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Wuchiapingian (Lopingian, late Permian) brachiopod fauna from Guangdong Province, southeastern China: systematics and contribution to the Lopingian recovery

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Abstract.—A diverse Wuchiapingian brachiopod fauna, which contains 57 species in 28 genera, is described from the Shuizhutang Formation at the Liannan section, Guangdong province, southeastern China. Four new species *Tyloplecta liannanensis* n. sp., *Linoproductus huananensis* n. sp., *Araxathyris minor* n. sp., and *Permophricodothyris flata* n. sp. are proposed. From well-preserved Liannan specimens, characteristics of the shell microstructures in *Permianella* are revised, and different morphologies of muscle scars in *Permophricodothyris* are distinctly shown. Until now, only several Wuchiapingian brachiopod faunas have been found in South China. Compared with these faunas, the Liannan fauna shows much higher α diversity and is more like faunas from southeastern China than those from the Yangtze area in faunal composition. The Liannan fauna is dominated with *Neochonetes*, *Transennatia*, *Orthothetina*, *Permophricodothyris*, and *Cathaysia*, which are normally larger and more strongly ornamented than their Changhsingian counterparts. The Wuchiapingian brachiopods in South China are represented mainly by the Douling fauna and Shuizhutang fauna. The Douling fauna has relatively low diversity and presents the survival stage after the Guadalupian–Lopingian boundary crisis. The Shuizhutang fauna has a much higher diversity and more key Changhsingian taxa and shows a rapid radiation stage. Faunal compositions of the two faunas indicate that the initial recovery of brachiopods occurred mainly at the genus level followed by a more rapid radiation at both genus and species levels.

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Introduction

The Guadalupian–Lopingian boundary (GLB) biotic crisis has been regarded as one of the least understood crisis events in the Phanerozoic era (Raup and Sepkoski, 1982; Bambach, 2002; Jost et al., 2014). There remain debates about whether it was a sudden extinction (Stanley and Yang, 1994; Isozaki and Servais, 2018; Arefifard and Payne, 2020; Rampino and Shen, 2020) or a gradual diversity reduction (Clapham et al., 2009; Fan et al., 2020; Shen et al., 2020; Lee et al., 2022), which may be related to the varied crisis times over different areas and selective extinctions among different marine organisms. During the GLB crisis, brachiopods were severely affected, and 30% of genera and 87% of species became extinct (Shen and Shi, 1996; Sun and Shen, 2004), but this crisis was restricted to the genus and species level (Shen et al., 2006). Following this, the brachiopod fauna had relatively low diversity in the initial early Wuchiapingian recovery and then rapidly radiated in the late Wuchiapingian (Chen et al., 2005; Shen et al., 2006; Shen and Zhang, 2008; Shen and Shi, 2009; Fan et al., 2020). During the GLB crisis, the dominant Guadalupian brachiopod genera, *Neoplicatifera*, *Urushtenoidea*, and *Vediproductus*, were replaced by *Permophricodothyris*, *Haydenella*. and *Edriosteges* in the Wuchiapingian (Shen et al., 2019). However, due to the widespread absence of marine strata related to the global regression event (Shen et al., 2020), brachiopod fossil data in the GLB interval remain deficient (Shen and Zhang, 2008; Shen and Clapham, 2009; Ghaderi et al., 2014; Tazawa et al., 2015; Xu et al., 2018). More robust, section-based studies on GLB brachiopod faunas are required to investigate the crisis and recovery/radiation patterns.

In the 1980s, numerous works gave overviews of the Lopingian brachiopod faunas from both the Yangtze block and southeastern China (Zhan in Hou et al., 1979; Liao, 1980; Wang et al., 1982; Yang, 1984; Liao in Yang et al., 1987; Hu, 1989; Li et al., 1989). Later, several more-extensive systematic works for Wuchiapingian brachiopods from South China were published (Chen et al., 2005; Li and Shen, 2008; Shen and Zhang, 2008; Shen and Shi, 2009), most of which focused on brachiopod fauna from the Yangtze block. The present paper provides a detailed description of a brachiopod fauna from the

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Liannan area of Guangdong Province, southeastern China, and discusses the faunal changes across different environments in the Wuchiapingian and the implications for brachiopod faunal recovery/radiation after the GLB crisis.

Geological setting and age

The described specimens were collected from the Shuizhutang Formation at the Liannan section, which is located about 10 km southeast of Liannan County in Qingyuan, northern Guangdong Province (Fig. 1). In the Lopingian (late Permian), the studied area recorded two regressive–transgressive cycles, represented by the Wuchiapingian Longtan Formation and Shuizhutang Formation (from coal-bearing deposits to carbonates) and the Changhsingian Wangpanli Formation and Changxing Formation (from coal-bearing deposits to carbonates), respectively (Hou et al., 1979). The Shuizhutang Formation represented in the Liannan section was deposited in a conjunction area between the shallow-water restricted carbonate platform (Lianshan–Yangshan area) and the clastic shelf, which is close to the Yunkai old land (Fig. 2). The Shuizhutang Formation comprises mainly dark grey siliceous mudstone in the lower part and yellowish siliceous and calcareous mudstone in the middle to upper part (Fig. 3).

Judging from the yielded fusulinids *Codonofusiella kwangsiana* Sheng, 1963 and *Gallowayinella meitienensis* Chen, 1934 and ammonoids *Prototoceras*, *Araxoceras*, and *Konglingites* (Hou et al., 1979), the age of the Shuizhutang Formation should be assigned to the late Wuchiapingian (Shen and Zhang, 2008; Shen, 2018). In addition, the Liannan brachiopod fauna, which is dominated mainly by *Fusichonetes*, *Neochonetes*, *Transennatia*, *Cathaysia*, and *Orthothetina,* should belong to the *Transennatia–Orthothetina* Assemblage and also indicates the late Wuchiapingian age (Yang et al., 1987).

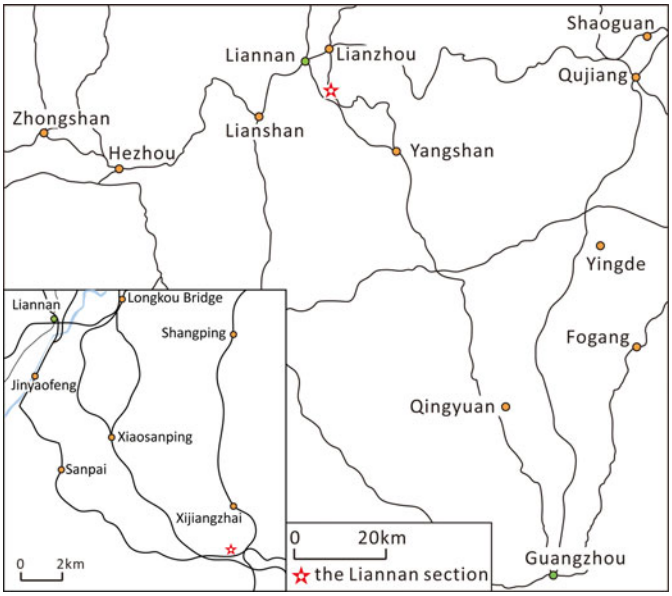

Figure 1. Location of the Liannan section, northern Guangdong Province, southeastern China.

Materials and methods

In total, 1,900 complete brachiopod specimens were collected from the upper Wuchiapingian of the Liannan section. The Liannan fauna contains 57 brachiopod species in 28 genera and is summarized in Figure 3.

To verify the distinctness of the spondylium development of *A. minor* n. sp., spondylium length and width and total shell length and width of all *Araxathyris* specimens from the Liannan section were measured. To highlight the large variation in width/length ratios of *Cathaysia chonetoides* (Chao, 1927), shell width and length of all *Cathaysia* specimens from the Liannan section were also measured. Further, to present the shell outline and size of the subgenus *Neochonetes* (*Zhongyingia*), we measured shell width and length of all specimens of this subgenus from the Liannan section and Lopingian specimens in the literature. Both the shell size and spondylium size were approximated with the geometric mean of length and width, following Jablonski (1996). To show the similarity of brachiopod faunas from selected sections, absence–presence data at genus level were collected, and cluster analysis using the unweighted paired group algorithm and the Raup–Crick index were adopted. All analyses were carried out using the software PAST (Hammer et al., 2001).

Repository and institutional abbreviation.—Types and other specimens examined in this study are deposited in the Faculty of Earth Science and Resources, China University of Geosciences (Beijing) (CUGB), China, with the prefix LN for the Liannan section in Guangdong Province, South China.

Results and discussion

Comparison of the Liannan fauna with other contemporaneous faunas from South China.—There have been only several Wuchiapingian brachiopod faunas reported from South China, including faunas from the Yansha and Xiaoyuanchong sections (Shen and Zhang, 2008) and the Daijiagou section (Chen et al., 2005) (Fig. 2). In addition, there are Wuchiapingian brachiopod faunas described by Shen and Zhang (2008) and Chen et al. (2005) from the Yanhu, Sanhe, Yejiwo, and Chuanmu sections. Since these latter four sections all yielded fewer than five species, they are not included herein.

Compared with the three aforementioned sections, the Liannan fauna shows much higher α diversity. There are 57 species in the Liannan section, 11 species from the Xiaoyuanchong section, 34 species from the Yansha section, and 16 species from the Daijiagou section. According to the result of cluster analysis, the Liannan fauna shows greatest similarity to the Xiaoyuanchong and Yansha faunas and least similarity to the Daijiagou fauna (Fig. 4). Some common genera in the Lopingian of South China, including *Spinomarginifera*, *Neochonetes*, *Transennatia*, *Tyloplecta*, and *Haydenella*, all occurred in the Liannan, Yansha, and Xiaoyuanchong sections (Fig. 5). Although *Spinomarginifera* and *Transennatia* also occurred in the Daijiagou section, genera that only occasionally occurred in the Yangtze and other blocks, such as *Magniderbyia* and *Niutoushania,* existed only in the Daijiagou fauna.

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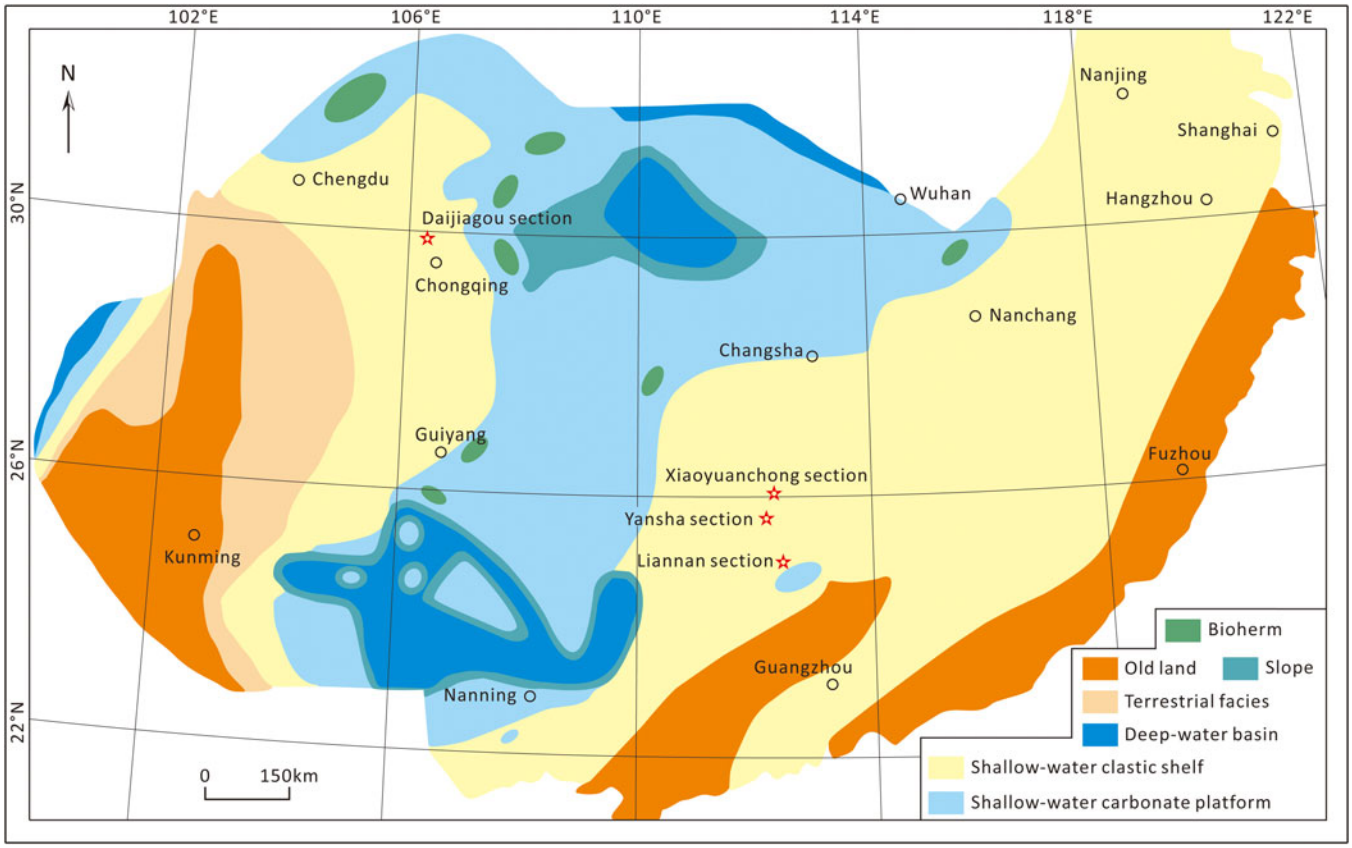

Figure 2. Paleogeographical map of South China during Wuchiapingian (from Feng et al., 1997), showing the location of the Liannan section as well as the sites of the Yansha, Xiaoyuanchong, and Daijiagou sections also referred to in this paper.

