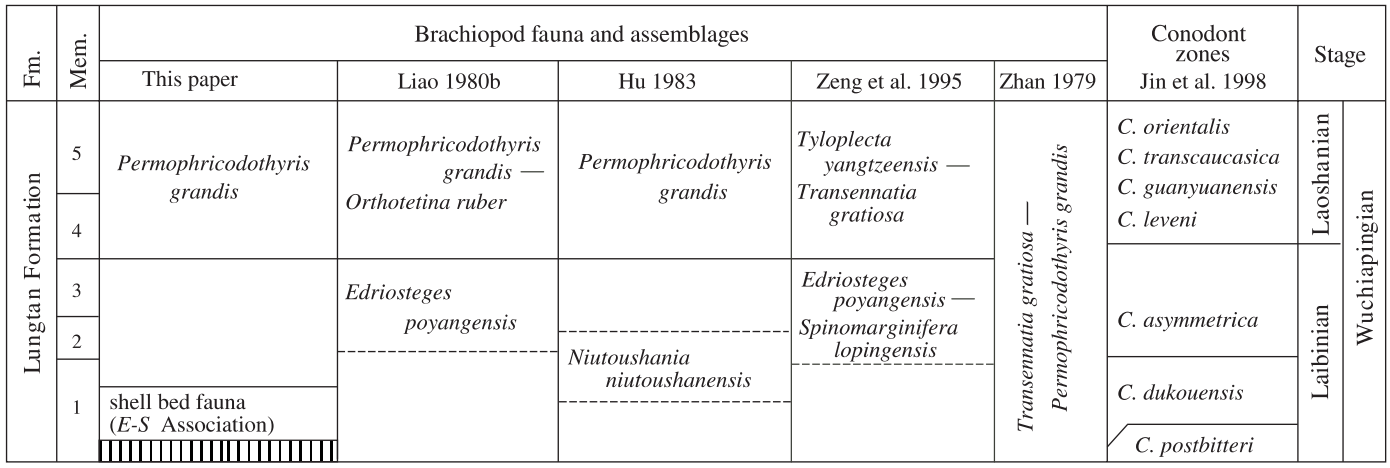


Fig. 3. Correlations of the described faunas with previously published brachiopod assemblages from South China. The dashed lines indicate that the zonal boundaries are not well defined.

a half distinctive third-order sequences (Shi et al. 2002). The intrabasin sequence stratigraphic correlation (Chen et al. 1998) shows that the first member of the Lungtan Formation containing the described fauna is correlated with the lower Laibinian (early Wuchiapingian) (Fig. 3), as defined by the conodonts *Clarkina postbitteri*, *C. dukouensis*, and *C. asymmetrica* zones, ammonoid *Roadoceras–Doulingoceras* Zone and fusulinid *Codonofusiella kweichowensis* Zone in the deep-water facies sequences (Mei et al. 1994; Jin et al. 1998). The brachiopod shell bed at the basal Lungtan Formation of Daijiagou indicates the first flooding event of the Wuchiapingian transgression in South China (Zeng et al. 1995; Chen et al. 1998), and its counterpart in the deep-water facies sequence is constrained as an early Laibinian age by the presence of the conodont *Clarkina dukouensis* Zone (Mei et al. 1999).

The brachiopod faunas from the 5th member of the Lungtan Formation at both the Daijiagou and Chuanmu sections are comparable and are dominated by a great abundance of *Permophricodothyris grandis*. Other important forms include *Peltichia zigzag*, *Transennatia gratiosa*, and *Spinomarginifera alpha*. Of these, *P. grandis* has been regarded as the nominal species of the Wuchiapingian *P. grandis–Orthotetina ruber* Assemblage from the southern Guizhou by Liao (1980b); *Transennatia gratiosa* was also referred to as the nominal species of the *Tyloplecta yangtzeensis–Transennatia gratiosa* Assemblage from the Huayinshan areas (Zeng et al. 1995). Zhan (1979) also proposed the *Transennatia gratiosa–Permophricodothyris grandis* Assemblage to accommodate the Lungtan faunas from northern Guangdong (Fig. 3). However, *Orthotetina ruber* and *Tyloplecta yangtzeensis*, both having a stratigraphic range from the Capitanian to Wuchiapingian (Liang 1990), are not present in our collection. As a result, these brachiopods from the 5th member are considered to be late Wuchiapingian in age.

Taphonomy and paleoecology of the Wuchiapingian faunas

***Edriosteges poyangensis–Spinomarginifera lopingensis* (*E–S*) Association**.—This association is preserved in the gray calcareous mudstone to argillaceous limestone of the basal Lungtan Formation (1st member; Fig. 2A) at the Daijiagou section, thus the substratum, inhabited by this association, may have been a muddy limestone (Fig. 4). As discussed above, this association is stratigraphically lower than the *Edriosteges poyangensis–Spinomarginifera lopingensis* Assemblage of Zeng et al. (1995), although they share the nominal species (Fig. 3). The taxa comprise seven brachiopod species: *Magniderbyia* sp., *Perigeyerella costellata*, *Edriosteges poyangensis*, *Chengxianoproductus* cf. *changxingensis*, *Spinomarginifera lopingensis*, *Niutoushania chongqingensis*, *Permophricodothyris grandis*, and *Paraspiriferina* sp. Of these, the productids are the most abundant and are represented by four species (about 57% of total species diversity). The orthotetids form the second largest group (two species), and the Spiriferida and Spiriferinida are each represented by one species.

Shell material of most brachiopod specimens in the *E–S* Association is relatively well preserved. Preservation as molds is observed where calcite shell material was subject to dissolution at the edges of sampled slabs due to solution of calcite leaving voids during burial. All specimens were recovered on surfaces of slabs split parallel to bedding to expose the concentrated shell material on resulting parts and counterparts. Whole and fragmented shells of the small aulostegid brachiopod *Edriosteges* dominate this association (Fig. 4). The second most abundant genus is *Spinomarginifera*. Other brachiopods common in the Lungtan fauna include *Magniderbyia*, *Chengxianoproductus*, and *Niutousha-*

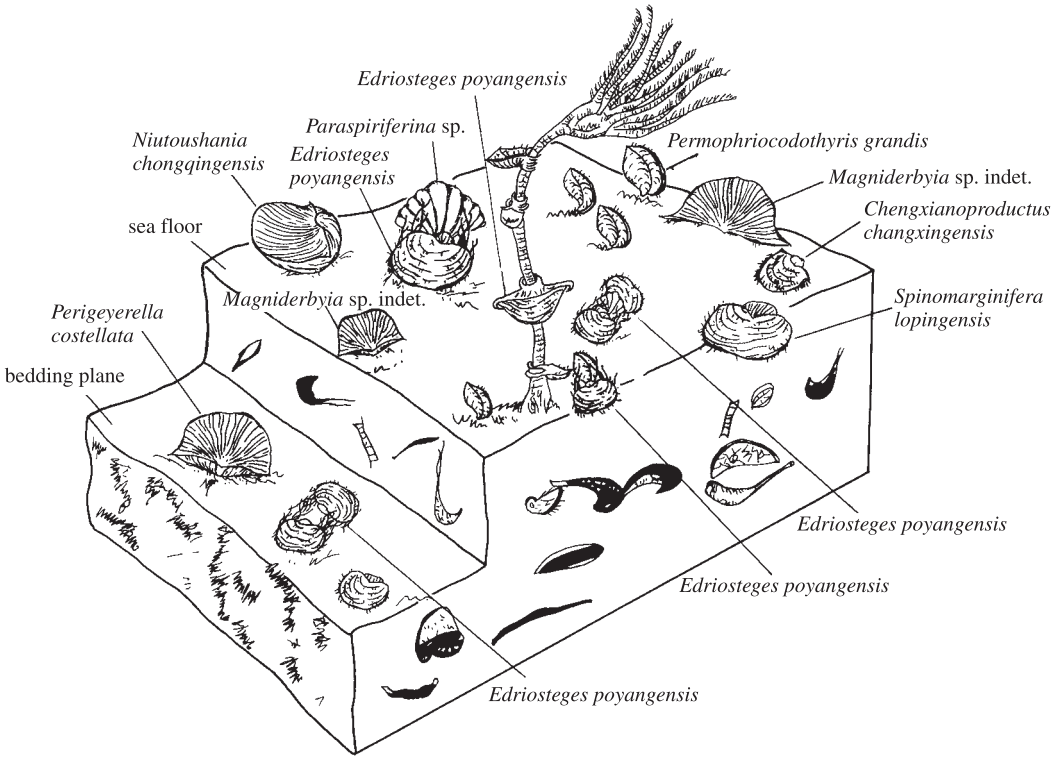


Fig. 4. Reconstruction of the *Edriosteges poyangensis–Spinomarginifera lopingensis* Association.

nia. Additional genera present include the orthotetid *Perigeyerella* and spiriferinid *Paraspiriferina* (both present in small numbers) and the poorly preserved spiriferid *Permophricodothyris*. Shells of *Permophricodothyris* are disarticulated and moderately fragmented with both valves orientated convex side up. The concavo-convex shells of the productids are randomly orientated, although significant numbers of specimens are convex side up. As a whole, other than *Permophricodothyris*, whose shells were mostly dissolved during burial, all valves are preserved articulated and without abrasion, indicating little post-mortem disturbance.

Of these constituents, both *Magniderbyia* and *Perigeyerella* possess large and strongly dorsibiconvex shells, an exaggeratedly posteriorly conical ventral umbo, and a large delthyrium from which the pedicle emerged. The reconstruction of the life habits of these forms (Grant 1976: 65) reveals that their strong pedicles were capable of attaching firmly to soft muddy or hard sandy substrates; the specialized, conical umbo was partly buried in mud to support the rest of the body above the substrate (Fig. 4).

Edriosteges has a concavo-convex profile, very thin shells with extremely strong, clasping spines along the hinge margin and some long, tubular body spines scattered on the ventral disc. In particular, these clasping spines suggest that *Edriosteges* had a similar life habit to that of *Linoproductus* (for reconstructions see Grant 1963). In both genera the spines grew from the hinge margins holding the shell to a crinoid stem or other floating objects so that the shells were suspended above the muddy substrate (Fig. 4). The tubular body spines anchored on or in the substrate and aided the stabilization of the much heavier valves (Brunton and Mundy 1988) when the shells continued to grow in size as the individual matured.

Both *Spinomarginifera* and *Chengxianoproductus*, which possess densely spinose concavo-convex shells, probably had a quasi-infaunal habit (*sensu* Rudwick 1970; Brunton 1987; Brunton and Mundy 1988) or quasi-endosedimentary (term of Walker and Miller 1992) habit. The functional morphology of *Spinomarginifera* is completely analogous to that of *Marginifera*. Accordingly, cluster spines of *Spinomarginifera*, like those of *Marginifera*, seem to have rooted the shell in a soft substrate (Fig. 4), as inferred by Grant (1968). *Chengxianoproductus* probably had a similar life habit to *Waagenoconcha* because both genera superficially resemble one another in all observed features of functional morphology. As such, like *Waagenoconcha*, *Chengxianoproductus* stabilized its shells using tubular body spines (Fig. 4), some of which possibly penetrated a little below the surface of a very soft sediment and prevented the shell from sinking too deeply (for further discussion see Grant 1966).

Niutoushania may have had an epifaunal (West 1977) or endosedimentary (Walker and Miller 1992) habit (Fig. 4). When compared with the above two productid genera, this genus has much larger and thicker shells, and thus its shells are much heavier than that of either *Chengxianoproductus* or *Spinomarginifera*. In addition, unlike these two genera, *Niutoushania* also has strongly concavo-convex valves and a

very shallow corpus cavity and thus required the support of its covering of dense spines to keep the heavy body from sinking into the mud.

Both spiriferids *Permophricodothyris* and *Paraspiriferina* (Fig. 4) had strong pedicle anchorage to the substrate, indicated by the presence of the open, large delthyrium in both genera. Furthermore, the dense, lamellose spines on both valves of *Permophricodothyris* imply that these spines may be employed to either stabilize the shell or prevent predation, similar to the body spines of some productids (see Leighton 2001).

Other taxa.—Several other taxa were collected from other levels above the shell bed in the Lungtan Formation. Of these other taxa, *Meekella pusilloplicata* was found in black mudstone interbedded with coal seams in the lower Lungtan Formation (3rd member; Fig. 2A) at the Daijiagou section. This species also has specialized shells with a high, irregularly conical ventral umbo and a large delthyrium, suggestive of a similar life habit to that of *Magniderbyia* and *Perigeyerella*.

At Daijiagou, *Meekella kueichowensis*, *Me. beipeiensis*, and *Transennatia gratiosa* are preserved in the dark bioclastic limestone directly overlying coal seams or black mudstones. The former two species stabilized their shells by a strong pedicle anchored firmly to the hard or soft substrate. The latter possesses a strongly concavo-convex shell and numerous tubular body spines, and thus can be inferred to have had a quasi-endosedimentary life habit similar to *Spinomarginifera*.

Permophricodothyris grandis, *Peltichia zigzag*, *Edriosteges poyangensis*, *Transennatia gratiosa*, and *Spinomarginifera alpha* are present in the yellow calcareous siltstone to sandstone in the upper part (5th member) of the Lungtan Formation at Chuanmu (Fig. 2B). These species are mostly preserved as molds. *Peltichia* was probably attached by pedicle-anchorage, indicated by the presence of a large foramen. Other fossils associated with these brachiopods include gastropods, bivalves, bryozoa and echinoids.

Implications for brachiopod recovery from the G/L extinction in South China

Like some opportunistic brachiopod faunas, the *Edriosteges poyangensis–Spinomarginifera lopingensis* Association occurring at the basal Lungtan Formation is also associated with an initial regional transgressive event of the early Wuchiapingian (Chen et al. 1998). However, the *E–S* Association contains a moderately diverse fauna (seven genera; see Figs. 4, 5). This is in contrast to opportunistic brachiopod faunas that usually have a rather low diversity and are dominated by one to two abundant elements (commonly chonetids) (e.g., Jacobs 1976; Alexander 1977; Simanauskas and Cisterna 2000; Campi and Shi 2002). In addition, possible

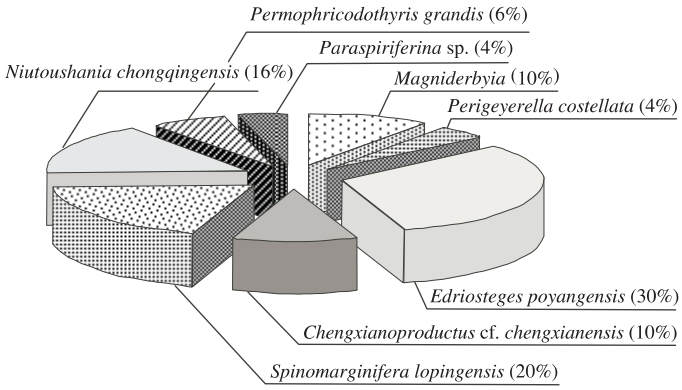


Fig. 5. Abundance of the *Edriosteges poyangensis–Spinomarginifera lopingensis* Association. A total of 51 specimens were collected from a shell bed at the basal Lungtan Formation.

opportunists such as the chonetids *Neochonetes* and *Tethyochonetes*, which are common in the Late Permian of South China (Chen et al. 2000), are not present in the *E–S* Association, although they do occur in the higher horizons of the formation. Therefore, the *E–S* Association represents a normal marine fauna. In addition, the above sequence stratigraphic and faunal correlations suggest that the *E–S* Association is an earliest Wuchiapingian shelly fauna. According to the biotic recovery model proposed by Kauffman and Harries (1996) and the definition of the recovery in biodiversity by Erwin (2000), the *E–S* Association therefore may represent the onset of recovery of shelly faunas in the aftermath of the G/L mass extinction.

To test the effect of the G/L extinction to the described faunas, we list the worldwide stratigraphic distributions of the described taxa (Fig. 6). Of the Wuchiapingian faunas, five of eleven brachiopod genera (*Edriosteges*, *Meekella*, *Transennatia*, *Perigeyerella*, and *Permophricodothyris*) first occurred in the Wordian or pre-Wordian strata worldwide, disappeared in the late Capitanian, and re-appeared in the early Wuchiapingian, with a gap equating to three conodont zones in the carbonate successions (Fig. 6). This strata interval is defined by the latest Capitanian conodont *Jinogondolella granti* Zone and earliest Wuchiapingian *Clarkinia postbitteri* Zone (Mei et al. 1998). Most benthos of the Middle Permian disappeared in this strata interval except for two brachiopod genera (*Tyloplecta* and *Spinomarginifera*) and numerous genera of fusulinids, corals, and ammonoids persisting into the overlying Wuchiapingian in the Laibin area, South China (Sha et al. 1990; Jin et al. 1998; Wang and Sugiyama 2001). This phase contains the G/L mass extinction horizon and thus is the extinction interval (Fig. 6) in accordance to Kauffman and Harries' (1996) subdivisions of biotic extinction-survival-recovery intervals. In addition, *Paraspiriferina* occurring in the Early Permian and Roadian–Wordian (Middle Permian), disappeared in the Capitanian, and reappeared in the early Wuchiapingian, with a gap of eight conodont zones (Fig. 6). These six genera are therefore Lazarus genera (terms of Jablonski 1986; Erwin

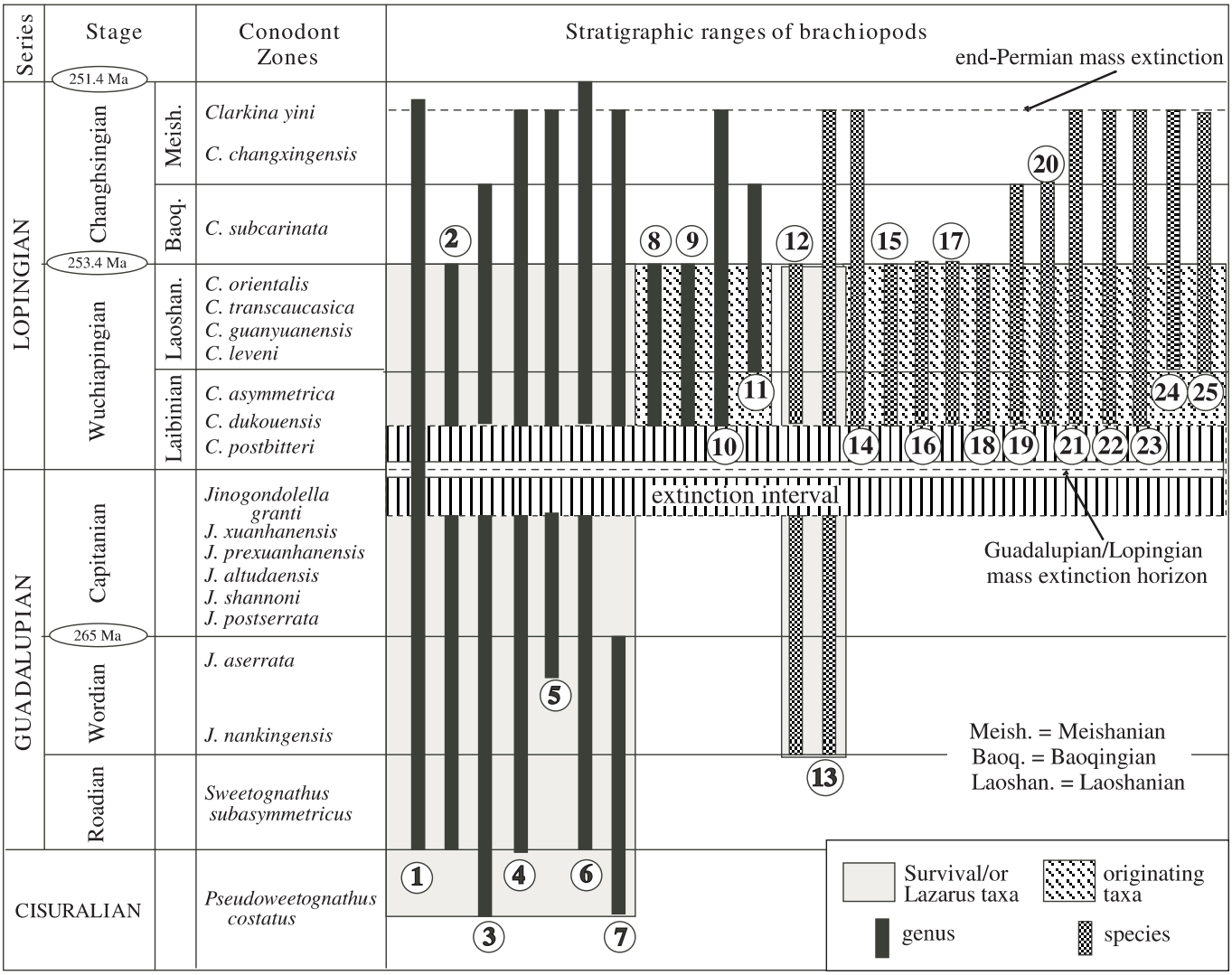


Fig. 6. Global stratigraphic distributions of the Lungtan brachiopod faunas. Permian chronostratigraphic framework follows International Union of Geological Sciences (2002). Conodont zones are after Mei et al. (1994) and Jin et al. (1998). The G/L mass extinction horizon corresponds to the biostratigraphic G/L boundary. The extinction interval is defined by the late Capitanian conodonts *Jinogondolella granti* Zone and the earliest Wuchiapingian *Clarkina postbitteri* Zone. Brachiopod genera include 1, *Spinomarginifera*; 2, *Edriosteges*; 3, *Meekella*; 4, *Transennatia*; 5, *Perigeyerella*; 6, *Permophricodothyris*; 7, *Paraspiriferina*; 8, *Magniderbyia*; 9, *Niutoushania*; 10, *Chengxianoproductus*; 11, *Peltichia*. Brachiopod species include 12, *Edriosteges poyangensis*; 13, *Transennatia gratiosa*; 14, *Permophricodothyris grandis*; 15, *Magniderbyia* sp. indet.; 16, *Meekella pusilloplicata*; 17, *Me. kueichowensis*; 18, *Me. beipeiensis*; 19, *Spinomarginifera lopingensis*; 20, *Niutoushania chongqingensis*; 21, *Chengxianoproductus* cf. *changxingensis*; 22, *Paraspiriferina* sp.; 23, *Perigeyerella costellata*; 24, *Peltichia zigzag*; 25, *Spinomarginifera alpha*.

and Droser 1993; Erwin 1997; Fara 2001) of the G/L extinction, suggesting the significant Lazarus effect during the event. Most of these genera are more diverse in terms of constituent species in the late Wuchiapingian to early Changhsingian in comparison to the early Wuchiapingian.

Spinomarginifera originated in early Middle Permian (Roadian) (Yang et al. 1977) and extends into the Capitanian and Wuchiapingian (e.g., Licharew and Kotlyar 1978; Feng and Jiang 1978; Liao 1980b; Liang 1990; Zeng et al., 1995). This genus is therefore a survivor of the G/L extinction (Fig. 6). Of the remaining four genera *Magniderbyia*, *Chengxianoproductus*, *Niutoushania*, and *Peltichia*, both *Magniderbyia* and *Niutoushania* originated and thrived during the recovery phase after the G/L mass extinction but were confined to the Wuchiapingian of South China; the remaining two genera initially appeared in the early Wuchiapingian and then proliferated in the Changhsingian.

At the species level, two species (*Edriosteges poyangensis* and *Transennatia gratiosa*), which are exceptionally abundant and characteristic of the Wuchiapingian, are actually Wordian (Middle Permian) holdovers. They disappeared during the extinction interval of the G/L extinction and re-occurred in the early Wuchiapingian (Fig. 6). These species are therefore Lazarus species, which went on to the early repopulation stage after the G/L mass extinction in South China. However, these forms were reef dwellers in the Capitanian (see Licharew and

Kotlyar 1978; Liang 1990), and, after the G/L crisis, they modified their life habits to be able to exploit vacant ecospace in the soft muddy or solid substrate (term of West 1977). After their adaptation to new niches, these species proliferated in the Wuchiapingian in South China and were dispersed rapidly over the eastern Tethyan region and its margin seas (Liao 1980b; Jin 1985; Liang 1990; Zeng et al. 1995). These species also persisted into the Changhsingian although none survived the end-Permian mass extinction.

The remaining species originated in the recovery phase of the G/L extinction. Of these, *Magniderbyia* sp., *Meekella pusilloplicata*, *Me. kueichowensis*, and *Me. beipeiensis* possess strikingly specialized shells, which are characterized by a high, irregularly cone-shaped ventral umbo and a high interarea. All of them are limited to the Wuchiapingian. Although they may extend into the Changhsingian, *Spinomarginifera lopingensis*, *Niutoushania chongqingensis*, *Chengxianoproductus* cf. *changxingensis*, and *Permophricodothyris grandis* are more abundant in the Wuchiapingian. In contrast, the proliferation of *Paraspiriferina* sp., *Perigeyerella costellata*, *Peltichia zigzag*, and *Spinomarginifera alpha* occurred in the Changhsingian, while they are relatively rare in the Wuchiapingian. Nevertheless, all of these forms have suffered severely in the end-Permian crisis.

When life habits are analyzed, the post-extinction survivors appear to have significantly diversified their habitats compared to their pre-extinction niches. Of the post-extinction brachiopods originating in the recovery period, a great number of species preferred a strong pedicle for anchoring to the soft substrate, reflected by the presence of a large delthyrium or foramen. Alternatively, there are also numerous productids, which attached their shells to the substrate by anchoring spines. As such no signals demonstrate a single life habit preference for these post-extinction forms in terms of the attachment patterns. However, these two attachment patterns enabled these brachiopods to inhabit both a soft muddy and a solid substrate.

Systematic paleontology

(by Z.Q. Chen)

Phylum Brachiopoda Dumeril, 1806
Subphylum Rhynchonelliformea Williams, Carlson, Brunton, Holmer, and Popov, 1996
Class Strophomenata Williams, Carlson, Brunton, Holmer, and Popov, 1996
Order Orthotetida Waagen, 1884
Suborder Orthotetidina Waagen, 1884
Superfamily Orthotetoidea Waagen, 1884
Family Meekellidae Stehli, 1954
Subfamily Meekellinae Stehli, 1954
Genus *Perigeyerella* Wang, 1955

Type species: *Perigeyerella costellata* Wang, 1955; Changhsingian (Late Permian), Guizhou, South China.

Perigeyerella costellata Wang, 1955

Figs. 7B, C, 8.

Perigeyerella costellata n. sp.; Wang 1955: 102–103, pl. 6: 1–10.
Perigeyerella costellata Wang; Feng and Jiang 1978: 239, pl. 87: 1.
Perigeyerella costellata Wang; Liao 1980a: pl. 2: 28.
Perigeyerella costellata Wang; Liao 1980b: pl. 2: 10, 11.
Perigeyerella costellata Wang; Xu and Grant 1994: fig. 13.
Perigeyerella costellata Wang; Zeng et al. 1995: pl. 1: 13, 14.

Locality and horizon.—Daijiagou section; 1st member of the Lungtan Formation.

Material.—NMV P309619–620.

Remarks.—The materials examined agree perfectly with Wang's (1955) description of the species. This species is defined by its transversely oval to subcircular outline, conical ventral umbo, and rectimarginate anterior commissure. Its external surfaces are weakly rugose and multicostellate, about 35 costellae in 10 mm at the midlength of the shell. Two thin, high dental plates are convergent toward the valve floor (Fig. 7). The Changhsingian *Perigeyerella altilosina* Xu and Grant, 1994 is the most closely allied species to *P. costellata*, from which the Changhsingian species is differentiated by its more elongate outline and proportionally higher ventral interarea. A transversely oval outline and a low ventral interarea of our specimens also recall those of *P. tricosa* Grant, 1976, but the loss of a dorsal median sulcus distinguishes Grant's species from *P. costellata*.