The similarity of the faunal composition but difference in α diversity among the four studied sections can be explained by their paleogeographical positions during the Wuchiapingian. Although they are all located in or close to the shallow-water clastic shelf, the Liannan, Yansha, and Xiaoyuanchong sections are all situated in southeastern China while the Daijiagou section is in the northwestern Yangtze block; thus, the former three faunas show greater similarity. A similar pattern is also seen in Changhsingian brachiopods from South China. The Sanhe and Dapaichong faunas (which are from southeastern China) are distinctly differentiated from the Daijiagou, Beifengjing, Yutianbao, Nantong, and Tuanxi faunas (which are from the Upper Yangtze) in the network diagram (Wu et al., 2020, fig. 4).

Implications for brachiopod faunal recovery/radiation from the GLB crisis.—After the GLB crisis, the brachiopods maintained a relatively low diversity in the early Wuchiapingian (survival stage) and then rapidly radiated in the late Wuchiapingian (radiation stage) in South China (Sun and Shen, 2004). During this transitional interval, southern Hunan Province–northern Guangdong Province serves as one of the key areas (Fig. 2), yielding unusually diverse brachiopod faunas (Shen and Zhang, 2008; this study).

In southern Hunan Province, an earliest Wuchiapingian brachiopod fauna was reported from the upper part of Douling Formation (which contains mainly calcareous mudstone interbedded with thin-bedded bioclastic limestone, deposited in the continental shelf sedimentary environment; see Shen and Zhang, 2008 for details) at the Yanshan, Xiaoyuanchong, Douling, Yanhu, Yejiwo, and Sanhe sections (Wang and Jin, 1991; Shen and Archbold, 2002; Shen and Zhang, 2008), which sheds light on the survival stage just after the GLB crisis. The Douling brachiopod fauna includes 39 species in 30 genera and 20 families (without undetermined species), which consist mainly of the Wuchiapingian taxa (e.g., *Acosarina minuta* (Abich, 1878), *Transennatia gratiosa* (Waagen, 1884), *Edriosteges poyangensis* (Kayser, 1883), *Haydenella kiangsiensis* (Kayser, 1883), *Tyloplecta yangtzeensis* (Chao, 1927); see Fig. 5 for details). However, this fauna still has relatively low diversity and contains only a few key Changhsingian brachiopod taxa (e.g., *Neochonetes* (*Huangichonetes*) *substrophomenoides* Shen and Archbold, 2002 and *Notothyris crassa* Reed, 1944; see Fig. 5).

In the northern Guangdong Province, late Wuchiapingian brachiopods were reported from the Shuizhutang Formation at Liannan, Lianshan, and Yangshan areas (Hou et al., 1979; this study). Compared with faunas from the Douling Formation, this fauna presents a much higher diversity (70 species in 31 genera and 22 families, without undetermined species), which shows the rapid recovery/radiation stage of brachiopods in the late Wuchiapingian. This fauna also presents many more key Changhsingian taxa (e.g., *Oldhamina squamosa* Huang, 1932, *Paryphella sinuata* (Zhan in Hou et al., 1979), *Spinomarginifera alpha* Huang, 1932; see Fig. 5 for details).

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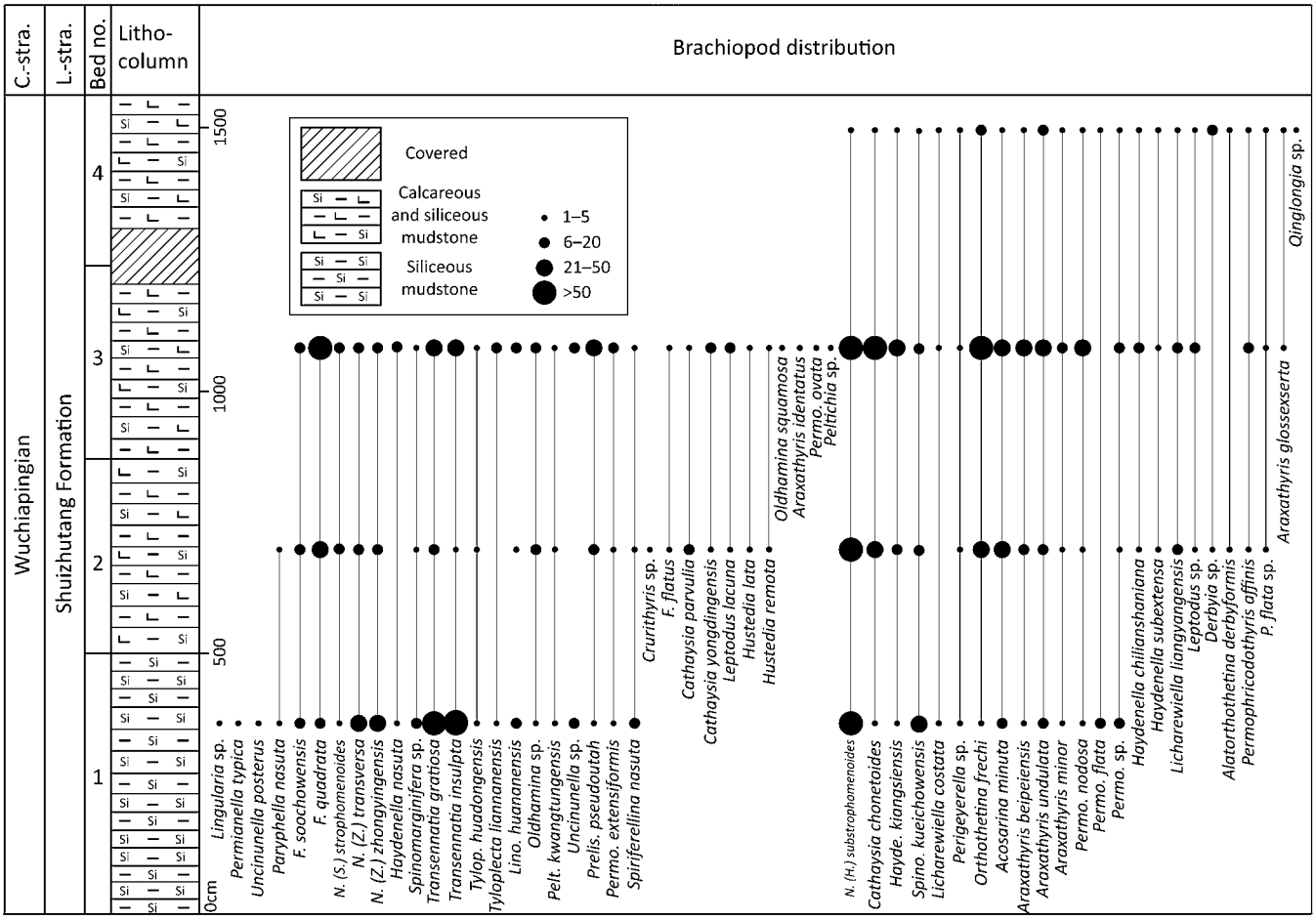

Figure 3. Distribution of brachiopods from the Shuizhutang Formation at the Liannan section.

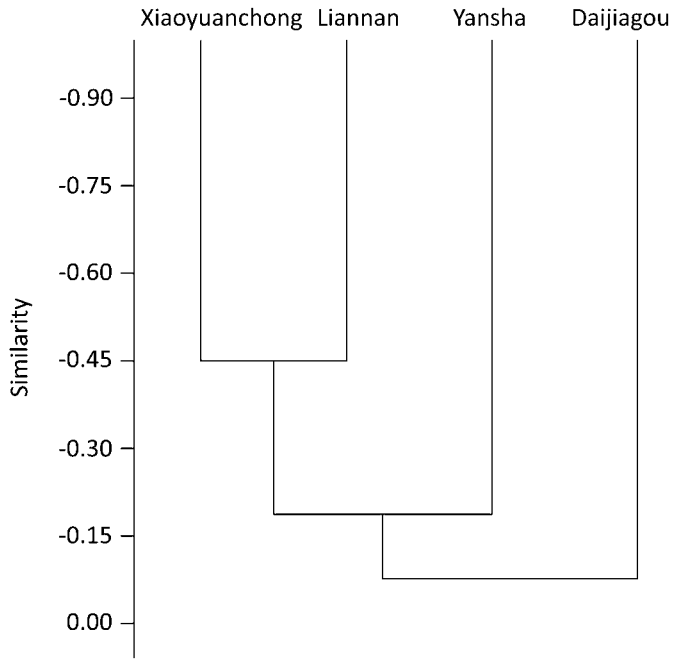

Figure 4. Q-mode cluster analysis of species abundance data using unweighted paired group algorithm and the Raup–Crick index.

It appears, therefore, that brachiopod faunas from the Douling Formation and Shuizhutang Formation, respectively, present the survival stage (early Wuchiapingian) and recovery/radiation stage (late Wuchiapingian) after the GLB major crisis. From comparison of these two faunas, it is clear that they share most brachiopod families, implying that the recovery/radiation occurred mainly in the genus-/species-level richness, which is consistent with the GLB brachiopod crisis pattern (Sun and Shen, 2004). The similar diversity of genera and species in the Douling fauna prove that, during the survival stage, the brachiopod initial recovery occurred mainly at the genus level. Finally, the highly diversified Shuizhutang fauna indicates that rapid radiation occurred at both genus and species levels, and the presence of more key Changhsingian taxa highlights the significant influence on the Changhsingian brachiopod fauna in South China.

Systematic paleontology

The classification above genus level adopted herein follows Kaesler (2000a, b, 2002, 2006) and Selden (2007). Herein, species that have been fully described in recent papers are only listed in Table 1 with illustrations (mainly Figs. 6—8 and a few specimens in the other figures), and their detailed descriptions are shown in the Supplementary text.

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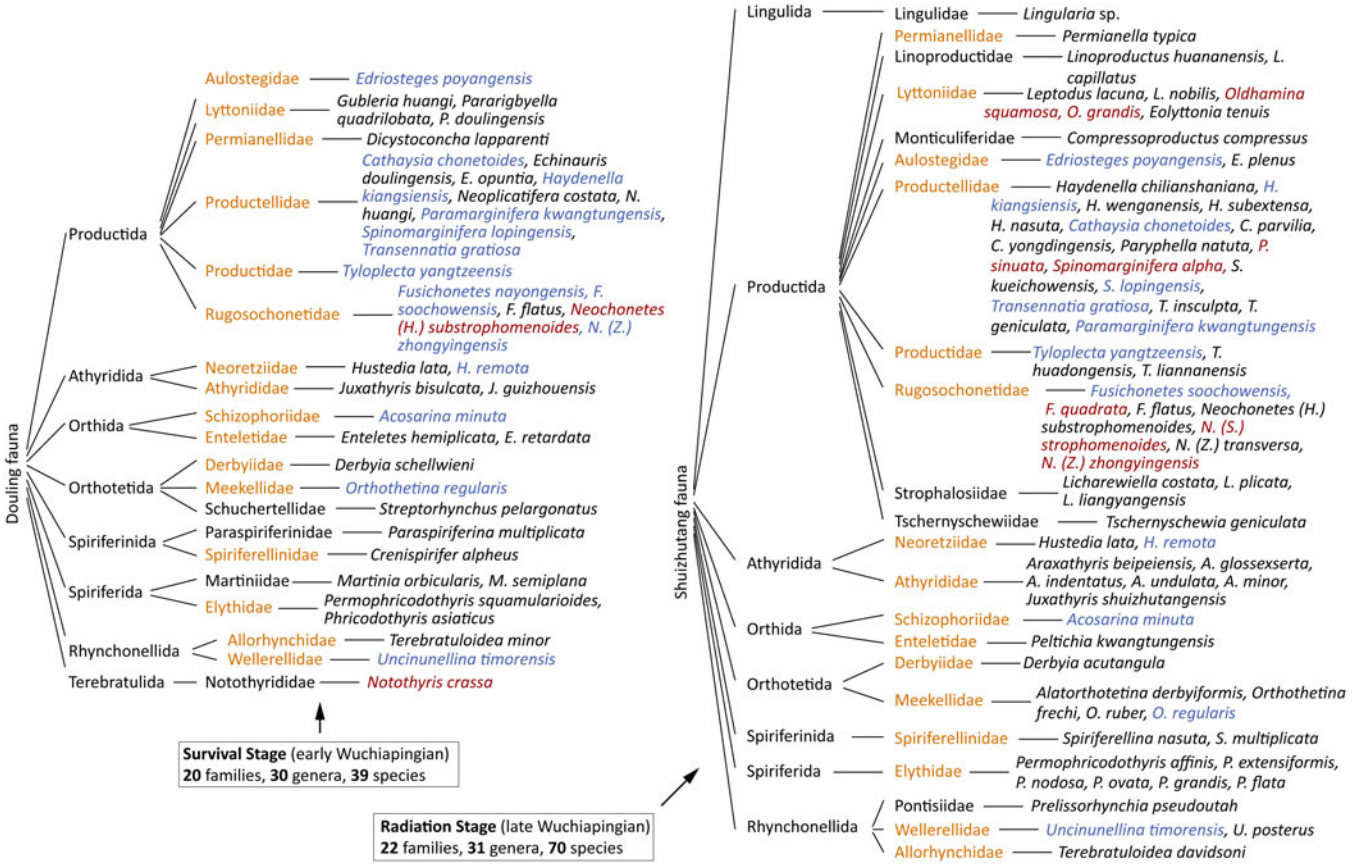

Figure 5. Faunal composition of the Douling fauna and the Shuizhutang fauna. Yellow words represent their shared families. Blue-gray words represent their shared species. Red words represent Changhsingian key taxa.