Genus *Meekella* White and St. John, 1867

Type species: *Plicatula striatocostata* Cox, 1858; Moscovian (Pennsylvanian), Iowa, USA.

Meekella beipeiensis Chen sp. nov.

Figs. 7D, E, 9.

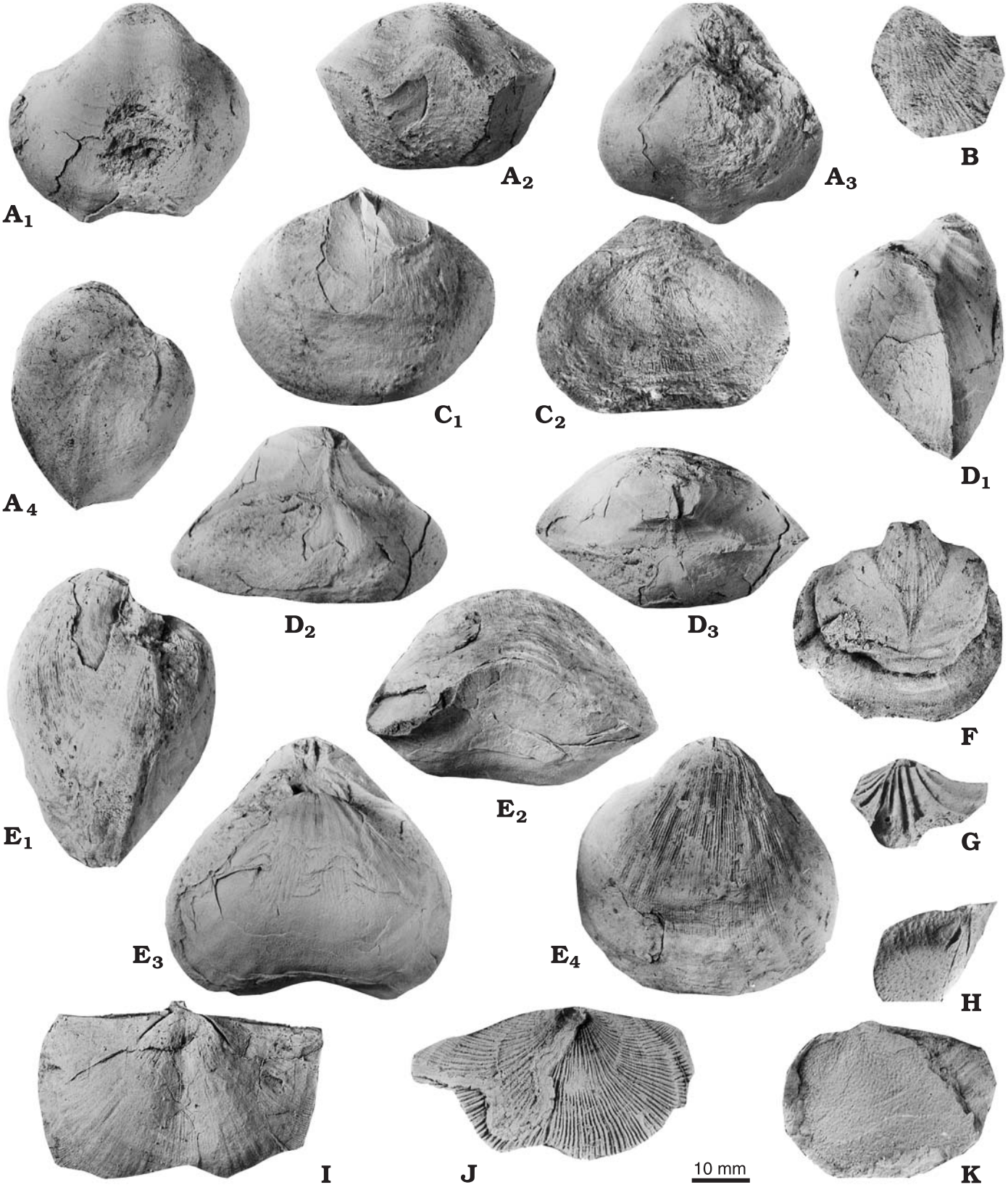
Holotype: NMV P309624 (Fig. 7E), 5.4 mm wide, 5.1 mm long and 3.9 mm thick.

Type locality: Daijiagou section, Beipei, Chongqing City, South China.

Type horizon: 4th member of the lower Lungtan Formation (early Wuchiapingian, Late Permian).

Derivation of the name: Named for the Beipei area, where the Daijiagou section is located.

Fig. 7. **A**. *Peltichia zigzag* (Huang, 1933), ventral (A_1), anterior (A_2), dorsal (A_3), and lateral (A_4) views of NMV P309618. **B**, **C**. *Perigeyerella costellata* Wang, 1955, ventral (B, C_1) and dorsal (C_2) views of a ventral external mold NMV P309619 (**B**) and a complete specimen NMV P309620 (**C**). **D**, **E**. *Meekella beipeiensis* Chen sp. nov., lateral (D_1, E_1), posterodorsal (D_2), posterior (D_3), anterior (E_2), dorsal (E_3), and ventral (E_4) views of a complete specimen NMV P309625 (**D**) and holotype NMV P309624 (**E**). **F**. *Permophricodothyris grandis* (Huang, 1933), ventral view of a ventral internal mold NMV P309621. **G**. *Paraspiriferina* sp., dorsal view of a dorsal external mold NMV P309635. **H**. *Spinomarginifera lopingensis* (Kayser, 1883), dorsal view →



of a dorsal internal mold NMV P309634. **I**. *Meekella pusilloplicata* Liao, 1980b, dorsal view of a dorsal internal mold NMV P309623. **J**. *Magniderbyia* sp. indet., ventral view of a ventral external mold NMV P309628. **K**. *Chengxianoproductus* cf. *changxingensis* Liao and Meng, 1986, dorsal view of a dorsal external mold NMV P309626. A, from the 5th member of the Lungtan Formation of Daijiagou. B, C, G, H, J, K, from the 1st member of the Lungtan Formation of Daijiagou; D, E, from the 4th member of the Lungtan Formation of Daijiagou; I, from the 3rd member of the Lungtan Formation of Daijiagou; F, from the 5th member of the Lungtan Formation of Chuanmu.

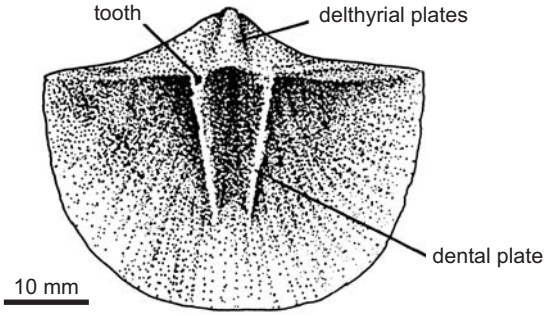


Fig. 8. Reconstruction of ventral interior of *Perigeyella costellata* Wang, 1955 (based on specimen NMV P309620).

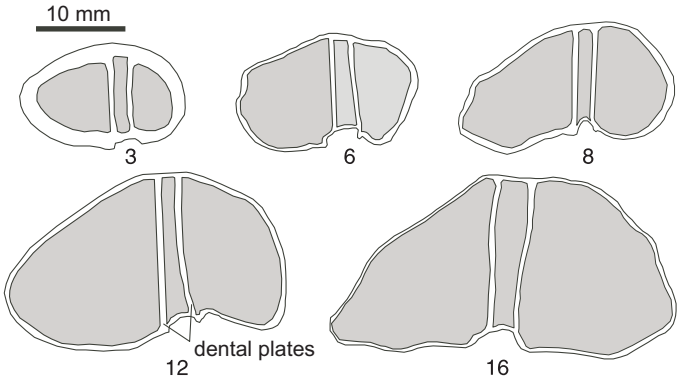


Fig. 9. Selected serial sections of the ventral umbo of *Meekella beipeiensis* Chen sp. nov. (based on specimen NMV P309627) showing closely situated, parallel dental plates. The numbers are distance from the ventral beak; the orientation of the sections is with ventral surfaces upward.

Material.—Of six studied specimens, NMV P309624–625 are figured and NMV P309627 is sectioned.

Diagnosis.—Large species for genus; elongate ovate to triangular in outline; ventral umbo moderately conical; dorsal median sulcus distinct, forming a lingual extension at anterior margin; external surfaces weakly plicate. The new species is distinguished from *Meekella dorsisulcata* Feng and Jiang, 1978 by its more anteriorly extended dorsal median sulcus and narrower, more rounded plicae, and from the Capitanian *Me. zhejiangensis* Liang, 1990 by its significantly lower ventral interarea.

Description.—Nearly biconvex in profile; shell width anterior to midvalve; extremities round. Ventral beak normally twisted slightly and deformed by cicatrix of attachment; interarea moderately high, concave to slightly flattened; pseudodeltidium with high sharp monticulus; umbo conical posteriorly; lateral slopes steep; median sulcus absent. Dorsal valve evenly convex, most convex at umbo; median sulcus broad, originating at beaks as shallow groove, abruptly broadening and deepening at umbonal region, forming deep lingual extension anteriorly.

Costellae fine, dense, rounded, frequently intercalate or bifurcate, about 40 per 10 mm at midlength, irregularly, moderately plicate; four plicae in 10 mm at midlength, those on umbo more conspicuous than others. Ventral interior dental plates high, long, slightly convergent anteriorly, extending to midlength. Cardinal process long, slightly projecting posteriorly; dorsal socket ridges strong; crural plates fused to base of cardinal process (Fig. 9).

Remarks.—Liao (1980b) described three new species *Meekella langdaiensis*, *Me. deltoides*, and *Me. pusilloplicata* from the Lungtan Formation of Guizhou, South China. They are contemporaneous to *Me. beipeiensis*, but all are distinct from the new species in the loss of a dorsal median sulcus. In addition, *Me. deltoides* is much smaller; *Me. pusilloplicata* has a proportionally longer hingeline; *Me. langdaiensis* embraces coarser plicae with sharper crests. Shen et al. (1992) created two new species, *Meekella sichuanensis* and *Me. perigeyerelloides*, from the Changhsingian of Chongqing, South China; they possess a higher, flat ventral interarea and a slightly shallower dorsal median sulcus, and thus cannot be confused with *Me. beipeiensis*.

Meekella pusilloplicata Liao, 1980b

Fig. 7I.

Meekella pusilloplicata sp. nov.; Liao 1980b: 256, pl. 3: 1–4.

Locality and horizon: Daijiagou section; 3rd member of the Lungtan Formation.

Remarks.—A dorsal internal mold (NMV P309623), pentagonal in outline, agrees fully with Liao's (1980b) description of the species. The diagnostic features include: maximum width at hingeline, costellae fine, weakly plicate, dorsal socket plates well developed, diverging laterally. *Meekella kueichowensis* Huang, 1933 shares a similar outline and size to the nominal species, from which this Huang's species is easily distinguished in the possession of a proportionally narrower hingeline and coarser ribs.

Meekella kueichowensis Huang, 1933

Fig. 10A.

Meekella kueichowensis n. sp.; Huang 1933: 27, pl. 3: 19–21, 4: 1–4.
Meekella kueichowensis Huang; Jin et al. 1974: 312, pl. 164: 15, 16.
Meekella kueichowensis Huang; Feng and Jiang 1978: 237, pl. 86: 5.
Meekella kueichowensis Huang; Zhan 1979: 64, pl. 10: 5, 6.
Meekella kueichowensis Huang; Liao 1980b: pl. 3: 24.
Meekella kueichowensis Huang; Liang 1990: 124, pl. 12: 13.
Meekella kueichowensis Huang; Zeng et al. 1995: pl. 3: 3.

Locality and horizon: Daijiagou section; 4th member of the Lungtan Formation.

Remarks.—This species is defined by its large size, subcircular to subtriangular outline, and robust plicae that are occasionally twisted. The Daijiagou specimen (NMV P309622) is identical in all observed aspects to the topotypes of Huang's species described by Jin et al. (1974) from the Lungtan Formation of Guizhou, South China. *Meekella megala* Grant, 1993 from the Wordian of the Khios Island, Greece is indistinguishable in shell outline, size and low plicae from Huang's species, however the Greek species can be differentiated from Huang's species by its relatively lower ventral interarea and more flattened pseudodeltidium.

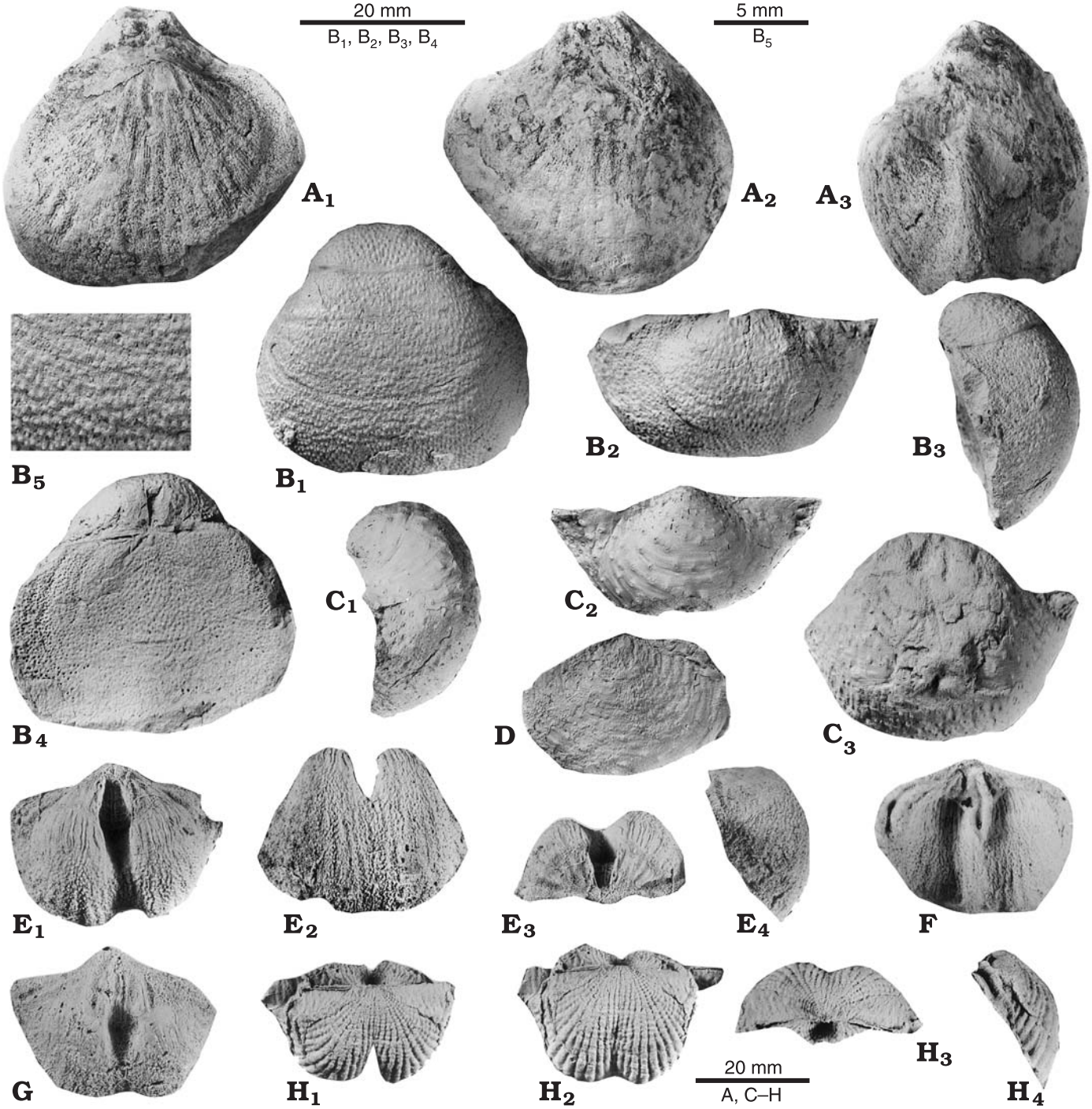


Fig. 10. **A**. *Meekella kueichowensis* (Huang, 1933), dorsal (A_1), ventral (A_2), and lateral (A_3) views of NMV P309622. **B**. *Chengxianoproductus* cf. *changxingensis* Liao and Meng, 1986, ventral (B_1), posterior (B_2), lateral (B_3), and dorsal (B_4) views of NMV P309640 (B); B_5, enlargement of fine, densely arranged spine bases of B_1. **C**, **D**. *Spinomarginifera alpha* Huang, 1932, lateral (C_1), posterior (C_2), ventral (C_3), and dorsal (D) views of a complete specimen NMV P309643 and a dorsal external mold NMV P309644. **E**–**H**. *Transennatia gratiosa* (Waagen, 1884), ventral (E_1, G, H_1), anteroventral (E_2, H_2), posterior (E_3, H_3), lateral (E_4, H_4), and internal (F) views of a ventral internal mold NMV P309639 (**E**), and latex replica NMV P309638 (**F**) of the ventral internal mold (E_1–E_4), a ventral internal mold NMV P309636 (**G**) and a dorsal external mold NMV P309637 (H_1–H_4). A, E, F, G, from the 4th member of the Lungtan Formation of Daijiagou; B, from the 1st member of the Lungtan Formation of Daijiagou; C, D, H, from the 5th member of the Lungtan Formation of Daijiagou.

Family Derbyidae Stehli, 1954

Genus *Magniderbyia* Ting, 1965

Type species: *Derbyia magnifica* Licharew, 1939; Late Permian, Caucasus region, Azerbaijan.

Magniderbyia sp. indet.

Fig. 7J.

Locality and horizon: Daijiagou section; 1st member of the Lungtan Formation.

Remarks.—Although *Magniderbyia* has been placed as a junior synonym under *Derbyia* by Williams and Brunton (2000), this genus is distinguished from *Derbyia* by its significantly large size, wider hingeline that almost equals the shell width, and pair of large, laterally extending ears. *Magniderbyia* therefore is treated as a valid genus. This genus is represented by several external molds in the Daijiagou collections. Of these, a ventral external mold (NMV P309628) is figured here to indicate the presence of *Magniderbyia* in the Wuchiapingian faunas. Our specimens approach both *Me. lata* Zhan, 1979 and *Me. mucronata* Liao, 1980b in fine, dense ribs and strongly laterally projecting cardinal extremities, however a meaningful comparison with these two species is difficult due to insufficient material. Like *Magniderbyia*, *Derbyia regis* Grant, 1995 from the Upper Permian of Hydra Island, Greece also has a transverse outline and a hingeline equating the shell width. However, the Greek species possesses rounded extremities rather than the laterally projecting ones of *Magniderbyia*.

Order Productida Sarycheva and Sokolskaya, 1959
Suborder Productidina Waagen, 1884
Superfamily Productoidea Gray, 1840
Family Productellidae Schuchert in Schuchert and LeVene, 1929
Subfamily Marginiferinae Stehli, 1954
Tribe Paucispiniferini Muir-Wood and Cooper, 1960
Genus *Transennatia* Waterhouse, 1975

Type species: *Productus gratiosus* Waagen, 1884; Capitanian (Middle Permian), Salt Range, Pakistan.

Transennatia gratiosa (Waagen, 1884)

Figs. 10E–H, 11.

Productus gratiosus n. sp.; Waagen 1884: 691, pl. 72: 3–7.
Productus gratiosus Waagen; Diener 1897: 23, pl. 3: 3–7; Mansuy 1913: 115, pl. 13: 1a, b; Broili 1916: 12, pl. 116: 4, 5, 7–11; Chao 1927: 44, pl. 4: 6–8; Chi-Thuan 1962: 491, pl. 2: 5–7.
Productus (*Dictyoclostus*) *gratiosus* Waagen; Huang 1932: 32–33, pl. 2: 3; 1933: 88, pl. 11: 14a, b.
Marginifera gratiosa (Waagen); Licharew 1936: 60, 118, pl. 4: 11–19; Reed 1944: 98, pl. 19: 6, 7.
Dictyoclostus gratiosus (Waagen); Zhang and Ching (Jin) 1961: 411, pl. 4: 12–18; Wang et al. 1964: 291, pl. 45: 14–19.
Transennatia gratiosa (Waagen); Waterhouse 1975: 10–11.
Gratiosina gratiosa (Waagen); Grant 1976: pl. 33: 19–26; Licharew and Kotlyar 1978: pl. 12: 5, 6; pl. 12: 1a, b.
Asioproductus gratiosus (Waagen); Yang et al. 1977: 350, pl. 140: 5a–c; Feng and Jiang 1978: 254, pl. 90: 1, 2; Tong 1978: 228, pl. 80: 7a, b; Li et al. 1980: 373, pl. 164: 14a–c; pl. 166: 5, 6.
Asioproductus bellus sp. nov.; Chan (Zhan) 1979: 85–86, pl. 7: 7–13, 9: 8–10.
Transennatia gratiosa (Waagen); Liao 1980b: pl. 3: 25; Liu et al. 1982: 185, pl. 132: 9a–d; Wang et al. 1982: 214, pl. 92: 6–8; pl. 102: 4–9; Yang 1984: 219, pl. 33: 7a–c; Zeng et al. 1995: pl. 5: 14, 15; Tazawa and Matsumoto 1998: 6, pl. 1: 4–8; Tazawa et al. 2000: 7, pl. 1: 3–5; Tazawa and Ibaraki 2001: 7, pl. 1: 1–3.

Locality and horizon: Daijiagou section; 4th and 5th members of the Lungtan Formation; Chuanmu section; 5th member of the Lungtan Formation.

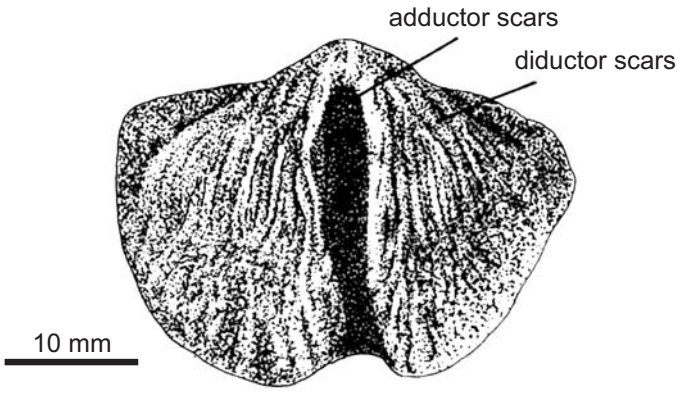


Fig. 11. Ventral interior of *Transennatia gratiosa* (Waagen, 1884); based on a ventral internal mold NMV P309639.

Material.—NMV P309636–639.

Remarks.—A restudy (Grant 1976) of the topotype specimens of *Productus gratiosus* Waagen, 1884 from the Wargal and Chhidru Formations at Chhidru and Jabbi of the Salt Range, Pakistan allows us to understand the internal features as following: the dorsal valve has a sessile W-shaped cardinal process; a pair of elongate, highly raised adductor scars are separated by a low, thin median septum; the ventral valve is tuberculate, and embraces an elongate, highly raised median adductor scar; the diductor scars are wide, flabellate and deeply grooved on the floor of each side of the scar platform. These features are confirmed in our specimen (Fig. 11). This Salt Range species has also been referred to as the type species of *Asioproductus* Zhan (in Yang et al. 1977). Later, Zhan (1979) altered his specimens to *Asioproductus bellus* Zhan, 1979, but did not compare his new material with Waagen's species. Liang (1990: 162) differentiated *Asioproductus* from *Transennatia* by the appearance of a *Marginifera*-type, bilobate cardinal process. However, one of Zhan's (1979: pl. 6: 9) illustrations clearly shows a W-shaped cardinal process. As a consequence, *Asioproductus* is synonymous to *Transennatia*. Another species *Transennatia insulpta* Grant, 1976 (see also Chen 2004) can be distinguished from the type species by its evidently smaller size and more extended ears.

Tribe Marginiferini Stehli, 1954
Genus *Spinomarginifera* Huang, 1932

Type species: *Spinomarginifera kueichowensis* Huang, 1932; Changhsingian (Late Permian), Guizhou, South China.

Spinomarginifera lopingensis (Kayser, 1883)

Fig. 7H.

Productus nystianus var. *lopingensis* n. var.; Kayser 1883: 187: pl. 28: 1–5.
Marginifera lopingensis (Kayser); Chao, 1928: 153: pl. 16: 8–12.
Spinomarginifera lopingensis (Kayser); Liao 1980b: pl. 5: 35–39.
Spinomarginifera lopingensis (Kayser); Liao 1987: pl. 5: 5, 7–18.
Spinomarginifera lopingensis (Kayser); Zeng et al. 1995: pl. 9: 1.

Locality and horizon: Daijiagou section; 1st member of the Lungtan Formation.

Material.—Of 10 specimens, NMV P309634 is figured.

Remarks.—This species usually exhibits a elongate outline, much longer than wide. The ventral beak is strongly incurved posteriorly. The dorsal interior is characterized by a pair of elongate but extremely narrow, highly raised ventral adductor scars that form an angle of less than 30°. *Spinomarginifera jiaozishanensis* Liao, 1980b can be differentiated from *S. lopingensis* by its more circular profile and deeper, broader ventral median sulcus. *S. plena* Liao, 1987 also from the Wuchiapingian of South China differs from *S. lopingensis* in possessing a more rounded ventral umbo and broader ears.

Spinomarginifera alpha Huang, 1932

Fig. 10C, D.

Spinomarginifera kueichowensis mut. *a* n. sp.; Huang 1932: 60–61, pl. 5: 12, 13.

Spinomarginifera alpha Huang; Liao 1980b: 259, pl. 5: 44–47.

Locality and horizon: Daijiagou and Chuanmu sections; 5th member of the Lungtan Formation.

Material.—NMV P309643–644.

Remarks.—The present species is the largest among the six species described originally by Huang (1932). It is elongately subrectangular in outline and the hingeline is the widest part of the shell. The ventral umbo is rounded, highly convex, and strongly curved posteriorly. *Spinomarginifera alpha* is differentiated from *S. kueichowensis* by its much larger size and more highly convex, posteriorly curved ventral umbo. In addition, when compared with *S. alpha*, *S. pseudosintanensis* Huang, 1932 is more strongly rugose and possesses more elongate spine bases on the trails, *S. lopingensis* is more elongate and ribbed anteriorly, and *S. chengyaoyenensis* Huang, 1932 is much smaller and more weakly rugose.

Family Productidae Gray, 1840
Subfamily Yakovleviinae Waterhouse, 1975
Tribe Reticulatiini Lazarev, 2000
Genus *Niutoushania* Liao, 1984

Type species: *Niutoushania niutoushanensis* Liao, 1984; Wuchiapingian (Late Permian), Anhui, South China.

Emended diagnosis.—Medium to large, suboval to subquadrate shell, geniculate anteriorly; corpus cavity moderately deep; sulcus and fold indistinct; fine spines on dense ventral ribs; rugae absent or weakly developed on umbo. Ventral interior adductor scars elongate, ridge-shaped; diductor scars broad, flabellate, deeply grooved (Fig. 12A). Cardinal process bilobate, supported by a thin median septum; cardinal ridges extending along hinge margins; anterior adductor scars elongate, highly raised, tear-shaped; posterior adductor scars strongly dendritic; brachial ridges hook-shaped, nearly horizontally given off; inner surfaces strongly tuberculate (Fig. 12B). The redefined *Niutoushania* shares similar size, shell outline and general ornamentation with both *Tyloplecta* Muir-Wood and Cooper, 1960 and *Tarimoplecta* Chen and Shi, 2000, but it differs clearly from the latter two in lacking a much deeper corpus cavity and fine capillae, which are diagnostic of both *Tyloplecta* and *Tarimoplecta* (Chen and Shi 2000; Shi and Chen 2003). Moreover, the conspicuous nodes characterize the ventral umbo of *Tyloplecta*, and the costae of *Tarimoplecta* broaden abruptly at the start of the geniculation. None of these characteristics is present in *Niutoushania*.