Order Productida Sarytcheva and Sokolskaja, 1959
Suborder Productidina Waagen, 1883
Superfamily Productoidea Gray, 1840
Family Productellidae Schuchert, 1929
Subfamily Productininae Muir-Wood and Cooper, 1960
Tribe Chonetellini Licharew in Sarytcheva et al., 1960
Genus *Haydenella* Reed, 1944

Type species.—*Productus kiangsiensis* Kayser, 1883 from upper Carboniferous of Loping, Jiangxi, China.

Remarks.—On the basis of the *Productus kiangsiensis* Kayser, 1883 collected from the *Productus* Limestones of the Salt Range as the type species, Reed (1944) proposed the genus *Haydenella*. However, there have been debates concerning the affiliation of type species before and after the nomenclature of *Haydenella*, and the classification position of this genus has remained confused for over 100 years. In this study, we follow the classification system of Brachiopoda in the *Treatise* (Brunton et al., 2000, p. 428).

Table 1. List of species with only illustrations in the text.

Species name	Illustration	Species name	Illustration
Lingularia sp.	Fig. 6.1	*Alatorthotetina derbyiformis*	Fig. 14.13, 14.14
Fusichonetes quadrata	Fig. 6.10–6.14	*Orthothetina frechi*	Fig. 14.18–14.23
Fusichonetes flatus	Fig. 6.15–6.17	*Perigeyerella* sp.	Fig. 14.9
Fusichonetes soochowensis	Fig. 6.2–6.9, 6.26, 6.27	*Peltichia kwangtungensis*	Fig. 14.24–14.29
Neochonetes (*H.*) *substrophomenoides*	Fig. 6.18–6.21	*Acosarina minuta*	Fig. 8.1–8.4
N. (*S.*) *strophomenoides*	Fig. 6.22–6.25	*Uncinunellina postera*	Fig. 8.19
N. (*Z.*) *transversa*	Fig. 7.1–7.6	*Uncinunellina* sp.	Fig. 8.20, 8.21
N. (*Z.*) *zhongyingensis*	Fig. 7.7–7.10	*Prelissorhynchia pseudoutah*	Fig. 8.12–8.18
Cathaysia chonetoides	Fig. 7.11–7.15	*Hustedia lata*	Fig. 8.5, 8.6
Cathaysia parvulia	Fig. 7.16–7.19	*Hustedia remota*	Fig. 8.7–8.11
Cathaysia yongdingensis	Fig. 7.20–7.22	*Crurithyris* sp.	Fig. 15.21
Paryphella nasuta	Fig. 7.23, 7.24	*Araxathyris indentatus*	Fig. 15.6–15.11
Spinomarginifera kueichowensis	Figs. 9.18–9.20, 10.1–10.3	*Araxathyris glossexserta*	Fig. 15.5
Spinomarginifera sp.	Fig. 10.4–10.8	*Araxathyris undulata*	Fig. 15.17–15.20
Leptodus lacuna	Figs. 13.25, 14.1–14.5	*Araxathyris beipeiensis*	Figs. 8.22–8.24, 15.1–15.4
Oldhamina squamosa	Fig. 14.6–14.8	*Spiriferellina nasuta*	Fig. 15.22–15.25
Derbyia sp.	Fig. 14.12	*Qinglongia* sp.	Fig. 15.26

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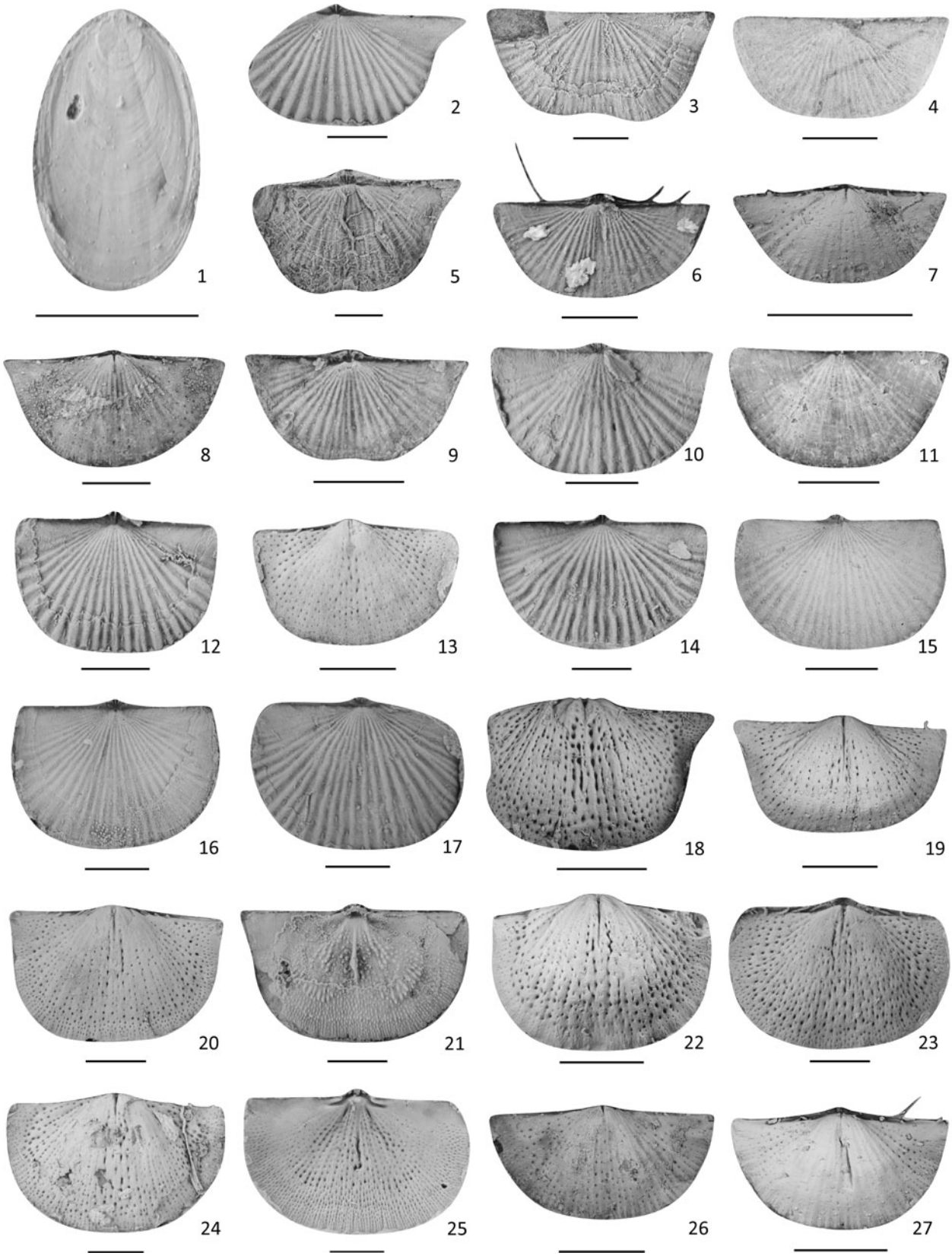

Figure 6. Brachiopods from the Shuizhutang Formation. (**1**) *Lingularia* sp., a ventral valve, LN191001. (**2–9, 26, 27**) *Fusichonetes soochowensis* (Chao, 1928): (**2–6, 9**) external molds of dorsal valves: (**2**) LN221803, (**3**) LN223301, (**4**) LN223402, (**5**) LN223601, (**6**) LN216601, (**9**) LN221701; (**7, 8, 26, 27**) internal molds of ventral valves: (**7**) LN001801, (**8**) LN221301, (**26**) LN001401, (**27**) LN001701. (**10–14**) *F. quadrata* (Zhan in Hou et al., 1979): (**10–12, 14**) external molds of dorsal valves: (**10**) LN188903, (**11**) LN222301, (**12**) LN222703, (**14**) LN223703; (**13**) an internal mold of a ventral valve, LN222802. (**15–17**) *F. flatus* (Shen and Archbold, 2002), external molds of dorsal valves: (**15**) LN002603, (**16**) LN221102, (**17**) LN222003. (**18–21**) *Neochonetes* (*Huangichonetes*) *substrophomenoides*: (**18–20**) internal molds of ventral valves: (**18**) LN001201, (**19**) LN002403, (**20**) LN216503; (**21**) dorsal interior, LN220503. (**22–25**) *N.* (*Sommeriella*) *strophomenoides* Waagen, 1884: (**22–24**) internal molds of ventral valves: (**22**) LN003403, (**23**) LN218003, (**24**) LN219901; (**25**) an internal mold of a dorsal valve, LN220303. Scale bars = 3 mm.

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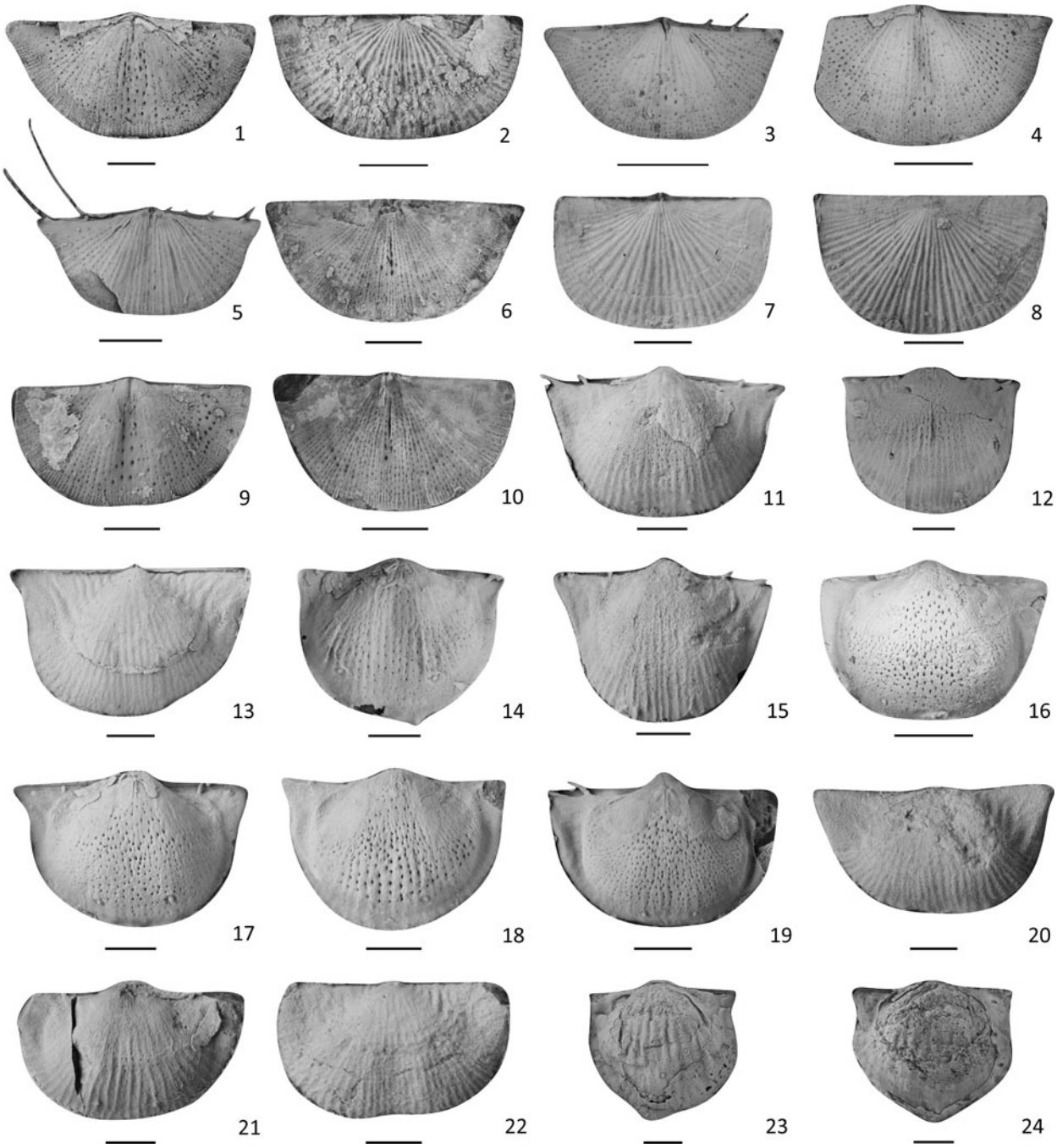