Remarks.—Generic diagnosis is emended here based on re-examining the type specimens of the type species housed in Nanjing Institute of Geology and Paleontology, Chinese Academy of Sciences. These type specimens, like the Daijiagou materials, were also collected from the Lungtan coal series in Changxing, South China; both bear some similarities. However, our new materials provide more detailed ventral internal features. *Niutoushania* can be separated from other dictyoclostines by its indistinct reticulations, a lower, thinner dorsal median septum, and more pronounced brachial scars, which are perpendicular to the median septum.

Niutoushania chongqingensis Chen sp. nov.

Figs. 12, 13A, B.

Holotype: NMV P309641.

Other material: Eight specimens; figured specimen: NMV P309641.

Type locality: Daijiagou section, Beipei, Chongqing, South China.

Type horizon: 1st member of the Lower Lungtan Formation, Wuchiapingian, Late Permian.

Derivation of the name: After Chongqing City, South China.

Diagnosis.—Large, subquadrate shells, with moderately deep corpus cavity, fine spines on ventral costae, and distinct brachial ridges. The new species shares similar in shell outline, concavo-convexity, ornamentation and internal structures with the type species *Niutoushania niutoushanensis* Liao, 1984, but is distinguished from the latter by its larger size, a relatively shallower corpus cavity and more pronounced brachial scars.

Description.—Geniculate anteriorly; widest at hingeline; ears broad, triangular, inflated, projecting laterally. Ventral valve highly evenly convex, strongly curved longitudinally; beak stout, strongly incurved, overhanging hingeline; umbonal region slightly flattened medially, incurved posteriorly; lateral slopes steep; median sulcus broad, shallow but distinct. Dorsal valve concave to slightly flattened. External costae irregularly spaced, bifurcate, about 5–6 in 10 mm at midlength of shell, relatively finer on disc, broadening near anterior margin; coarse spines arranged in row along hinge margin, scattered on disc and ears; fine spines densely covering on costae; dorsal ornament similar to that of ventral valve. Ventral adductor scars elongate, highly raised, separated by low median ridge; diductor scars broad, fan-like, flabellate (Fig. 12A); cardinal process bilobed anteriorly, supported by a low, thin median septum; cardinal ridges ex-

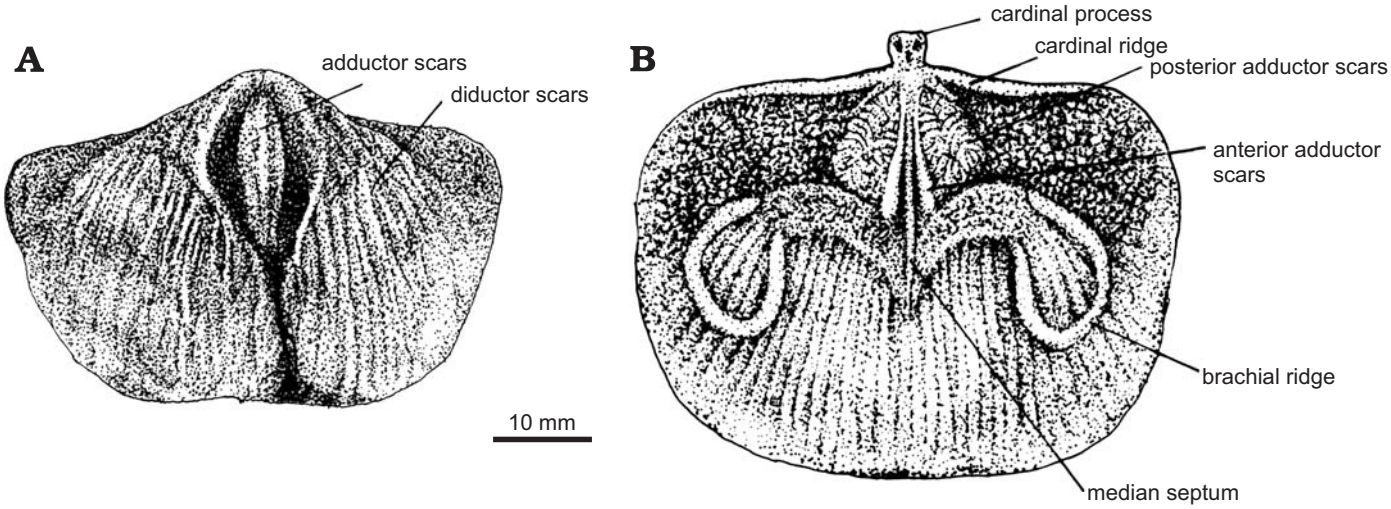


Fig. 12. Interiors of *Niutoushania chongqingensis* Chen sp. nov. (based on specimen NMV P309641); ventral valve (**A**) and dorsal valve (**B**).

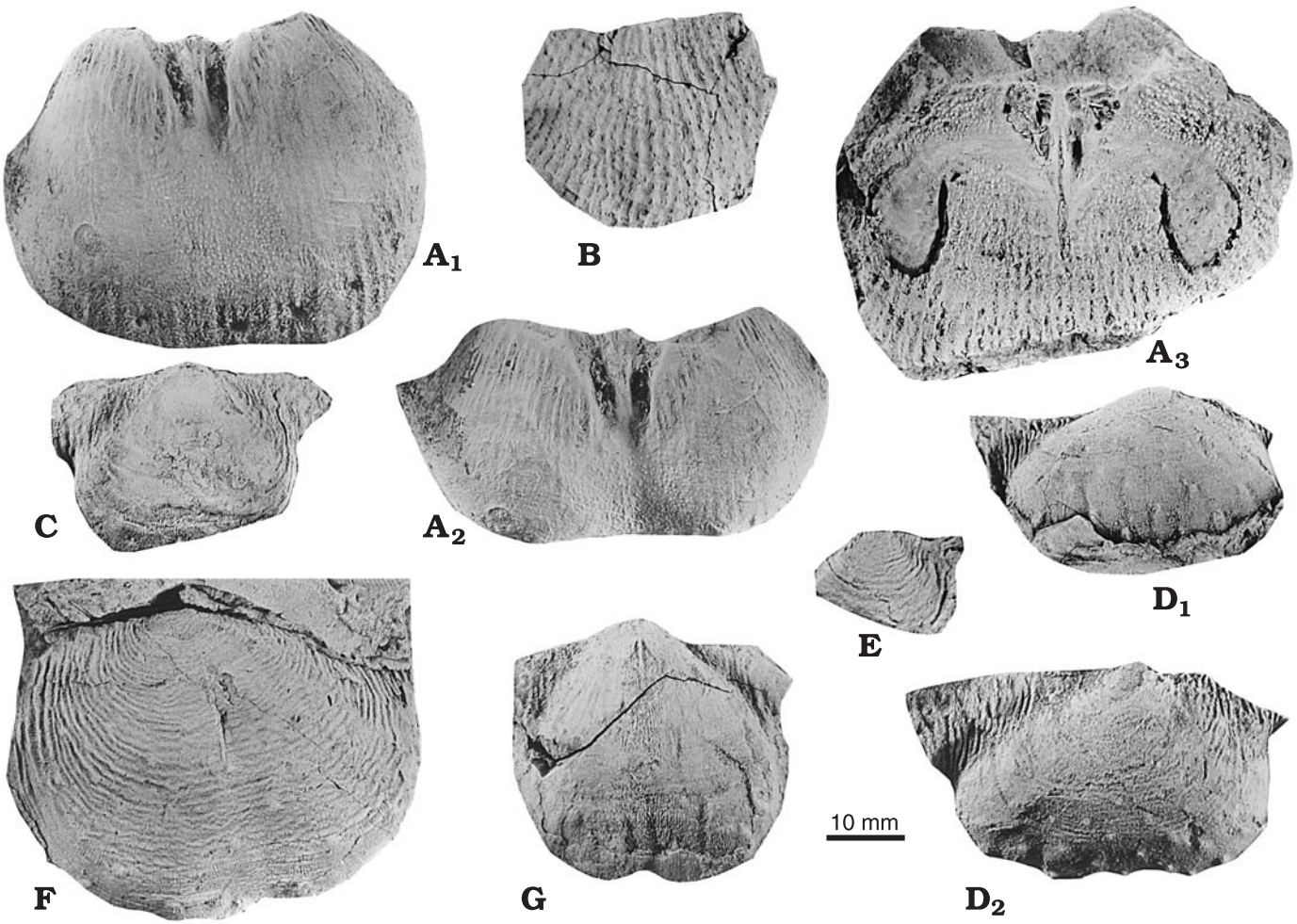


Fig. 13. *Niutoushania* (**A**, **B**) and *Edriosteges* (**C**–**G**) from the 1st member of the Lungtan Formation of Daijiagou. **A**, **B**. *Niutoushania chongqingensis* Chen sp. nov., anteroventral (A_1), posterior (A_2), and dorsal (A_3) views of holotype NMV P309641 (**A**). **B**. Fragment of a ventral external mold NMV P309642 showing regularly spaced costae and fine spine bases. **C**–**G**. *Edriosteges poyangensis* (Kayser, 1883), dorsal (C, D_2, E, F), anterodorsal (D_1), and ventral (**G**) views of four dorsal external molds NMV P309632 (**C**), NMV P309630 (**D**), NMV P309629 (**E**), NMV P309631 (**F**), and a ventral valve NMV P309633 (**G**).

tending laterally along hinge margins; dorsal adductor scars elongate, smooth, highly elevated; diductor scars strongly dendritic; brachial ridges hook-like, horizontally extending from median septum (Fig. 12B).

Remarks.—Beyond *Niutoushania*, the large-sized productid *Tyloplecta yangtzeensis* (Chao, 1927) is also overall comparable with the new species, from which Chao's species is distinguishable in having anteriorly broadened costae, fine capillae, and nodules on the ventral umbo.

Superfamily Echinoconchoidea Stehli, 1954
Family Echinoconchidae Stehli, 1954
Subfamily Echinoconchinae Stehli, 1954
Tribe Echinoconchiini Stehli, 1954
Genus *Chengxianoproductus* Liao and Meng, 1986

Type species: *Chengxianoproductus nitens* Liao and Meng, 1986, subsequent designation herein; Changhsingian (Late Permian), Hunan, South China.

Nomenclature discussion.—Liao and Meng (1986) applied two different species names, *Chenxianoproductus nitens* (Liao and Meng, 1986) and *C. typica* (Liao and Meng, 1986), for the same specimens. Both species have been regarded as the type species of *Chenxianoproductus*. However, according to the principal of page priority, *C. nitens* Liao and Meng, 1986 is treated as a valid species and selected here as the type species for the genus, while *C. typica* Liao and Meng, 1986 is an invalid species name and abandoned.

Emended diagnosis.—Medium-sized Echinoconchinae, with subcircular to triangular-oval outline; sulcus and fold variously developed; dorsal valve flat to slightly concave with a deep corpus cavity. Ventral exterior with broad bands, each bearing rows of alternatively arranged spine bases; spines suberect. Dorsal valve with similar ornament to ventral valve. Cardinal process small, bilobate; median septum low, extending over half disc-length; lateral ridges originating at cardinal process base, curving down inside ears; inner surface densely pustulate. *Chengxianoproductus* superficially resembles *Alatoproductus* Jin and Hu, 1978 in terms of shell outline, spinose exteriors and internal characteristics; however, *Chengxianoproductus* embraces conspicuous concentric bands and smaller alternatively arranged spine bases; whereas the spine bases of *Alatoproductus* are much coarser and randomly arranged. Another ally is *Stictozoster* Grant, 1976, which also possesses dense spines on concentric bands, a bilobate cardinal process, and a long, thin long dorsal median septum. However, *Chengxianoproductus* is distinct from Grant's genus in having a more weekly concavo-convex profile, a sulcus, a fold, and dorsal lateral ridges. *Chengxianoproductus* also approaches moderately both *Waagenoconcha* Chao (1927) and *Tschernyschewia* Stoyanow, 1910 in externally spinose ornamentation, but differs clearly from the latter two genera in having unvaried sizes of its spines and conspicuous concentric bands. In addition, *Chengxianoproductus* lacks the well-developed ventral interarea and a rather high ventral median septum, which are diagnostic of *Tschernyschewia*.

Remarks.—Shen et al. (1992: 178) treated *Chengxianoproductus* Liao and Meng, 1986 as a junior synonymy of *Parapulchratia* Zhan, 1979 because (1) both genera are generally comparable in many respects and (2) Liao and Meng (1986) assigned parts of specimens of *Productus pustulosus* var. *palliata* Kayser, 1883, type species of *Parapulchratia*, to their genus. However, Kayser's (1883) species has long remained poorly understood and later has broadly applied to Chinese Upper Permian specimens (e.g., Frech 1911; Chao 1927; Wang et al. 1964; Zhan 1979). In particular, Chao (1927) upgraded Kayser's variant species to species level and referred it to *Waagenoconcha*. Wang et al. (1964) refigured one of Chao's (1927) specimens to represent Kayser's species.

Kayser's figured materials include a broken ventral valve, one complete dorsal valve, and three broken dorsal internal molds. Of these, the ventral valve (see Kayser 1883: pl. 27: 9) possesses a rather narrow, inflated umbo and nearly centrally arranged, coarse spines, lacks a median sulcus and concentric lamellae, and thus is easily separated from *Chengxianoproductus* that is defined by a broad ventral umbo, a broad but distinct median sulcus, and numerous broad lamellae, each bearing rows of alternatively arranged spines. Alternatively, the overall appearance of Kayser's (1883) ventral valve is morphologically close to *Alatoproductus* Jin and Hu, 1978 or *Tschernyschewia* Stoyanow, 1910 or *Waagenoconcha* Chao, 1927. The complete dorsal valve (see Kayser 1883: pl. 27: 13) internally embraces a broad cardinal process and costal impressions and is suggestive of a *Haydenella* species. Other three incomplete dorsal internal molds (Kayser 1883: pl. 27: 10–12) are indeterminate but are morphologically close to *Waagenoconcha* or *Edriosteges*.

The materials ascribed to *Waagenoconcha palliata* species by Chao (1927) and Wang et al. (1964), housed in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, are re-examined in this study (by ZQC in 2004). Chao's *W. palliata* includes several specimens collected from various regions of South China. Of these, the specimen (Chao 1927: pl. 7: 5, NIGP 984) from the Changxing coal mine of Zhejiang Province and the specimen (Chao 1927: pl. 7: 6, unregistered) from the Fengcheng of Jiangxi Province are both possessing a strong, bilobed cardinal process and conspicuous cardinal ridges and are comparable with that of *Tschernyschewia*, as suggested by Liao and Meng (1986: 80). Both specimens (Chao 1927: pl. 7: 3, 4a, b, NIGP 986 and NIGP 985, respectively) are externally similar. Of these, the specimen (NIGP 986) was later re-illustrated by Wang et al. (1964: pl. 40: 22–24) under the name "*Waagenoconcha*" *palliata*. Our (ZQC) and Prof. Z.T. Liao (personal communication 2004) re-examination reveals that this specimen (NIGP 986) is sculptured with varied spines and conspicuous concentrical lamellae, and each lamella bears rows of fine spines at its front edges. As a result, the specimens figured by Chao (1927) and Wang et al. (1964) can not share the same species name with Kayser's figured

materials. It is also noteworthy that Zhan (1979: 88), when he created *Parapulchratia*, stated that his materials of *P. palliata* are almost same to Chao's (1927: pl. 7: 6) specimen from Jinagxi Province. The latter seems to be a *Tschernyschewia* species (Liao and Meng 1986). Accordingly, Zhan's specimens are readily different from Kayser's materials.

In summary, Kayser's (1883) species includes morphologically varied specimens. A re-examination of Kayser's original type materials is necessitated. The figured materials by Kayser (1883) seem to be generically different from *Chengxianoproductus*. These specimens ascribed to *Waagenoconcha palliata* (Kayser, 1883) by later workers (Chao 1927; Wang et al. 1964; Zhan 1979) are not conspecific with Kayser's figured materials. As such, *Chengxianoproductus* is tentatively regarded as an independent genus from *Parapulchratia*.

Depth of corpus cavity is crucial to the correct classification of *Chengxianoproductus* (C.H.C. Brunton, personal communication 2003). The slightly concave to flattened dorsal valve and highly convex ventral valve indicate that *Chengxianoproductus* possesses a rather deep corpus cavity, which is diagnostic of the genus. Placing stress on the deep corpus cavity, we consider that *Chengxianoproductus* fits better within the Echinoconchidae (C.H.C. Brunton, personal communication 2003) than the Sentosiidae McKellar, 1970 (see Brunton et al. 2000). However, the weak bands of spines on *Chengxianoproductus* are slightly more of a sentosiid character than echinoconchid character. This feature therefore also distinguishes *Chengxianoproductus* from other genera of the Echinoconchidae. Thus, the assignment of *Chengxianoproductus* to the Echinoconchini is tentative.

Chengxianoproductus cf. *changxingensis* Liao and Meng, 1986

Figs. 7K, 10B, 14.

cf. *Waagenoconcha palliata* (Kayser); Chao 1927: 90, pl. 7: 3, 4, not 5, 6.

cf. "*Waagenoconcha*" *palliata* (Kayser); Wang et al. 1964: 286, pl. 40: 22–24.

cf. *Chengxianoproductus changxingensis* n. sp.; Liao and Meng 1986: 80.

Locality and horizon: Daijiagou section; 1st member of the Lungtan Formation.

Material.—Of five studied specimens, NMV P309626 and NMV P309640 are figured.

Description.—Large size for genus; subquadrate in outline; nearly circular in lateral profile; widest at midlength of shell; ears broad, flat, well-demarcated from umbo. Ventral valve strongly convex; beak small, distinct, incurved, slightly overhanging hingeline; lateral slopes steep; median sulcus broad, distinct; dorsal valve slightly concave, flattening posteriorly; median fold low, originating anterior to umbo. Ventral exterior with broad, flattened concentric bands, bearing 6–7 rows of circular spine bases tending to be alternatively arranged; row of spines along hinge. Dorsal ornament similar to that of ventral valve. Ventral interior with dendritic muscle scars, without median septum. Cardinal process bilobed with a shallow, circular alveolus; lateral ridges extending from base of cardinal process, curving down inside ears; median septum low, extending over half disc length (Fig. 14).

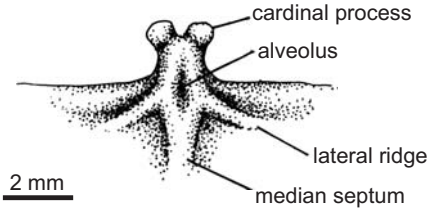


Fig. 14. Cardinal process of *Chengxianoproductus* cf. *changxingensis* Liao and Meng, 1986 (based on specimen NMV P309640).

Remarks.—When they established the present species, Liao and Meng (1986) questionably assigned parts of Kayser's (1883: pl. 27: 9–12) specimens to their new species *C. changxingensis*. However, as stated in the above generic discussion, the specimens figured by Chao (1927) and Wang et al. (1964) are not conspecific with the type specimens of *Parapulchratia palliata* Kayser, 1883. Accordingly, *C. changxingensis* only includes parts of the figured materials by Chao (1927: pl. 7: 3, 4). Of these, the specimen figured by Chao (1927: pl. 7: 3) and Wang et al. (1964: pl. 40: 22–24) was selected as the holotype of the species by Liao and Meng (1986).

The Daijiagou materials are comparable with the Changxing type in size, shell outline, spine arrangement and observed internal features. However, the conspicuous, smooth grooves separating lamellae are not preserved in Chao's original specimens. Consequently, the assignment of the Daijiagou materials to *C. changxingensis* is tentative. In addition, the specimen NMV P309640 also approaches *C. nitens* Liao and Meng, 1986 in many aspects, but *C. nitens* can not include the described material as it is smaller and has a greater number of lamellae and fewer rows of spines on each lamella. The Changhsingian species *C. intercedens* Liao and Meng, 1986 is differentiated from the described specimen (NMV P309640) by its deeper ventral median sulcus and a greater number of lamellae. *Tschernyschewia sinensis* (Chao, 1927) is also characteristic of the Lungtan Coal Series and morphologically indistinguishable from *C. changxingensis*, from which the *T. sinensis* differs in possessing a more elongate outline and the absence of conspicuous bands.

Suborder Strophalosiidina Schuchert, 1913

Superfamily Aulostegoidea Muir-Wood and Cooper, 1960

Family Aulostegidae Muir-Wood, 1960

Subfamily Echinosteginae Muir-Wood and Cooper, 1960

Genus *Edriosteges* Muir-Wood and Cooper, 1960

Type species: *Edriosteges multispinosa* Muir-Wood and Cooper, 1960; Kungurian (Early Permian), Texas, USA.

Edriosteges poyangensis (Kayser, 1883)

Fig. 13C–G.

Strophalosia poyangensis n. sp.; Kayser 1883: 190, pl. 28: 8, 10.
Aulosteges poyangensis (Kayser); Frech 1911: 134, pl. 20: 4a–d.
Aulosteges poyangensis (Kayser); Chao 1928: 73–74, pl. 3: 23.
Aulosteges poyangensis (Kayser); Huang 1932: 66–68, pl. 4: 7–13, pl. 5: 25.
Aulosteges poyangensis (Kayser); Wang et al. 1964: 345, pl. 56: 2–4.
Edriosteges poyangensis (Kayser); Sarycheva 1965: pl. 32: 4–6.
Edriosteges poyangensis (Kayser); Jin et al. 1974: 312, pl. 164: 14.
Edriosteges poyangensis (Kayser); Zhan 1979: 73, pl. 7: 1–4.
Edriosteges poyangensis plena subsp. nov.; Zhan 1979: 73–74, pl. 7: 5–8.
Edriosteges poyangensis (Kayser); Liao 1980b: pl. 3: 10–13.
Edriosteges poyangensis (Kayser); Liang 1990: 148–150, pl. 17: 4, 5.

Locality and horizon: Daijiagou section; 1st member of the Lungtan Formation; Chuanmu section; 5th member of the Lungtan Formation.

Material.—Total 15 specimens; figured specimens: NMV P309629–633.

Description.—Medium to large shells; outline semicircular in posterior view; slightly transversely trapezoidal in anterior view; hingeline slightly narrower than or equal with shell width; both valves geniculate anteriorly; trails short; ventral interarea relatively low; ears broad, slightly inflated; ventral umbo evenly convex; lateral slopes gentle; median sulcus variously developed, when present, originating anterior to umbo. Dorsal disc concave; median fold indistinct; corpus cavity moderately deep; ventral rugae irregularly spaced, conspicuous on discs, weakening anteriorly, sometime absent on trail; tubercules scatted over valves; spines scattered over ears, ventral corpus and trail, a row along hinge; radial striae fine, prominent when outer shell layer removed; shell thin.

Remarks.—This species is characteristic of the Lungtan Formation in South China. The allied species *Edriosteges tumita* Liao, 1980b is differentiated from *E. poyangensis* by an anteriorly convex and strongly geniculated ventral valve. *E. subplicatilis* Frech, 1911 (see also Liao 1980b: pl. 4: 15–17) is characterized by the presence of more pronounced rugae over the discs, *E. acuminata* Liao, 1980b is distinct in having the hingeline equal to the maximum shell width and pair of conspicuously projecting ears.

Class Rhynchonellata Williams, Carlson, Brunton, Holmer, and Popov, 1996
Order Orthida Schuchert and Cooper, 1931
Superfamily Enteletoidea Waagen, 1884
Family Enteletidae Waagen, 1884
Genus *Peltichia* Jin and Liao (in Jin and Sun, 1981)

Type species: *Parenteletes sinensis* mut. *zigzag* Huang, 1933; Changhsingian (Late Permian), Guizhou, South China.

Peltichia zigzag (Huang, 1933)

Fig. 7A.

Parenteletes sinensis mut. *zigzag* n. sp.; Huang 1933: 13, pl. 2: 7a–e.
Enteletina sinensis mut. *zigzag* (Huang); Wang et al. 1964: 153, pl. 20: 18–21.
Enteletina sinensis mut. *zigzag* (Huang); Jin et al. 1974: 313, pl. 165: 14–16.
Enteletina sinensis mut. *zigzag* (Huang); Yang et al. 1977: 309, pl. 129: 9.
Peltichia zigzag (Huang); Liao 1979: pl. 1: 28.
Peltichia zigzag (Huang); Liao 1980a: pl. 1: 25, 26.
Enteletina sinensis mut. *zigzag* (Huang); Liao 1980b: pl. 1: 53–55.
Enteletina sinensis mut. *zigzag* (Huang); Xu 1987: pl. 8: 11.
Peltichia zigzag (Huang); Xu and Grant 1994: 9.25, 9.26, 9.28–9.31.
Peltichia zigzag (Huang); Zeng et al. 1995: pl. 2: 2, 3.
Peltichia zigzag (Huang); Shen et al. 1999: 60, figs 10.1–5, 10. 26–29, 11.

Locality and horizon: Daijiagou section; 5th member of the Lungtan Formation; Chuanmu section; 5th member of the Lungtan Formation.

Remarks.—The material (NMV P309618) examined agrees fully with the description of the species given by Shen et al. (1999). According to these authors, *Peltichia* is generally confined to the Changhsingian. However, the presence of *P. zigzag* in the upper Lungtan Formation places its origin in the late Wuchiapingian. Within the genus, *P. zigzag* is separated from *P. transversa* (Huang, 1933) by its larger size, more elongate outline and strongly parasulcate anterior commissure.

Order Spiriferida Waagen, 1883
Suborder Delthyridina Ivanova, 1972
Superfamily Reticulariodiea Waagen, 1883
Family Elythidae Fredericks, 1924
Subfamily Phricodothyridinae Caster, 1939
Genus *Permophricodothyris* Pavlova, 1965

Type species: *Permophricodothyris ovata* Pavlova, 1965; Wuchiapingian (Late Permian), Caucasus, Azerbaijan.

Permophricodothyris grandis (Chao, 1929)

Figs. 7F, 15.

Squamularia grandis n. sp.; Chao 1929: 97, pl. 11: 1–3.
Squamularia cf. *grandis* Chao; Huang 1933: 36, pl. 5: 4–7, pl. 7: 3.
Squamularia grandis Chao; Wang et al. 1964: 557, pl. 106: 14–19.
Squamularia grandis Chao; Jin et al. 1974: 312, pl. 164: 17–19.
Squamularia grandis Chao; Feng and Jiang 1978: 296, pl. 105: 2, 3.
Squamularia grandis Chao; Tong 1978: 261, pl. 91: 2.
Permophricodothyris grandis Chao; Zhan 1979: 97–98, pl. 8: 1–2, 4–6.
Squamularia grandis Chao; Wang et al. 1982: 248, pl. 94: 10.
Squamularia grandis Chao; Xu 1987: 235, pl. 16: 4–9.
Squamularia grandis Chao; Zeng et al. 1995: pl. 13: 1, 2.
Permophricodothyris grandis (Chao); Shi et al. 2002: 378, figs. 3B, C, E, 4B, 5.1–5.13, 6.1–6.9.

Locality and horizon: Daijiagou section; 1st and 5th members of the Lungtan Formation; Chuanmu section; 5th member of the Lungtan Formation.