Figure 7. Brachiopods from the Shuizhutang Formation. (**1–6**) *N.* (*Zhongyingia*) *transversa* Zhang et al., 2015: (**1, 3–5**) internal molds of ventral valves: (**1**) LN217101, (**3**) LN000501, (**4**) LN002001, (**5**) LN217801; (**2**) an external mold of a dorsal valve, LN216301; (**6**) an internal mold of a dorsal valve, LN217401. (**7–10**) *N.* (*Z.*) *zhongyingensis* Liao, 1980: (**7, 8**) external molds of dorsal valves: (**7**) LN217703, (**8**) LN218301; (**9**) an internal mold of a ventral valve, LN218501; (**10**) an internal mold of a dorsal valve, LN218601. (**11–15**) *Cathaysia chonetoides*: (**11, 12, 14, 15**) internal molds of ventral valves: (**11**) LN200402, (**12**) LN183703, (**14**) LN197803, (**15**) LN198403; (**13**) an external mold of a dorsal valve, LN195502. (**16–19**) *C. parvulia* Chang in Yang, 1977, internal molds of ventral valves: (**16**) LN002503, (**17**) LN195102, (**18**) LN196703, (**19**) LN197102. (**20–22**) *C. yongdingensis* Liao in Wang et al., 1982: (**20, 22**) external molds of dorsal valves: (**20**) LN196103, (**22**) LN200503; (**21**) an internal mold of a ventral valve, LN196903. (**23, 24**) *Paryphella nasuta* Liao, 1984, internal molds of ventral valves: (**23**) LN209201, (**24**) LN209601. Scale bars = 3 mm.

By having a nearly globose ventral valve, *Argentiproductus* Cooper and Muir-Wood, 1951 is similar to this genus but differs in the presence of lamellae and absence of rugae on ears. *Ogbinia* Sarytcheva in Ruzhentsev and Sarytcheva, 1965 resembles *Haydenella* in the low ribs and short dorsal medium septum, but the former has an elongate outline and no rugae on the ears. *Avonia* Thomas, 1914 is similar to the present genus in the concavoconvex profile, weak ribs, and short dorsal medium septum, but the former possesses weak lamellae and bifid cardinal processes. In the ribs on shell surface and rugae on ears and weakly marked brachial ridges, *Linoproductus* Chao, 1927 is very similar to *Haydenella*, but the former has an elongate subcircular outline and maximum shell width at the hingeline.

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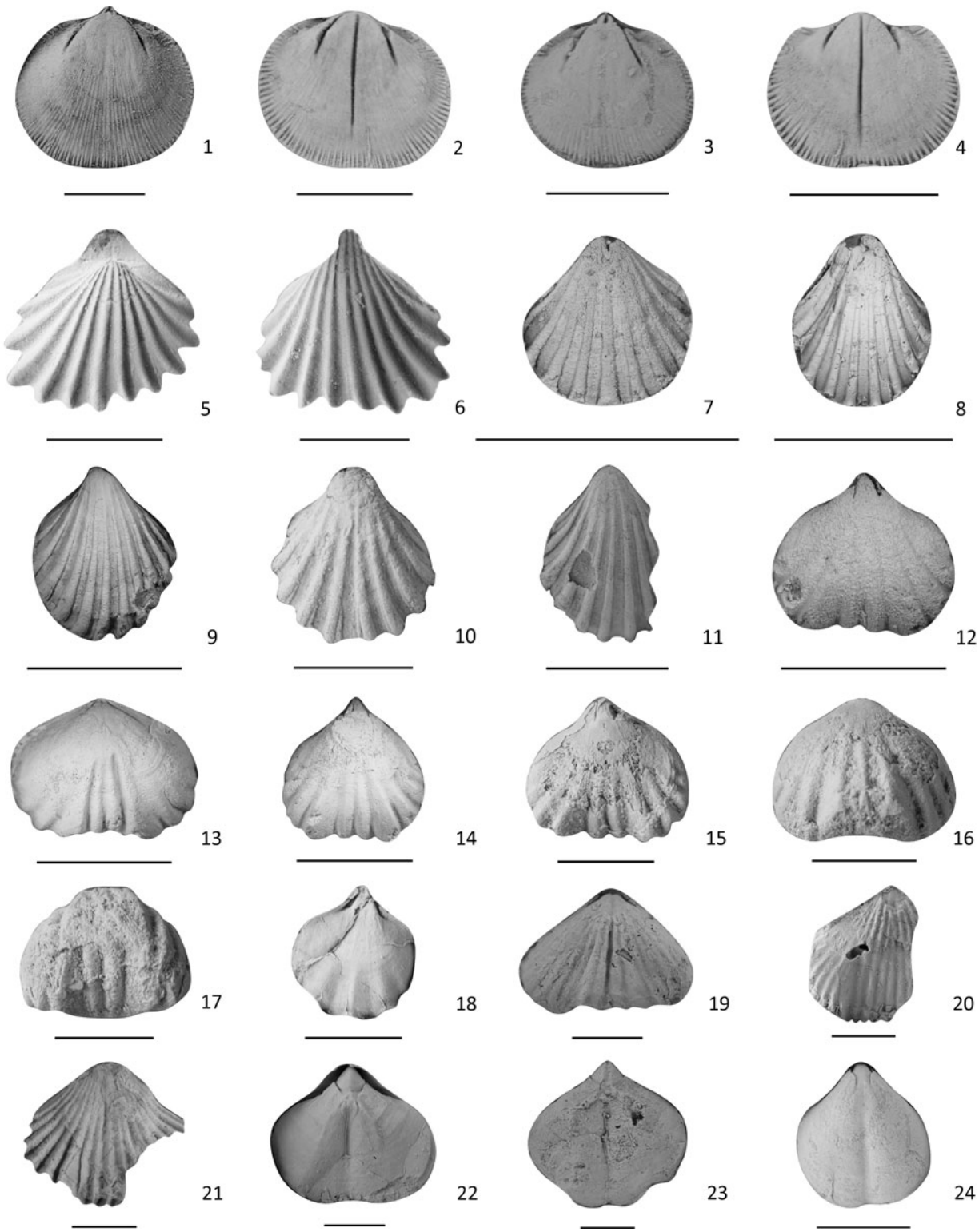

Figure 8. Brachiopods from the Shuizhutang Formation. (**1–4**) *Acosarina minuta*: (**1, 3**) internal molds of dorsal valves: (**1**) LN242203, (**3**) LN243302; (**2, 4**) internal molds of ventral valves: (**2**) LN243002, (**4**) LN243802. (**5, 6**) *Hustedia lata* Grabau, 1931: (**5**) an external mold of a dorsal valve, LN191502, (**6**) an external mold of a ventral valve, LN191702. (**7–11**) *H. remota* (Eichwald, 1860): (**7, 8**) internal molds of dorsal valves: (**7**) LN001902, (**8**) LN000803; (**9–11**) internal molds of ventral valves: (**9**) LN001003, (**10**) LN192503, (**11**) LN212203. (**12–18**) *Prelissorhynchia pseudoutah* (Huang, 1933): (**12, 14**) internal molds of ventral valves: (**12**) LN000602, (**14**) LN001903; (**13, 18**) internal molds of dorsal valves: (**13**) LN000702, (**18**) LN191101; (**15–17**) an inner core of a conjoined shell, LN192702: (**15**) ventral view, (**16**) dorsal view, (**17**) anterior view. (**19**) *Uncinunellina postera* (Waagen, 1883), an internal mold of a dorsal valve, LN177501. (**20, 21**) *Uncinunellina* sp., ventral valves: (**20**) LN186603, (**21**) LN188801. (**22–24**) *Araxathyris beipeiensis* Xu and Grant, 1994, internal molds of ventral valves: (**22**) LN169903, (**23**) LN176104, (**24**) LN187802. Scale bars = 5 mm.

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Haydenella chilianshaniana Jin and Ye, 1979
Figure 9.1

1979 *Haydenella chilianshaniana* Jin and Ye, p. 84, pl. 24, figs. 7–12.

Holotype.—42631, Bayinhe Group, Tianjun County, Qinghai, China (Jin and Ye, 1979, pl. 24, figs. 11, 12).

Occurrence.—Permian; China.

Description.—Medium size for genus, semicircular outline; cardinal extremities blunt, with a cardinal angle of about 100°; hingeline slightly shorter than the maximum width. Ventral valve moderately convex, with maximum convexity posteriorly; ears small, triangular, and well demarcated from visceral region; visceral disk rounded; sulcus absent. Ornamentation of costellae, absent at ears; several indistinct rugae on ears arranged perpendicularly to hinge.

Material.—A ventral valve (LN179103).

Remarks.—The lack of a sulcus in the ventral valve makes the present species different from many of its counterparts in the genus. *Haydenella bofengensis* Zhu, 1990 resembles the present species in the lack of sulcus, convexity of ventral valve, and semicircular outline but differs in having a long trail. *Haydenella minuta* Sarytcheva in Ruzhentsev and Sarytcheva, 1965 also has no sulcus but differs in possessing a more pointed and less inflated umbo.

Haydenella kiangsiensis (Kayser, 1883)
Figure 9.2–9.11

1883 *Productus kiangsiensis* Kayser, p. 185, pl. 26, figs. 6–11.
1927 *Avonia kiangsiensis*; Chao, p. 125, pl. 14, figs. 14–16.
1928 *Thomasia kiangsiensis*; Chao, p. 50, pl. 6, fig. 18.
1932 *Linoproductus kiangsiensis*; Huang, p. 46, pl. 3, figs. 13–19.
1944 *Productus* (*Haydenella*) *kiangsiensis*; Reed, p. 78, pl. 19, fig. 2.
1960 *Haydenella kiangsiensis*; Muir-Wood and Cooper, pl. 65, figs. 1–14.
1961 *Argentiproductus kiangsiensis*; Zhang and Jin, p. 411, pl. 3, figs. 13, 14.
1978 *Haydenella kiangsiensis*; Jin and Hu, pl. 2, fig. 25.
1979 *Haydenella kiangsiensis*; Zhan in Hou et al., p. 81, pl. 5, figs. 3, 4.
1995 *Haydenella kiangsiensis*; Zeng et al., pl. 5, fig. 8.
2005 *Haydenella kiangsiensis*; Campi and Shi, p. 111, figs. Z, bb, cc, ee.
2008 *Haydenella kiangsiensis*; He et al., p. 815, fig. 4.17–4.19.
2008 *Haydenella kiangsiensis*; Li and Shen, p. 311, fig. 4(7).
2009 *Haydenella kiangsiensis*; Shen and Clapham, p. 721, pl. 1, fig. 28, pl. 2, fig. 1.
2012 *Haydenella kiangsiensis*; Crippa and Angiolini, p. 138, fig. 11c–j.
2014 *Haydenella kiangsiensis*; Ghaderi et al., p. 35, pl. 1, figs. 1, 2.

Holotype.—Unknown. Kayser (1883) did not designate a holotype for this species.

Occurrence.—Permian to the earliest Triassic; Armenia, Azerbaijan, Cambodia, China, Greece, Iran, Japan, Malaysia, Pakistan, the Russian Federation, Tajikistan.

Description.—Medium size for genus, outline semicircular to suboval; cardinal extremities blunt; hingeline shorter than the maximum width; maximum width at middle to posterior part. Ventral valve moderately convex, with maximum convexity at posterior part, becoming flattened anteriorly; sulcus absent; costellae low and coarse, bifurcated from midvalve in some specimens and originating from anterior of beak; spines in row between ears and corpus and scattered on the valve; interior with fine and radially distributed papillae, mostly distinct only at posterior part. Dorsal valve moderately concave, with maximum concavity at middle to anterior part; fold absent; ears small, ornamented by regularly distributed and distinct rugae; costellae bifurcated at posterior part in some specimens; cardinal process quadrivalve.

Material.—Six external molds of dorsal valves (LN202903, LN204702, LN207103, LN207302, LN208103, LN208603) and three internal molds of ventral valves (LN184303, LN211103, LN172003).

Remarks.—*H. kiangsiensis* is like *H. bofengensis* in that both have semicircular outline and no sulcus, but the latter has a more convex ventral valve and long trail. The current species differs from *H. chilianshaniana* by its more rounded outline and more pointed ventral umbo. It resembles *Haydenella granti* Yanagida and Nakornsri, 1999 in rounded outline and pointed umbo, but the latter has relatively more transverse outline and more-developed concentric growth lines.

Haydenella nasuta Zeng, 1993
Figure 9.13–9.17

1993 *Haydenella nasuta* Zeng, p. 751, pl. 1, figs. 4, 5.

Holotype.—MPUM 10770, Ruteh Limestone, North Iran (Crippa and Angiolini, 2012, fig. 11l).

Occurrence.—Guadalupian to Lopingian; China, Iran.

Description.—Small to medium for genus; transversely to slightly elongated subrounded; hingeline slightly shorter than the maximum width; cardinal extremities right-angled to blunt. Ventral valve moderately convex with maximum convexity at umbonal region; flanks gently inclined; nasute protrusion short; sulcus not observed or very weakly developed; ears small, distinct from corpus with a row of spine between them. External surface ornamented by low costellae originating from slightly anterior to umbo; rugae very strong on ears, about 2–3 on each ear, disposed nearly at about right angle to hingeline; erect body spines sporadically scattered on surface. Internal surface with fine and radially distributed papillae.

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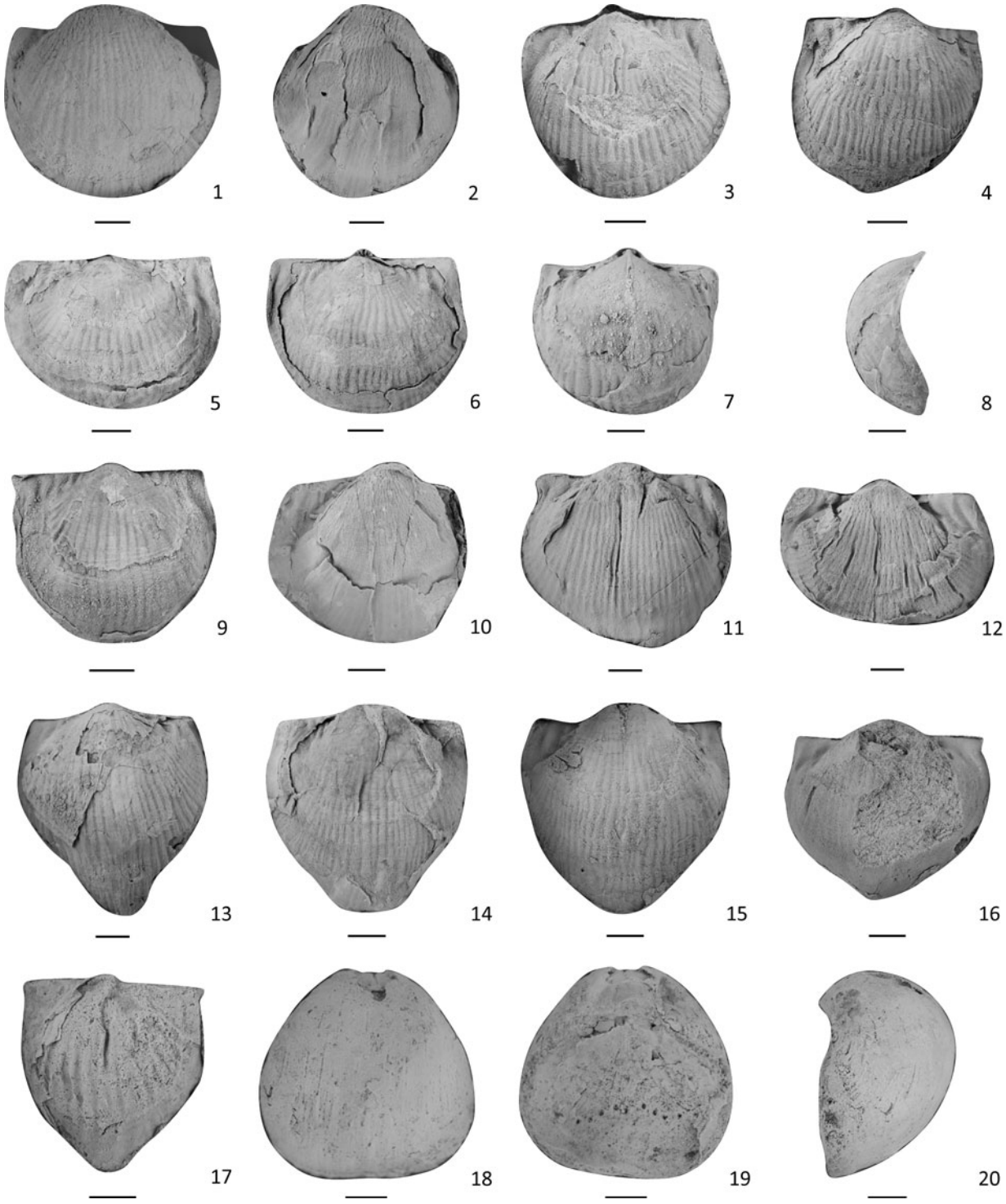

Figure 9. Brachiopods from the Shuizhutang Formation. (**1**) *Haydenella chilianshaniana*, a ventral valve, LN179103. (**2–11**) *H. kiangsiensis*: (**2, 10, 11**) internal molds of ventral valves: (**2**) LN184303, (**10**) LN211103, (**11**) LN172003; (**3–7, 9**) external molds of dorsal valves: (**3**) LN202903, (**4**) LN204702, (**5**) LN207103, (**6**) LN207302, (**7**) LN208103, (**9**) LN208603; (**8**) lateral view of (**7**). (**12**) *H. subextensa*, an internal mold of a ventral valve, LN201403. (**13–17**) *H. nasuta*: (**13–15, 17**) external molds of dorsal valves: (**13**) LN201303, (**14**) LN202003, (**15**) LN204303, (**17**) LN208801; (**16**) an internal mold of a ventral valve, LN207603. (**18–20**) *Spinomarginifera kueichowensis* Huang, 1932, an internal mold of a conjoined shell, LN268503. Scale bars = 3 mm.

Dorsal valve slightly to moderately concave, with maximum concavity at middle to anterior part; umbo normally not or slightly over hingeline; ears small; a long and wide nasute protrusion developed, beginning from anterior part of midvalve; fold not observed. External surface with coarse costellae originating from anterior part of umbo, bifurcated into several much finer costellae from midvalve in some specimens; 3–4 pairs of rugae developed on ears.

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Material.—Four external molds of dorsal valves (LN201303, LN202003, LN204303, LN208801) and an internal mold of a ventral valve (LN207603).

Remarks.—This species is most similar to *Haydenella eminens* Crippa and Angiolini, 2012 in both having a prominent nasute protrusion, but the latter has much finer costellae.

Haydenella subextensa Zhan in Hou et al., 1979
Figure 9.12

1979 *Haydenella subextensa* Zhan in Hou et al., p. 82, pl. 11, figs. 9–13.
1995 *Haydenella subextensa*; Zeng et al., pl. 6, fig. 5.
2021 *Haydenella*? sp.; Wu et al., p. 874, fig. 10S–V.

Holotype.—K0125, Wangpanli Formation, Guangdong Province, China (Hou et al., 1979, pl. 11, fig. 11).

Occurrence.—Lopingian; China.

Description.—Shell medium size for genus, transversely suboval in outline; hingeline shorter than shell maximum width. Ventral valve moderately convex, somewhat flattened transversely; umbo pointed and slightly over hingeline; ears small and ornamented with rugae. External surface ornamented with faint costellae; body spine sporadically scattered on visceral region. Internal surface with fine papillae radially distributed on visceral region.

Material.—An internal mold of a ventral valve (LN201403).

Remarks.—*Haydenella heilongjiangensis* Li and Gu, 1980 and *Haydenella libera* Li in Li et al., 1986 are similar to the present species with their shared transverse outlines, but the former two have acuter cardinal extremities and a hingeline equal to the maximum width.

Tribe Paucispiniferini Muir-Wood and Cooper, 1960
Genus *Transennatia* Waterhouse, 1975

Type species.—*Productus gratiosus* Waagen, 1884 from the Capitanian of Salt Range, Pakistan.

Remarks.—With the type species *Productus gratiosus* Waagen, 1884, Waterhouse (1975, p. 10) and Grant (1976, p. 131), respectively, proposed the genera *Transennatia* and *Gratiosina*. On the basis of the Law of Priority, *Transennatia*, which was characterized by its typical reticulation formed by strong costae and rugae on the visceral part, was formally accepted in the *Treatise* (Brunton et al., 2000, p. 447). In South China, Zhan (in Hou et al., 1979) established the genus *Asioproductus* (with the type species *Asioproductus bellus*), which is widely distributed in Lopingian strata and was considered a junior subjective synonym of *Transenatia* (Brunton et al., 2000, p. 447; for detailed discussions see Shi et al., 2003).

Transennatia gratiosa (Waagen, 1884)
Figure 10.9–10.20

1884 *Productus gratiosus* Waagen, p. 691, pl. 72, figs. 3–7.
1911 *Productus gratiosus*; Frech, p. 127, pl. 19, fig. 4a, b.
1927 *Productus gratiosus*; Chao, p, 44, pl. 4, figs. 6–10.
1932 *Productus (Dictyoclostus)* aff. *gratiosus*; Huang, p. 32, pl. 2, fig. 3.
1932 *Productus (Dictyoclostus)* cf. *P. gratiosus*; Huang, p. 33, pl. 2, fig. 4–5.
1934 *Productus gratiosus*; Grabau, p. 34, pl. 10, figs. 4–6.
1937 *Productus (Marginifera) gratiosus* var. *timorensis* Hamlet; Licharew, p. 118, pl. 4, figs. 11–19; pl. 9, fig. 37.
1961 *Dictyoclostus gratiosus*; Zhang and Jin, p. 411, pl. 4, figs. 12–18.
1964 *Dictyoclostus gratiosus*; Wang et al., p. 291, pl. 45, figs. 14–19.
1977 *Asioproductus gratiosus*; Zhan in Yang et al., p. 350, pl. 140, fig. 5.
1978 *Asioproductus gratiosus* Zhan in Yang et al.; Feng and Jiang, p. 254, pl. 90, figs. 1, 2.
1978 *Asioproductus gratiosus* Zhan in Yang et al.; Tong, p. 228, pl. 80, fig. 7.
1978 *Gratiosina gratiosa* (Waagen); Licharew and Kotlyar, pl. 20, fig. 1a, b.
1979 *Asioproductus gratiosus*; Zhan in Hou et al., p. 85, pl. 6, figs. 7–13; pl. 9, figs. 8–10.
1982 *Transenatia gratiosa* (Waagen); Wang et al., p. 214, pl. 92, figs. 6–8; pl. 103, figs. 4–9.
2003 *Transenatia gratiosa* (Waagen); Shi et al., p. 1059, fig. 3.15–3.19.

Holotype.—Cephalopod bed, Salt Range, Pakistan (Waagen, 1884, pl. 72, fig. 3).

Occurrence.—Carboniferous to Permian; cosmopolitan.

Description.—Shell medium to large for genus, outline subquadrate, maximum width at hingeline or midvalve. Ventral valve strongly convex, geniculate at posterior part; ears small; sulcus narrow and deep. External surface with strong costae, converging into ventral sulcus, sometimes inconsistent in breadth in some specimens; concentric rugae developed, resulting in reticulated at visceral disc; body spine sparsely scattered, absent from sulcus, with a pair of spines located on the anterolateral slope. Interior with dense endospines, variable in size; a weak and short median septum developed.

Dorsal valve slightly to moderately concave, maximum concavity at middle to anterior part; ears medium in size, well demarcated from visceral disc; fold distinct and narrow, originating from beak. Exterior with strong costae, originating from beak, bifurcating at the most anterior part, covering the whole shell but ears; concentric rugae strongly developed on the whole shell except for a narrow circle near the margins, resulting in the very distinctly and densely reticulate ornament. Interior with radically distributed endospines, becoming thicker around brachial ridges; a pair of elongate adductor marks distinctly developed; a thin and weak median septum originating from umbo, extending about one-third of shell length.