Remarks.—This species has long been regarded as the most typical representative of *Squamularia* Gemmellaro, 1899 in South China (e.g., Liao 1987; Liang 1990; Xu and Grant 1994; Zeng et al. 1995), though the comparable specimens outside China have been assigned to *Permophricodothyris* (e.g., Pavlova 1965; Grant 1993). More recently, Shi et al. (2002) altered Chao's species to *Permophricodothyris* and described a number of specimens from the 5th member of the Daijiagou section. It is noteworthy that abundant fragments of the species are preserved in the basal Lungtan Formation at Daijiagou, while a great number of excellent internal molds are present in the 5th member of the Lungtan

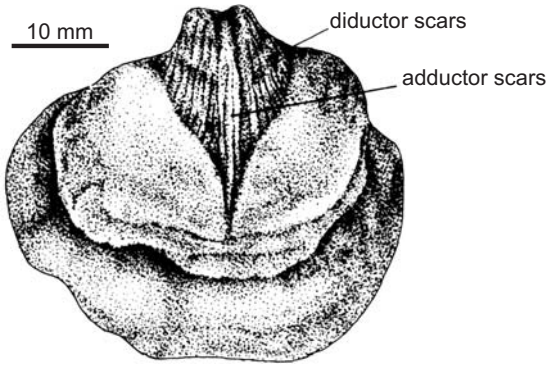


Fig. 15. Ventral interior of *Permophricodothyris grandis* (Huang, 1933) showing well-developed muscle scars (based on specimen NMV P309621).

Formation at Chuanmu. Of these, a ventral internal mold (NMV P309621) from Chuanmu is figured here to indicate the presence of Chao's species in the Lungtan Formation. The muscle scars are well defined on the figured internal mold, they are heart-shaped and raised on a muscle platform; the adductor scars are narrow, elongate, situated medially, and lightly grooved; the diductor scars are broad, chevron in shape with curved sides, meeting anteriorly with one another; the muscle markings of diductor scars are strongly grooved, about 6–7 radial lobes on each area (Fig. 15).

Order Spiriferinida Ivanova, 1972
Suborder Spiriferinidina Ivanova, 1972
Superfamily Pennospiriferinoidea Dagys, 1972
Family Paraspiriferinidae Cooper and Grant, 1976
Genus *Paraspiriferina* Reed, 1944

Type species: *Spiriferina* (*Paraspiriferina*) *ghundiensis* Reed, 1944; Capitanian (Middle Permian), Salt Range, Pakistan.

Paraspiriferina sp.

Fig. 7G.

Locality and horizon: Daijiagou section; 1st member of the Lungtan Formation.

Remarks.—An incomplete dorsal external mold (NMV P309635) is figured here to indicate the presence of *Paraspiriferina* in the basal Lungtan Coal Series. It is characterized by the coarse, sharp costae, numbering 4–5 on each flank. Of these, a median costa dominates the others and serves as the median fold. These features approach *Paraspiriferina alpha* (Huang, 1933), characteristic of the Lopingian of South China (e.g., Huang 1933; Liao 1980a; Xu 1987). However, insufficient material prevents a full comparison with Huang's species.

Conclusions

The fauna from the basal Lungtan Formation of the Wuchiapingian appears to represent the onset of the recovery of brachiopod faunas in the aftermath of the G/L mass extinction in South China. The post-extinction brachiopod faunas are characterized by the presence of numerous Lazarus taxa, survivors, and newly originating taxa. Those elements capable of adapting to a wide variety of ecologic niches could more easily survive from the G/L crisis. The post-extinction recovery forms have no life habit preference, but they were all adapted to a variety of newly vacated niches in the Late Permian oceans.

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References

Alexander, R.R. 1977. Growth, morphology and ecology of Paleozoic and Mesozoic opportunistic species of brachiopods from Idaho-Utah. *Journal of Paleontology* 51: 1133–1149.

Broili, F. 1916. Die Permischen Brachiopoden von Timor. *Paläontologie von Timor* 7: 1–104.

Brunton, C.H.C. 1987. The palaeoecology of brachiopods, and other faunas, of Lower Carboniferous (Asbian) limestones in West Fermanagh. *Irish Journal of Earth Sciences* 8 (2): 97–112.

Brunton, C.H.C., Lazarev, S.S., Grant, R.E., and Jin, Y.G. 2000. Productidina. *In*: A. Williams, C.H.C. Brunton, and S.J. Carlson (eds.), *Treatise on Invertebrate Palaeontology*, Part H, Revised (*Brachiopoda*, 2–3), H424–H644. Geological Society of America and University of Kansas Press, Lawrence.

Brunton, C.H.C. and Mundy, D.J.C. 1988. Strophalosiacean and aulostegacean productoids (Brachiopoda) from the Craven Reef Belt (late Visean) of North Yorkshire. *Proceedings of Yorkshire Geological Society* 47: 55–88.

Caster, K.E. 1939. A Devonian fauna from Colombia. *Bulletins of American Paleontology* 24: 1–218.

Campi, M.J. and Shi, G.R. 2002. *Linshuichonetes* gen. nov., a new rugosochonetid (Brachiopoda) genus from the Liangshan Formation (Early Permian) in Sichuan, China, and its ecology. *Acta Palaeontologica Sinica* 41: 105–118.

Chao, Y.T. 1927. Productidae of China, Part 1: Producti. *China Geological Survey, Palaeontologica Sinica, Series B* 5 (2): 1–192.

Chao, Y.T. 1928. Productidae of China. Part 2. Chonetinae, Productinae, and Richthofeninae. *Palaeontologia Sinica, Series B* 5 (3): 1–81.

Chao, Y.T. 1929. Carboniferous and Permian spiriferids of China. *Palaeontologica Sinica, Series B* 11 (1): 1–101.

Chen, Z.Q. 2004. Lower Permian reef-dwelling brachiopod faunas from the Tarim Basin, Northwest China: biostratigraphy, palaeoecology and biogeography. *Palaeontographica A* 272 (1–4), 1–96.

Chen, Z.Q., Jin, Y.G., and Shi, G.R. 1998. Permian transgression-regression sequences and sea-level changes of South China. *Proceedings of the Royal Society of Victoria* 110: 345–367.

Chen, Z.Q. and Shi, G.R. 2000. A new Tribe of dictyoclostid brachiopods from the Lower Permian of the Tarim Basin, Northwest China. *Palaeontology* 43: 325–342.

Chen Z.Q., Shi G.R., Shen, S.Z., and Archbold, N.W. 2000. *Tethyochonetes* gen. nov. (Chonetida, Brachiopoda) from Late Permian of China. *Proceedings of the Royal Society of Victoria* 112: 1–15.

Chi-Thuan, T.T. 1962. Les brachiopodes permiens de Cam-l (Province de Quang-Tri). *Annales de la Facult des Sciences, Universit de Saigon* 1962: 485–498.

Cooper, G.A. and Grant, R.E. 1976. Permian brachiopods of West Texas, V. *Smithsonian Contributions to Paleobiology* 24: 2609–3159.

Cox, E.T. 1857. A description of some of the most characteristic shells of the principal coal-seams in the western basin of Kentucky. *Geological Survey of Kentucky Report* 3: 566–576.

Dagys, A.S. 1972. Morphology and systematics of Mesozoic retsioid brachiopods [in Russian]. *Akademiâ Nauk SSSR, Sibirskoe Otdelenie, Institut Geologii i Geofiziki, Trudy* 112: 94–105.

Diener, C. 1897. Himalayan fossils. The Permian fossils of the *Productus* Shales of Kumaon and Gurhwal. *Geological Survey of India, Memoirs, Palaeontologia Indica, Series 15* 1 (4): 1–54.

Dumeril, A.M.C. 1806. *Zoologie analytique ou methode naturelle de classification des animaux*. 344 pp. Allais, Paris.

Erwin, D.H. 1993. *The Great Paleozoic Crisis*. 327 pp. Columbia University Press, New York.

Erwin, D.H. 1997. Understanding biotic recoveries: extinction, survival, and preservation during the end-Permian mass extinction. *In*: D. Jablonski, Erwin, D.H., and J.M. Lipps (eds.), *Evolutionary Paleobiology*, 399–418. University of Chicago Press, Chicago.

Erwin, D.H. 2000. Life's downs and ups. *Nature* 404: 129–130.

Erwin, D.H. 2001. Lessons from the past: Biotic recoveries from mass extinctions. The end and the beginning: recoveries from mass extinctions. *Proceedings of the National Academy of Sciences of the United States of America* 98: 5399–5403.

Erwin, D.H. and Droser, M.L. 1993. Elvis taxa. *Palaios* 8: 623–624.

Fara, E. 2001. What are Lazarus taxa? *Geological Journal* 36: 291–303.

Feng, R.L. and Jiang, Z.L. 1978. Brachiopods [in Chinese]. *In*: *Palaeontological Atlas of Southwestern China*, 231–305. Geological Publishing House, Beijing.

Frech, F. 1911. Die Dyas. *In*: F. von Richthofen (ed.), *China*, vol. 5, 116–137. Verlag von Dietrich Reimer, Berlin.

Fredericks, G.N. 1924. Paleontological studies. 2. On Upper Carboniferous spiriferids of Ural [in Russian]. *Izvestiâ Geologičeskogo Komiteta* 38: 295–324.

Gemmellaro, G.C. 1899. La fauna dei Calcari con Fusulina della Valle del Fuime Sosionella Provincia de Palemo. *Giornale di Scienze Naturali ed Economiche di Palermo* 22: 95–214.

Grant, R.E. 1963. Unusual attachment of a Permian linoproductid brachiopod. *Journal of Paleontology* 37: 134–140.

Grant, R.E. 1966. Spine arrangment and life habits of the productoid brachiopod *Waagenoconcha*. *Journal of Paleontology* 40: 1063–1069.

Grant, R.E. 1968. Structural adaptation in two Permian brachiopod genera, Salt Range, West Pakistan. *Journal of Paleontology* 42: 1–32.

Grant, R.E. 1976. Permian brachiopods from southern Thailand. *Journal of Paleontology* 50 (Supplement to No. 3), *The Paleontological Society Memoir* 9: 1–269.

Grant, R.E. 1993. Permian Brachiopods from Khios Island, Greece. *Journal of Paleontology* 67 (Supplement to No. 4) *The Paleontological Society Memoir* 33: 1–21.

Grant, R.E. 1995. Upper Permian brachiopods of the Superfamily Orthotetoidea from Hydra Island, Greece. *Journal of Paleontology* 69: 655–670.

Gray, J.E. 1840. *Synopsis of the Contents of the British Museum*, 42nd edition. 370 pp. British Museum, London.

Hallam, A. and Wignall, P.B. 1997. *Mass Extinctions and Their Aftermath*. 320 pp. Oxford University Press, Oxford.

Hu, S.Z. 1989. Discovery of brachiopods from coal-bearing member of Lungtan Formation and its significance—A new understanding of Lungtan Formation coal-forming environment [in Chinese]. *Acta Palaeontologica Sinica* 28: 474–479.

Huang, T.K. 1932. Late Permian brachiopods of southwestern China. Part 1. *Geological Survey of China, Palaeontologia Sinica B* 9 (1): 1–138.

Huang, T.K. 1933. Late Permian brachiopods of southwestern China, Part 2. *Geological Survey of China, Palaeontologia Sinica B* 9 (2): 1–172.

International Union of Geological Sciences (IUGS). 2002. *International Stratigraphic Chart*. Commission on Geological Map of the World, Paris.

Ivanova, E.A. 1972. Principal trends in the evolution of spiriferids (Brachiopoda) [in Russian]. *Paleontologičeskii žurnal* 1972 (3): 28–42.

Jablonski, D. 1986. Causes and consequences of mass extinction: a comparative approach. *In*: D.K. Elliott (ed.), *Dynamics of Extinction*, 183–229. Wiley & Sons, New York.

Jacobs, S.E. 1976. *Neochonetes granulifer*, an explosive opportunist from the Stull Shale (Upper Pensylvanian) in southwestern Iowa. *Proceedings of the Iowa Academic Sciences* 83: 20–22.

Jin, Y.G. 1985. Permian Brachiopoda and paleogeography of the Qinghai-Xizang (Tibet) Plateau. *Palaeontologia Cathayana* 2: 19–71.

Jin, Y.G. and Hu, S.Z. 1978. Brachiopods of the Kuhfeng Formation in South Anhui and Nanking Hills [in Chinese]. *Acta Palaeontologica Sinica* 17: 101–123.

Jin, Y.G., Liao, Z.T., and Hou, H.F. 1974. Permian Brachiopoda [in Chinese]. *In*: Nanjing Institute of Geology and Palaeontology, Academia Sinica (ed.), *Handbook of Stratigraphy and Palaeontology of Southwestern China*, 308–314. Science Press, Beijing.

Jin, Y.G., Mei, S.L., Wang, W., Wang, X.D., Shen, S.Z., Shang, Q.H., and Chen, Z.Q. 1998. On the Lopingian Series of the Permian System. *Palaeoworld* 9: 1–18.

Jin, Y.G. and Sun, D.L. 1981. Palaeozoic brachiopods from Xizang [in Chinese]. *In*: Nanjing Institute of Geology and Palaeontology, Academia Sinica (ed.), *Palaeontology of Xizang, Book III, The Series of the Scientific Expedition to the Qinghai-Xizang Plateau*, 127–176. Science Press, Beijing.

Jin, Y.G., Zhang, J., and Shang, Q.H. 1994. Two phases of the end-Permian mass extinction. *Canadian Society of Petroleum Geologists, Memoir* 17: 813–822.

Kauffman, E.G. and Harries, P.J. 1996. The importance of crisis progenitors in recovery from mass extinction. *In*: M.B. Hart (ed.), Biotic Recovery from Extinction Events. *Geological Society, Special Publication* 102: 15–39.

Kayser, E. 1883. Obercarbonische Fauna von Lo-Ping. *In*: F. von Richthofen (ed.), *China*, vol. 4 (8), 160–208. Verlag von Dietrich Reimer, Berlin.

Lazarev, S.S. 2000. Brachiopods of the new Tribe Reticulatiini from the Carboniferous of the Moscow region. 1. Merenomic basis for phylogeny and taxonomy. *Paleontological Journal* 34: 400–410.

Leighton, L.R. 2001. New example of Devonian predatory boreholes and the influence of brachiopod spines on predator success. *Palaeogeography, Palaeoclimatology, Palaeoecology* 165: 53–69.