Material.—Three internal molds of ventral valves (LN182901, LN215901, LN234801), five external molds of dorsal valves

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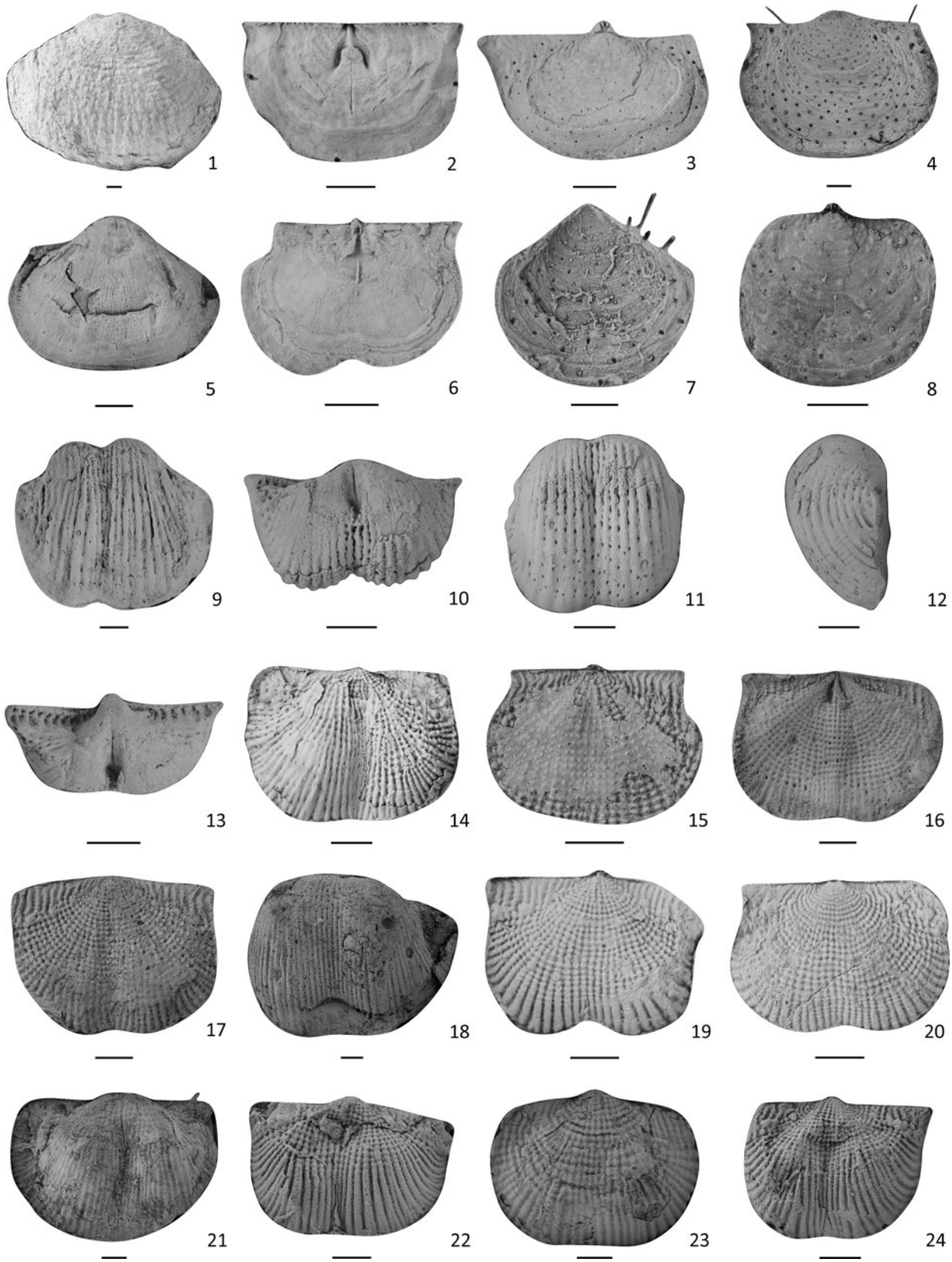

Figure 10. Brachiopods from the Shuizhutang Formation. (**1–3**) *Spinomarginifera kueichowensis*: (**1**) an internal mold of a ventral valve, LN186803; (**2**) an internal mold of a dorsal valve, LN213702; (**3**) an external mold of a dorsal valve, LN214800. (**4–8**) *S.* sp.: (**4, 7**) external molds of ventral valves: (**4**) LN213401, (**7**) LN214901; (**5**) an internal mold of a ventral valve, LN214401; (**6**) dorsal interior, LN214600; (**8**) an external mold of a dorsal valve, LN215001. (**9–20**) *Transennatia gratiosa*: (**9, 11, 18**) internal molds of ventral valves: (**9**) LN182901, (**11**) LN215901, (**18**) LN234801; (**10, 13**) posterior views of (**11**); (**12**) lateral view of (**11**); (**14, 15, 17, 19, 20**) external molds of dorsal valves: (**14**) LN227301, (**15**) LN233001, (**17**) LN233201, (**19**) LN234903, (**20**) LN235403; (**16**) an internal mold of a dorsal valve, LN233101. (**21–24**) *T. insculpta*: (**21**) ventral valve, LN205201; (**22–24**) external molds of dorsal valves: (**22**) LN224403, (**23**) LN224901, (**24**) LN225203. Scale bars = 3 mm.

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(LN227301, LN233001, LN233201, LN234903, LN235403), and an internal mold of a dorsal valve (LN233101).

Remarks.—The present species is like *Transennatia sulcata* Campi and Shi, 2007 with a ventral convexity and outline, but the latter has much coarser costae without converging into sulcus. It also resembles *Transennatia anshunensis* Liao, 1980 in the development of sulcus and shell outline, but the latter differs in having much coarser costae.

Transennatia insculpta (Grant, 1976)
Figures 10.21–10.24, 11, 12.1–12.12

1976 *Gratiosina insculpta* Grant, p. 135, pl. 32, figs. 1–37, pl. 33, figs. 1–16.

Holotype.—USNM 212386, Ko Muk, southern Thailand (Grant, 1976, pl. 32, figs. 25–28).

Occurrence.—Permian; China, Malaysia, Thailand.

Description.—Shell medium to large for genus, reverse trapezoid to subtriangular in outline, maximum width mostly at hingeline. Ventral valve strongly convex, with maximum convexity at middle to posterior part; ears large, moderately extended, ornamented with concentric rugae; sulcus moderately developed, originating from beak or midvalve. External surface covered with distinct costae, beginning from beak and bifurcating at middle to anterior part, becoming thinner and convergent in sulcus; concentric rugae evenly and densely distributed; visceral disc strongly geniculate by crossing of costae and rugae; several body spines scattered on valve. Interior with radially distributed endospines.

Dorsal valve slightly to moderately concave, with maximum concavity at anterior part where a distinct geniculation normally developed; beak narrow and pointed; ears large; fold moderately to distinctly developed. Exterior with costae, distinctly originating from beak, with bifurcation at middle to anterior valve; concentric rugae strong and densely distributed, resulting in prominently reticulate visceral region; 2–3 columns of microspines observed in the anterior part of costae between geniculation and margins (Fig. 11.17). Interior with fine endospines, becoming coarse around brachial ridges; a pair of elongate adductor marks distinctly developed; cardinal process trilobed or quadrivalve.

Material.—A ventral valve (LN205201), 23 external molds of dorsal valves (LN224403, LN224901, LN225203, LN227001, LN228601, LN230401, LN235003, LN238001, LN224603, LN170103, LN225801, LN227701, LN227903, LN229003, LN229603, LN229703, LN230201, LN232403, LN233901, LN234303, LN235302, LN238303, LN238803), a conjoined shell (LN226203), an internal mold of a dorsal valve (LN236301), and four internal molds of ventral valves (LN229203, LN232001, LN236503, LN225403).

Remarks.—Grant (1976, p. 136) compared the differences between *T. insculpta* and *T. gratiosa* and argued that the "Thailand species (*T. insculpta*) differs from the Pakistan species (*T. gratiosa*) in being only about half the size, having somewhat more extended ears, a proportionately shorter, narrower and less distinctly lobate cardinal process, weaker lateral adductor muscle marks, indistinct taleolae in the ventral valve, and a single row of about 5 lateral spines along each flank rather than a dense band that may be considered as many as 3 rows as in *T. gratiosa*." However, the Pakistan specimens are weathered and too obscure to identify the type of cardinal process and development of adductor muscle and taleolae in the interior. Both the Thailand and Pakistan specimens have spines on the flank area of ventral valve. Herein, we suggest that *T. gratiosa* can be distinguished from the current species by having less-extended ears, geniculate ventral valve, and sometimes more-distinct sulcus and fold. *Transennatia timorensis* Hamlet, 1928 is comparable to the present species in that both have a moderately convex ventral valve, but it differs in having much coarser costae and rugae.

Family Productidae Gray, 1840
Subfamily Leioproductinae Muir-Wood and Cooper, 1960
Tribe Tyloplectini Termier and Termier, 1970
Genus *Tyloplecta* Muir-Wood and Cooper, 1960

Type species.—*Productus scabriculus* mut. *nankingensis* Frech, 1911 from the early Permian of Anhui Province, China.

Remarks.—A global review of morphology and classification of the genus has been given in Shi and Chen (2003).

Tyloplecta huadongensis Liang, 1990
Figure 12.13–12.19

1990 *Tyloplecta huadongensis* Liang, p. 191, pl. 32, figs. 1–9, pl. 33, fig. 10.

Holotype.—ZB50088, Lengwu Formation, Lengwu, Zhejiang Province, China (Liang, 1990, pl. 32, figs. 1–4).

Occurrence.—Permian; Asia, Europe.

Description.—Shell large, suboval to elongate oval in outline, hingeline slightly shorter than the greatest width of the shell. Ventral valve strongly inflated, strongly geniculated at the posterior part, becoming moderately convex and regularly inclined after this geniculation; beak pointed and enrolled; ears small and inflated; sulcus moderately developed, beginning from anterior part of beak. External surface marked by thin and distinct costae, visible on margins of internal mold. Internal surface with a pair of radial adductor muscle scars at the anterior part of beak, a pair of large and pectinate diductor muscle scars at each side of adductor muscle scars; endospines observed on ears; fine and densely distributed pits on the surface anterior to muscle scars.

Dorsal valve moderately concave, marginal area of anterior and lateral parts of the shell geniculated, with maximum concavity at anterior part; ears small and inflated; beak slightly concave, not or slightly over hingeline; fold absent to slightly developed. External surface with low costae, developed mainly on visceral region; concentric rugae covering the whole shell, especially strong on ears.

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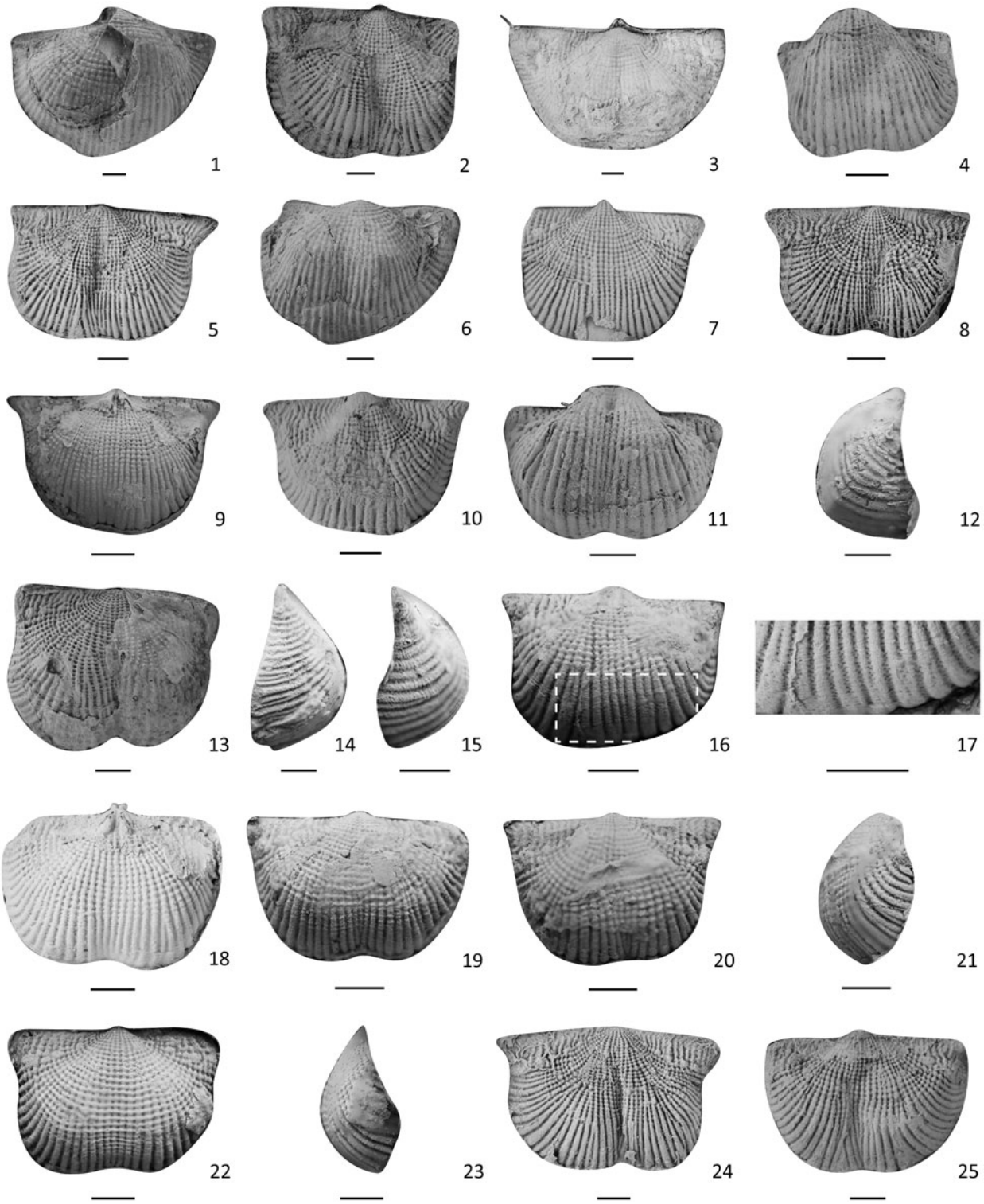

Figure 11. Brachiopods from the Shuizhutang Formation: *T. insculpta*. (**1**) a conjoined shell, LN226203; (**2, 3, 5, 7–10, 13, 16, 18–20, 22, 24, 25**) external molds of dorsal valves: (**2**) LN227001, (**3**) LN228601, (**5**) LN230401, (**7**) LN235003, (**8**) LN238001, (**9**) LN224603, (**10**) LN170103, (**13**) LN225801, (**16**) LN227701, (**18**) LN227903, (**19**) LN229003, (**20**) LN229603, (**22**) LN229703, (**24**) LN230201, (**25**) LN232403; (**17**) enlarged rectangular area in (**16**); (**4, 6, 11**) internal molds of ventral valves: (**4**) LN229203, (**6**) LN232001, (**11**) LN225403; (**12, 14, 15, 21, 23**) lateral views of (**11, 13, 16, 20, 22**), respectively. Scale bars = 3 mm.

Material.—Two external molds of dorsal valves (LN161303, LN163903), a dorsal interior (LN184902), and three internal molds of ventral valves (LN261403, LN261703, LN261903).

Remarks.—The present species differs from most species in the genus by its thin costae on the ventral valve and weak nodules caused by crossing costae and rugae. It is similar to *Tyloplecta bulangensis* Liao, 1980 in that both have thin costae, but the

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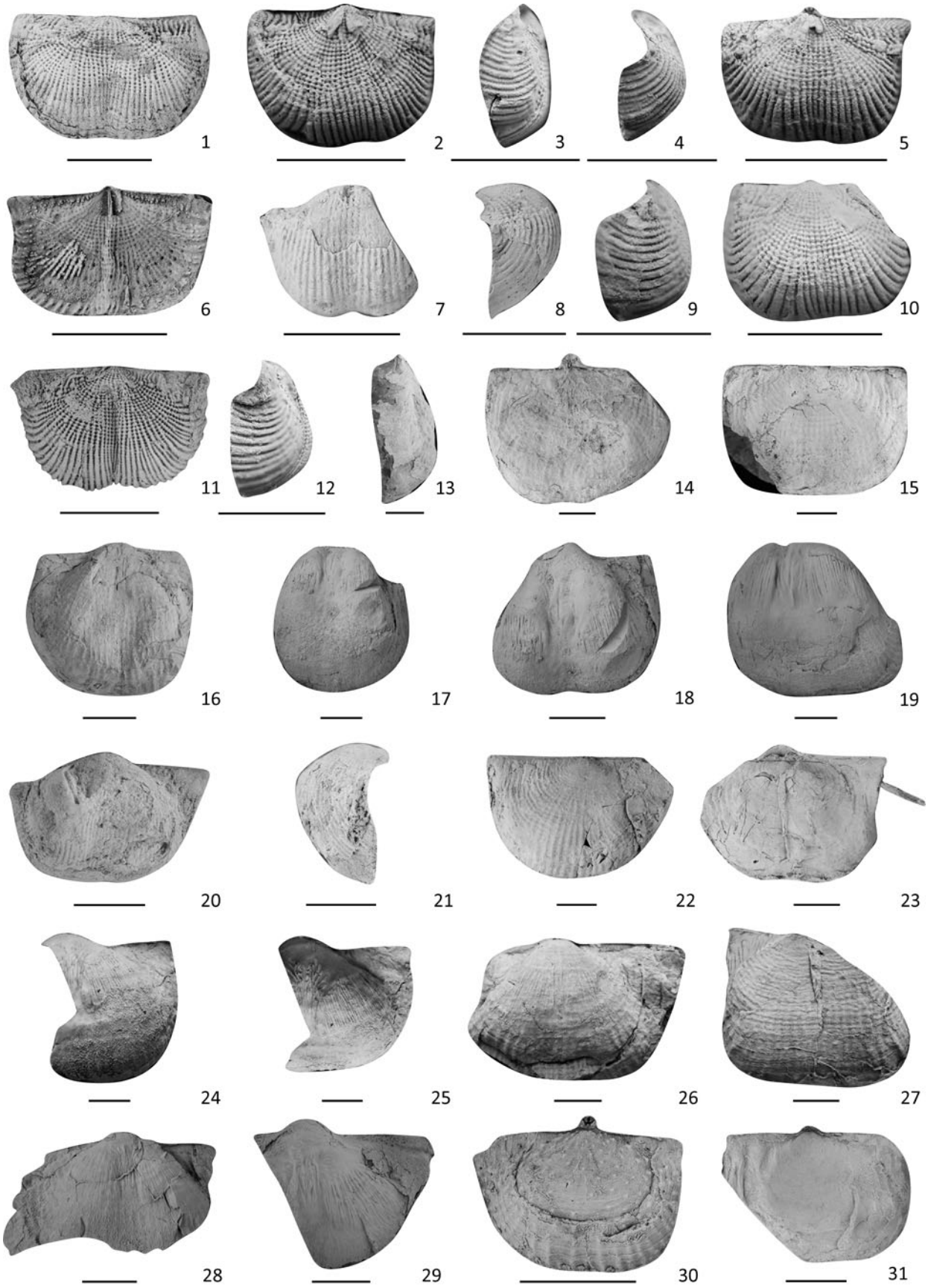

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Figure 12. Brachiopods from the Shuizhutang Formation. (**1–12**) *T. insculpta*: (**1, 2, 5, 10, 11**) external molds of dorsal valves: (**1**) LN233901, (**2**) LN234303, (**5**) LN235302, (**10**) LN238303, (**11**) LN238803; (**3, 4, 9, 12**) lateral views of (**2, 5, 10, 11**), respectively; (**6**) an internal mold of a dorsal valve, LN236301; (**7**) an internal mold of a ventral valve, LN236503; (**8**) lateral view of (**7**). (**13–19**) *Tyloplecta huadongensis*: (**14, 15**) external molds of dorsal valves: (**14**) LN161303, (**15**) LN163903; (**13**) lateral view of (**14**); (**16**) dorsal interior, LN184902; (**17, 19**) internal molds of ventral valves: (**17**) LN261403, (**19**) LN261903; (**18**) posterior view of (**16**). (**20–29**) *T. liannanensis* n. sp.: (**20**) ventral exterior, LN185601; (**21**) lateral view of (**20**); (**22, 27**) external molds of dorsal valves: (**22**) LN160803, (**27**) LN165903; (**23**) an internal mold of a dorsal valve, LN163703; (**24, 26, 28, 29**) internal molds of ventral valves: (**24**) LN164803, (**26**) LN165403, (**28**) LN173103, (**29**) LN175203; (**25**) posterior view of (**24**). (**30**) *Tyloplecta* sp., an external mold of a dorsal valve, LN214001. (**31**) *Linoproductus huananensis* n. sp., an external mold of a ventral valve, LN163303. Scale bars = 1 cm.

latter has a lower beak and large and flat ears. By having obscure nodes and thinner costae, the present species could be distinguished from *Tyloplecta yangtzeensis*.

Tyloplecta liannanensis new species
Figure 12.20–12.29

Type specimens.—Holotype, an external mold of a dorsal valve (LN160803); paratype, an internal mold of a ventral valve (LN175203).

Diagnosis.—Medium to large *Tyloplecta* with not enrolled ventral beak, moderately convex ventral valve, and thin costae.

Occurrence.—Wuchiapingian; China.

Description.—Shell medium to large, reverse trapezoid in outline, with hingeline marking the greatest width of the shell. Ventral valve moderately convex and regularly inflated; the longitudinal curve regular and gradual; in the transverse direction, the median portion almost flat and gently inclined toward both sides; beak narrow and pointed, not enrolled, slightly over hingeline, with an angle of umbonal region of about 100°; ears flat to slightly convex, large and marked off from the reminder of the valve by a distinct concavity; cardinal extremities slightly extended, with cardinal angles of about 60°–90°; sulcus absent or very weakly developed, represented mostly by a very shallow impression along the median portion of the shell. Costae thin, rarely bifurcating anteriorly, about 6–8 at anterior margin; rugae thin, present only on visceral disc, formed obscure nodes with costae. Interior with a pair of distinct radial adductor muscle scars in the middle at the anterior part of beak, a pair of wide and strong diductor muscle scars at each side; endospines randomly arranged on ears, umbonal region and anterior part, varied in size; strong pits developed on the anterior region of muscle scars.

Dorsal valve moderately concave, maximum concavity at anterior part; in the longitudinal direction, the anterior portion distinctly inclined dorsally; ears large, triangular, slightly concave; cardinal extremities slightly extended; fold weak, beginning from midvalve. Exterior covered with low costae, originating from anterior part of beak; secondary capillae developed on the whole shell except ears; concentric rugae existed from beak to margins, strong on shell from hingeline to lateral slope, very weak or nearly absent. Interior with very fine pits.

Etymology.—Named for the Liannan County where the Liannan section is located.

Other material.—A ventral exterior (LN185601), an external mold of a dorsal valve (LN165903), an internal mold of a dorsal valve (LN163703), and three internal molds of ventral valves (LN164803, LN165403, LN173103).

Remarks.—The species can be distinguished from most species in the genus as it lacks an enrolled ventral beak and has a less convex ventral valve and thinner costae. *Tyloplecta bulangensis* Liao, 1980 and *Tyloplecta fulingensis* Zhu, 1990 also have a low ventral beak that is not enrolled, but the former differs from the present species due to a subcircular outline and wider umbonal region, and the latter is differentiated from the present species by its more obtuse cardinal extremities.

Tyloplecta sp.
Figure 12.30

Occurrence.—Wuchiapingian; China.

Description.—Shell medium size, reverse trapezoid in outline, maximum width at hingeline. Dorsal valve moderately convex, maximum convexity at midvalve, regularly curved in longitudinal and transverse directions; ears moderate in size and inflated; cardinal extremities blunt, with cardinal angles of about 90°; sulcus absent. Exterior with randomly scattered body spines; costae sparsely distributed; concentric lirae developed mainly on ears and marginal areas; coarse nodes prominently developed mainly on the visceral region. Interior with quadrivalve cardinal process.

Material.—An external mold of a dorsal valve (LN214001).

Remarks.—The present species differs from all known species in the genus by its much smaller size, reverse trapezoid outline, and prominent nodes.

Superfamily Linoproductoidea Stehli, 1954
Family Linoproductidae Stehli, 1954
Genus *Linoproductus* Chao, 1927

Type species.—*Productus cora* d'Orbigny, 1842 from the Moscovian of Patapatani, Bolivia, and the Asselian of Yaurichambi, Bolivia.

Linoproductus huananensis new species
Figures 12.31, 13.1–13.8

Type specimens.—Holotype, an external mold of a dorsal valve (LN228302); paratype, a ventral exterior (LN213601).

Diagnosis.—Medium-sized *Linoproductus* with moderately convex ventral valve and slightly inflated ventral beak.

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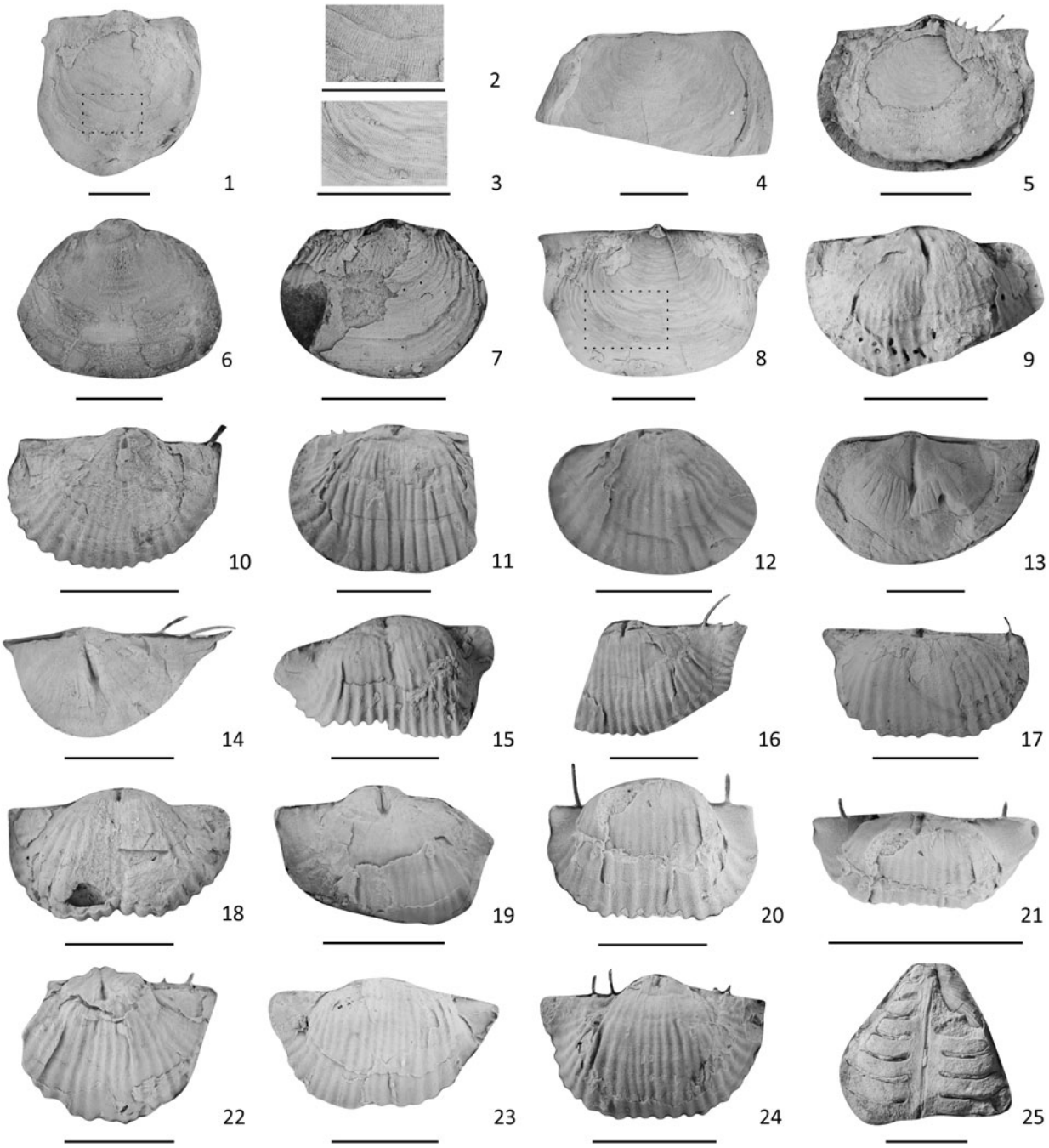