Li, L., Gu, F., and Su, Y.Z. 1980. Brachiopoda (Carboniferous–Permian) [in Chinese]. *In*: *Paleontological Atlas of Northeast China, Volume 1*, 327–428. Geological Publishing House, Beijing.

Liang, W.P. 1990. Lengwu Formation of Permian and its brachiopod fauna in Zhejiang Province [in Chinese]. *Geological Memoirs, Series 2* 10: 1–522.

Liao, Z.T. 1979. Uppermost Carboniferous brachiopods from western Guizhou [in Chinese]. *Acta Palaeontologica Sinica* 18: 527–546.

Liao, Z.T. 1980a. Brachiopod assemblages from the Upper Permian and Permian–Triassic boundary beds, South China. *Canadian Journal of Earth Sciences* 17: 289–295.

Liao, Z.T. 1980b. Upper Permian brachiopods from western Guizhou [in Chinese]. *In*: Nanjing Institute of Geology and Palaeontology, Academia Sinica (ed.), *Stratigraphy and Palaeontology of Upper Permian Coal-bearing Formations in Western Guizhou and Eastern Yunnan, China*, 241–277. Science Press, Beijing.

Liao, Z.T. 1984. New genera and species of Late Permian and earliest Triassic brachiopods from Jiangsu, Zhejiang and Anhui provinces [in Chinese]. *Acta Palaeontologica Sinica* 23: 276–285.

Liao, Z.T. 1987. Paleoecological characters and stratigraphic significance of silicified brachiopods of the Upper Permian from Heshan, Laibin, Guangxi [in Chinese]. *In*: Nanjing Institute of Geology and Paleontology, Academia Sinica (ed.), *Stratigraphy and Palaeontology of Systemic Boundaries in China, Permian and Triassic Boundary 1*, 81–125. Nanjing University Press, Nanjing.

Liao, Z.T. and Meng, F.Y. 1986. Late Chanxsingian brachiopods from Huatang of Cheng Xian County, southern Hunan [in Chinese]. *Nanjing Institute of Geology and Palaeontology, Memoirs* 22: 71–94.

Licharew, B.K. [Liharev, B.K.] 1936. On some representatives of rare Upper Palaeozoic brachiopods [in Russian]. *Bûlleten Moskovskogo Obŝestva Ispytatelej Prirody, Otdelenie Geologičeskie* 14: 133–158.

Licharew, B.K. [Liharev, B.K.] 1939. Class Brachiopoda [in Russian]. *In*: B.K. Ličarev (ed.), *Atlas rukovodiaŝih form iskopaemyh faun SSSR. Tom VI. Permskaâ sistema*, 76–1219. GONTI NKTP SSSR, Moskva.

Licharew, B.K. [Liharev, B.K.] and Kotlyar, G.V. [Kotlâr, G.V.] 1978. Permian brachiopods of southern Primorye [in Russian]. *In*: L.I. Popeko (ed.), *Verhnij Paleozoj Severo-Vostočnoj Azii*, 63–75, 96–99. AN SSSR DNTS Institut Tektoniki i Geofiziki, Vladivostok.

Liu, Z.H., Tan, Z.X., and Ding, Y.L. 1982. Brachiopoda [in Chinese]. *In*: *The Paleontological Atlas of Hunan. Geological Memoirs, Series 2* 1: 172–216.

Mansuy, H. 1913. Faunes des Calcaires à *Productus* de l'Indochine, Première série. *Service Géologique de l'Indochine, Mémoires* 2 (4): 1–133.

Mei, S.L. Jin, Y.G., and Wardlaw, B.R. 1994. Succession of Wuchiapingian conodonts from northeastern Sichuan and its worldwide correlation. *Acta Palaeontologica Sinica* 11: 1–19.

McKellar, R.G. 1970. The Devonian productoid brachiopod faunas of Queensland. *Geological Survey of Queensland, Publications* 342: 1–40.

Muir-Wood, H.M. 1960. Proposed use of the plenary powers to designate a type-species for the nominal genus *Strophalosia* King, 1844, (Phylum Brachiopoda). Z.N. (S.) 784. *Bulletin of Zoological Nomenclature* 17: 316–322.

Muir-Wood, H.M. and Cooper, G.A. 1960. Morphology, classification and life habits of the Productoidea (Brachiopoda). *The Geological Society of America Memoir* 81: 1–447.

Pavlova, Y.Y. [Pavlova, Û.Û.] 1965. Revision of the genus *Neophricodothyris* (order Spiriferida) [in Russian]. *Palaeontologičeskij žurnal* 2: 133–137.

Reed, F.R.C. 1944. Brachiopoda and Mollusca from the *Productus* Limestones of the Salt Range. *Geological Survey of India, Memoirs, Palaeontologia Indica* 23 (2): 1–678.

Rudwick, M.J.S. 1970. *Living and Fossil Brachiopods*. 199 pp. Hutchinson University Library, London.

Sarycheva, T.G. [Saryčeva, T.G.] 1965. Order Productida [in Russian]. *In*: V.E. Ružencev and T.G. Saryčeva (eds.), Razvitie i Smena Morskih Organizmov na Rubeže Paleozoâ i Mezozoâ. *Akademiâ Nauk SSSR, Paleontologičeskij Institut, Trudy* 108: 209–232.

Sarycheva, T.G. [Saryčeva, T.G.] and Sokolskaya, A.V.N. [Sokolskaâ, A.V.N.] 1959. On classification of lozhnoporistyh brachiopods [in Russian]. *Akademiâ Nauk SSSR, Doklady* 125: 181–184.

Schuchert, C. 1913. Brachiopoda. *In*: K.A. von Zittel (ed.), *Paleontology,* 2nd edition, vol. 1, 355–420. MacMillian & Co. Ltd., London.

Schuchert, C. and Cooper, G.A. 1931. Synopsis of the brachiopod genera of the suborders Orthoidea and Pentameroidea, with notes on the *Telotremata*. *American Journal of Science, Series 5* 22: 241–251.

Schuchert, C. and LeVene, C.M. 1929. Brachiopoda (Generum et genotyporum index et bibliographia). *In*: J.F. Pompeckj (ed.), *Fossilium Catalogus I: Animalia 42*, 1–140. W. Junk, Berlin.

Shen, S.Z., He, X.L., and Zhu, M.L. 1992. Changxingian brachiopods from Zhongliang Hill of Chongqing, Sichuan Province [in Chinese]. *In*: D.Y. Gu (ed.), *Stratigraphy and Palaeontology of Oil and Gas Bearing Areas in China 3*, 171–196. Petroleum Industry Press, Beijing.

Shen, S.Z. and Shi, G.R. 1996. Diversity and extinction patterns of Permian Brachiopoda of South China. *Historical Biology* 12: 93–110.

Shen, S.Z., Tazawa, J., and Shi, G.R. 1999. *Peltichia* Jin and Liao, 1981 (Enteletidae, Brachiopoda) from Asia: Taxonomy, biostratigraphy and paleobiogeography. *Journal of Paleontology* 73: 49–62.

Sheng, J.Z. and Jin, Y.G. 1994. Correlation of Permian deposits of China. *Palaeoworld* 4: 14–113.

Shi G.R. and Chen Z. Q. 2003. Global review of Permian *Tyloplecta* Muir-Wood and Cooper, 1960 (Brachiopoda): morphology, biogeographical and palaeogeographical implications. *Gondwana Research* 6: 777–790.

Shi, G.R., Chen, Z.Q., and Han, N.R. 2002. *Permophricodothyris* Pavlova, 1965 (Brachiopoda, Spiriferida) from the Permian of South China: its morphology, biostratigraphy and distribution. *Palaontologische Zeitschrift* 76: 369–383.

Shi, G.R., Shen, S.Z., and Tong, J.N. 1999. Two discrete, possibly unconnected, Permian marine mass extinctions. *In*: H.F. Yin and J.N. Tong (eds.), *Proceedings of the International Conference on Pangea and the Paleozoic-Mesozoic Transition*, 148–151. China University of Geosciences Press, Wuhan.

Simanauskas, T. and Cisterna, G. 2000. A palaeo-opportunistic brachiopod from the Early Permian of Argentina. *Alcheringa* 24: 45–53.

Stanley, S.M. and Yang, X.N. 1994. A double mass extinction at the end of the Paleozoic Era. *Science* 266: 1340–1344.

Stehli, F.G. 1954. Lower Leonardian Brachiopoda of the Sierra Diablo. *American Museum of Natural History, Bulletin* 105: 257–358.

Stoyanow, A.A. [Stoânov, A.A.] 1910. On new brachiopod species [in Russian]. *Bulletin de l'Academie Imperiale des Sciences de St. Petersbourg, Series 6* 4: 853–855.

Tazawa, J. and Ibaraki, Y. 2001. Middle Permian brachiopods from Stamai, the type locality of the Kanokura Formation, southern Kitakami Mountains, northeast Japan. *Science Reports of Niigata University, Series E (Geology)* 16: 1–33.

Tazawa, J. and Matsumoto, T. 1998. Middle Permian brachiopods from the Oguradani Formation, Ise district, Hida Gaien Belt, central Japan. *Science Reports of Niigata University, Series E (Geology)* 13: 1–19.

Tazawa, J., Takizawa, F., and Kamada, K. 2000. A Middle Permian Boreal-Tethyan mixed brachiopod fauna from Yakejima, southern Kitakami Mountains, NE Japan. *Science Reports of Niigata University, Series E (Geology)* 15: 1–21.

Ting, P.C. 1965. The Permian and Triassic brachiopods from Yangkang Valley, Tienchung district, Tsinghai Province [in Chinese]. *Acta Palaeontologica Sinica* 13: 260–290.

Tong, Z.X. 1978. Permian and Carboniferous brachiopods [in Chinese]. *In*: *Palaeontological Atlas of Southwestern China, Sichuan Volume*, 210–267. Geological Publishing House, Beijing.

Waagen, W.H. 1882–1885. Salt range fossils: *Productus* limestone fossils, Part 4 (2–4): Brachiopoda. *Memoirs of the Geological Survey of India, Palaeontologia Indica, Series 13* 1: 329–770.

Walker, S.E. and Miller, W. III. 1992. Organism-substrate relations: Toward a logical terminology. *Palaios* 7: 236–238.

Wang, G.P., Liu, Q.Z., Jin, Y.G., Hu, S.Z., Liang, W.P., and Liao, Z.T. 1982. Brachiopoda [in Chinese]. *In*: *Palaeontological Atlas of Eastern China*, 186–256. Geological Publishing House, Beijing.

Wang, X.D. and Sugiyama, T. 2000. Diversity and extinction patterns of Permian coral faunas of China. *Lethaia* 33: 285–294.

Wang, Y. 1955. New genera of brachiopods. *Scientia Sinica* 4: 327–357.

Wang, Y., Jin Y.G., and Fang, D.W. 1964. *Brachiopods from China* [in Chinese]. 686 pp. Science Press, Beijing.

Waterhouse, J.B. 1975. New Permian and Triassic brachiopod taxa. *University of Queensland, Department of Geology, Papers* 7 (1): 1–23.

West, R.R. 1977. Organism-substrate relations: terminology for ecology and palaeoecology. *Lethaia* 10: 71–82.

White, C.A. and St. John, O. 1867. Description of new subcarboniferous and coal measure fossils, collected upon the Geological Survey of Iowa, together with a notice of new generic characters involved in two species of brachiopods. *Chicago Academy of Sciences, Transactions* 1: 115–127.

Williams, A. and Brunton, C.H.C. 2000. Orthotetidina. *In* A. Williams, C.H.C. Brunton, and S.J. Carlson (eds.), *Treatise on Invertebrate Paleontology*, Part H, *Brachiopoda* (revised) Vol. 3, 644–681. The Geological Society of America and The University of Kansas, Lawrence.

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

Xu, G.R. 1987. Brachiopods [in Chinese]. *In*: Z.Y. Yang, H.F. Yin, S.B. Wu, F.Q. Yang, M.H. Ding, and G.R. Xu (eds.), Permian–Triassic Boundary Stratigraphy and fauna of South China. *Geological Memoirs, Series 2*, 6: 215–235.

Xu, G.R. and Grant, R.E. 1994. Brachiopods near the Permian–Triassic boundary in South China. *Smithsonian Contributions to Paleobiology* 76: 1–68.

Yang, D.L. 1984. Brachiopoda [in Chinese]. *In*: S.N. Feng, S.Y. Xu, J.X. Lin, and D.L. Yang (eds.), *Biostratigraphy of the Yangtze Gorge area, 3—Late Paleozoic Era*, 203–239. Geological Publishing House, Beijing.

Yang, D.L., Ni, S.Z., Chang, M.L., and Zhao, R.X. 1977. Brachiopods [in Chinese]. *In*: *Palaeontological Atlas of Central-South China 2*, 306–470. Geological Publishing House, Beijing.

Yang, X.N., Shi, G.J., Liu, J.R., Chen, Y.T., and Zhou, J. 2000. Inter-taxa differences in extinction process of Maokouan (Middle Permian) fusulinaceans. *Science in China, Series D-Earth Sciences* 43: 633–637.

Zeng, Y. 1996. Lungtanian strata and brachiopod fauna from Yuechi, Sichuan [in Chinese]. *Journal of Stratigraphy* (Nanjing) 20: 35–39.

Zeng, Y., He, X.L. and Zhu, M.L. 1995. *Permian brachiopods and community succession in the Huayin mountains*, *Sichuan* [in Chinese]. 187 pp. China University of Mineralogy Press, Xuzhou.

Zhan, L.P. 1979. Brachiopods [in Chinese]. *In*: H.F. Hou, L.P. Zhan, and B.W. Chen (eds.), *The Coal-bearing Strata and Fossils of Late Permian from Guangtung*, 20–30. Geological Publishing House, Beijing.

Zhang, Y. and Ching, Y.K. (Jin, Y.G.) 1961. An Upper Permian brachiopod fauna from Jingxian, Anhui Province [in Chinese]. *Acta Palaeontologica Sinica* 9: 401–425.