Figure 13. Brachiopods from the Shuizhutang Formation. (**1–8**) *Linoproductus huananensis* n. sp.: (**1**) an external mold of a dorsal valve, LN163103; (**2, 3**) enlargements of rectangles in (**1**) and (**8**), respectively; (**4, 8**) external molds of dorsal valves: (**4**) LN182103, (**8**) LN228302; (**5**) an external mold of a dorsal valve with part of internal mold of a ventral valve and part of ventral valve, LN212601; (**6**) an internal mold of a ventral valve, LN212901; (**7**) a ventral exterior, LN213601. (**9–12**) *Licharewiella costata*, internal molds of ventral valves: (**9**) LN194901, (**10**) LN202503, (**11**) LN206501, (**12**) LN210001. (**13–24**) *L. liangyangensis*, internal molds of ventral valves: (**13**) LN168200, (**14**) LN204000, (**15**) LN166603, (**16**) LN201603, (**17**) LN201803, (**18**) LN202203, (**19**) LN202703, (**20**) LN203102, (**21**) LN203302, (**22**) LN203703, (**23**) LN203902, (**24**) LN205702. (**25**) *Leptodus lacuna* Liang, 1990, an internal mold of a ventral valve, LN240403. Scale bars = 1 cm.

Occurrence.—Wuchiapingian; China.

Description.—Medium size for genus, outline rounded quadrate to transversely suboval, maximum width at midvalve. Ventral valve slightly to moderately convex, maximum convexity at umbo; ears small and slightly convex, not marked off from body of valve; umbo slightly overhanging hingeline; sulcus absent. External surface covered with very fine and closely set capillae; concentric rugae strongly and densely developed on ears, weak on visceral region; coarse body spines scattered on the whole valve. Interior with densely arranged endospines, coarse and water-drop-shaped in the middle part, fine and rounded in other areas.

Dorsal valve slightly to moderately concave, maximum concavity normally at midvalve; ears small and slightly concave; umbo pointed to moderately wide; fold absent. External surface

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with very fine capillae, with lots of bifurcations and intercalations; concentric rugae strong on ears and weaken toward midvalve.

Etymology.—Named for the South China area (Huanan) where the Liannan section is located.

Other material.—Three external molds of dorsal valves (LN163103, LN182103, LN228302), an external mold of a ventral valve (LN163303), an external mold of a dorsal valve with part of internal mold of a ventral valve and part of ventral valve (LN212601), and an internal mold of a ventral valve (LN212901).

Remarks.—This species can be easily differentiated from most counterparts in the genus by its moderately convex ventral valve and absence of an enrolled ventral beak. *Linoproductus capillatus* Zhan in Hou et al., 1979 and *Linoproductus fujianensis* Wang et al., 1982 also have rounded outlines and low convexity of ventral valve but differ from the present species by much more developed rugae, and *L. fujianensis* has coarser capillae. *Linoproductus pigrami* Archbold, 1981 is similar to the present species in the low convexity of ventral valve and development of capillae and rugae but differs by having larger and pointed ears and more flattened profile.

Suborder Strophalosiidina Schuchert, 1913
Superfamily Strophalosioidea Schuchert, 1913
Family Strophalosiidae Schuchert, 1913
Subfamily Strophalosiinae Schuchert, 1913
Genus *Licharewiella* Ustritsky in Ustritsky, Hu, and Chan, 1960

Type species.—*Strophalosia costata* Waagen, 1884 from the Wordian of Salt Range, Pakistan.

Remarks.—The internal structure of the genus has rarely been reported. The Liannan section yields some well-preserved ventral valves, providing interior information of the genus. The ventral interior of *Licharewiella* has a very strong and short median septum, a series of linear diductor muscle scars in the posterior part, and endospines variably developed.

Licharewiella costata (Waagen, 1884)
Figure 13.9–13.12

1882 *Strophalosia costata* Waagen, p. 655, pl. 63, figs. 7, 8, pl. 64, fig. 1.
1977 *Licharewiella costata*; Yang et al., p. 335, pl. 136, fig. 14.

Holotype.—Unknown. Waagen (1884) did not designate a holotype for this species.

Occurrence.—Permian; China, Pakistan.

Description.—Shell medium size, transversely oval in outline, maximum width at midvalve. Ventral valve moderately convex; ears small and slightly inflated; beak truncated or moderately pointed; sulcus slightly developed, originating from anterior part of beak. Interior with strong and short median septum, about one-eighth to one-fourth of shell length; linear diductor muscle scars developed on both sides of median septum; endospines coarse, restricted to anterior part of shell. Exterior with strong costae, beginning from anterior part of beak, becoming coarser and stronger forward.

Material.—Four internal molds of ventral valves (LN194901, LN202503, LN206501, LN210001).

Remarks.—The species is similar to *Licharewiella plicosa* Waagen, 1884 in the rounded outline, but the latter has thinner costae and more-pointed ventral beak.

Licharewiella liangyangensis Zhan in Hou et al., 1979
Figure 13.13–13.24

1979 *Licharewiella liangyangensis* Zhan in Hou et al., p. 75, pl. 6, fig. 18.
1982 *Truncatenia heshanensis* Liao, p. 540, pl. 1, figs. 10–15, 18–23.

Holotype.—K0083, Shuizhutang Formation, Lianxian, Guangdong, China (Hou et al., 1979, pl. 6, fig. 18).

Occurrence.—Wuchiapingian; China.

Description.—Shell medium size for genus, transversely reverse trapezoid to subquadrate in outline, maximum width at hingeline. Ventral valve moderately to strongly convex, maximum convexity at posterior part; ears variable in size, slightly inflated, smooth or partly covered with costae; umbonal region wide and obtuse, sometimes strongly truncated; sulcus absent. Interior with very strong and short median septum, about one-tenth to one-sixth of shell length; a series of linear diductor muscle scars developed in the front of median septum; fine endospines observed mainly in the visceral region. Exterior with strong and simple costae, beginning from the front of beak, occasionally intercalation and bifurcation in the anterior part; one to three pairs of spines distributed on each side of hinge.

Material.—Twelve internal molds of ventral valves (LN168200, LN204000, LN166603, LN201603, LN201803, LN202203, LN202703, LN203102, LN203302, LN203703, LN203902, LN205702).

Remarks.—The species can be easily differentiated from its counterparts by its outline and wide hingeline. *Truncatenia* Liao, 1982 was considered a synonym of *Licharewiella* by Kaesler (2000b). *Truncatenia heshanensis* Liao, 1982 is characterized by a reverse trapezoid outline and coarse costae on the valve and has no difference from the current species; thus, it should be a synonym of *L. liangyangensis*.

Suborder Lyttoniidina Williams, Harper, and Grant in Kaesler, 2000
Superfamily Permianelloidea He and Zhu, 1979
Family Permianellidae He and Zhu, 1979
Genus *Permianella* He and Zhu, 1979

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Type species.—*Permianella typica* He and Zhu, 1979 from the Lopingian of Jiangxi and Sichuan Province, China.

Remarks.—When He and Zhu (1979) first reported this genus, they stated that the shell featured pseudopunctae on the inner surface and had a smooth outer surface with sparse and weak concentric striae. Later, Wang and Jin (1991) provided a detailed discussion of permianellids, covering their shape, ornament, and shell structures. Although based on *Dicystoconcha* and lyttoniids specimens instead of *Permianella*, Wang and Jin (1991) concluded that the shell of the whole group developed tubercles on the outer surface and pseudopunctae on the inner surface. They stated that the tubercles are about 150 µm in diameter and unevenly distributed, and pseudopunctae are about 10 µm in diameter and also unevenly distributed. However, on the basis of the very well-preserved specimens from the Liannan section, it was found that the tubercles and pseudopunctae are very similar in size. Tubercles are evenly distributed and somewhat concentrically arranged in the middle to anterior part and number about 30–50 per mm^2. Pseudopunctae are also evenly distributed, absent at marginal brims, and number about 40–50 per mm^2.

Permianella typica He and Zhu, 1979
Figure 14.10, 14.11, 14.15–14.17

1979 *Permianella typica* He and Zhu, p. 132, pl. 1, fig. 1, pl. 2, 3.
1991 *Permianella typica*; Wang and Jin, p. 496, pl. 2, figs. 1–3.

Syntype.—Specimens 19791, 19796, 19799, Longtan Formation, Jiangxi and Sichuan Province, China (He and Zhu, 1979, pl. 1, fig. 1; pl. 2, fig. 3; pl. 3, fig. 3).

Occurrence.—Permian; China, Japan, Malaysia.

Description.—Shell of large size for genus, elongated bilobate in outline, greatest width at middle to anterior part; length 63.3 mm, width 25.3 mm, hingeline width 6.7 mm, length of incision 45.3 mm; posterolateral margins converging posteriorly at an umbonal angle about 70°, lateral margins nearly parallel. Ventral valve slightly convex in anterior profile and nearly flat in lateral profile; sulcus distinct, about one-fourth of shell length; external surface ornamented with fine and dense tubercles, sometimes concentrically arranged at the visceral region, randomly and more densely distributed at marginal brim; internal surface with randomly arranged pseudopunctae, absent near margins. Dorsal valve also flattened in lateral profile and slightly concave in anterior profile; fold beginning from the front of beak, widening and heightening anteriorly; exterior with very fine and densely distributed tubercles.

Material.—An external mold of a ventral valve (LN262201) and an external mold of a dorsal valve with a part of inner core (LN262101).

Remarks.—There are only two species and a few specimens of the genus reported. It differs from *Permianella grunti* Shen and Shi, 1997 by its larger umbonal angle, parallel lateral margins, and flattened shells. The specimen is slightly different from the material in Campi et al. (2000) by the latter having a smooth shell except fine radial fila on posterior half of valve.

Suborder Athyrididina Boucot, Johnson, and Staton, 1964
Superfamily Athyridoidea Davidson, 1881
Family Athyrididae Davidson, 1881
Genus *Araxathyris* Grunt in Ruzhentsev and Sarytcheva, 1965

Type species.—*Spirigera protea* Abich, 1878 from the Lopingian of Azerbaijan.

Araxathyris minor new species
Figure 15.12–15.16

Type specimens.—Holotype, an internal mold of a ventral valve (LN245303); paratype, an internal mold of a ventral valve (LN000101).

Diagnosis.—Small *Araxathyris* with large and strong spondylium.

Occurrence.—Wuchiapingian; China.

Description.—Shell small for genus, transversely suboval in outline, greatest width around shell midlength. Ventral valve moderately convex, posterior sides nearly straight and horizontal, lateral sides rounded, and anterior side slightly concave; sulcus slightly to moderately developed, beginning from midlength, deepening and widening anteriorly. Interior with very strong and large spondylium, highly overhanging hingeline, extending about half to two-thirds of shell length.

Etymology.—Named for its very small size.

Other materials.—Three internal molds of ventral valves (LN000104, LN245200, LN245903).

Remarks.—This species can be easily differentiated from other species by its very small size and very strong and large spondylium. Data for spondylium size and body-size of all specimens of the genus in the Liannan section were collected and are shown in Figure 16. It is clear that spondylium size in the present species is distinctly separated from, and larger than, other species and is a stable character because it steadily grows as body size increases.

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

Type species.—*Permophricodothyris ovata* Pavlova, 1965 from the Wuchiapingian of Azerbaijan.

Remarks.—There are 24 species in the genus. Most species are distinguished by shell size, convexity, development of the sulcus

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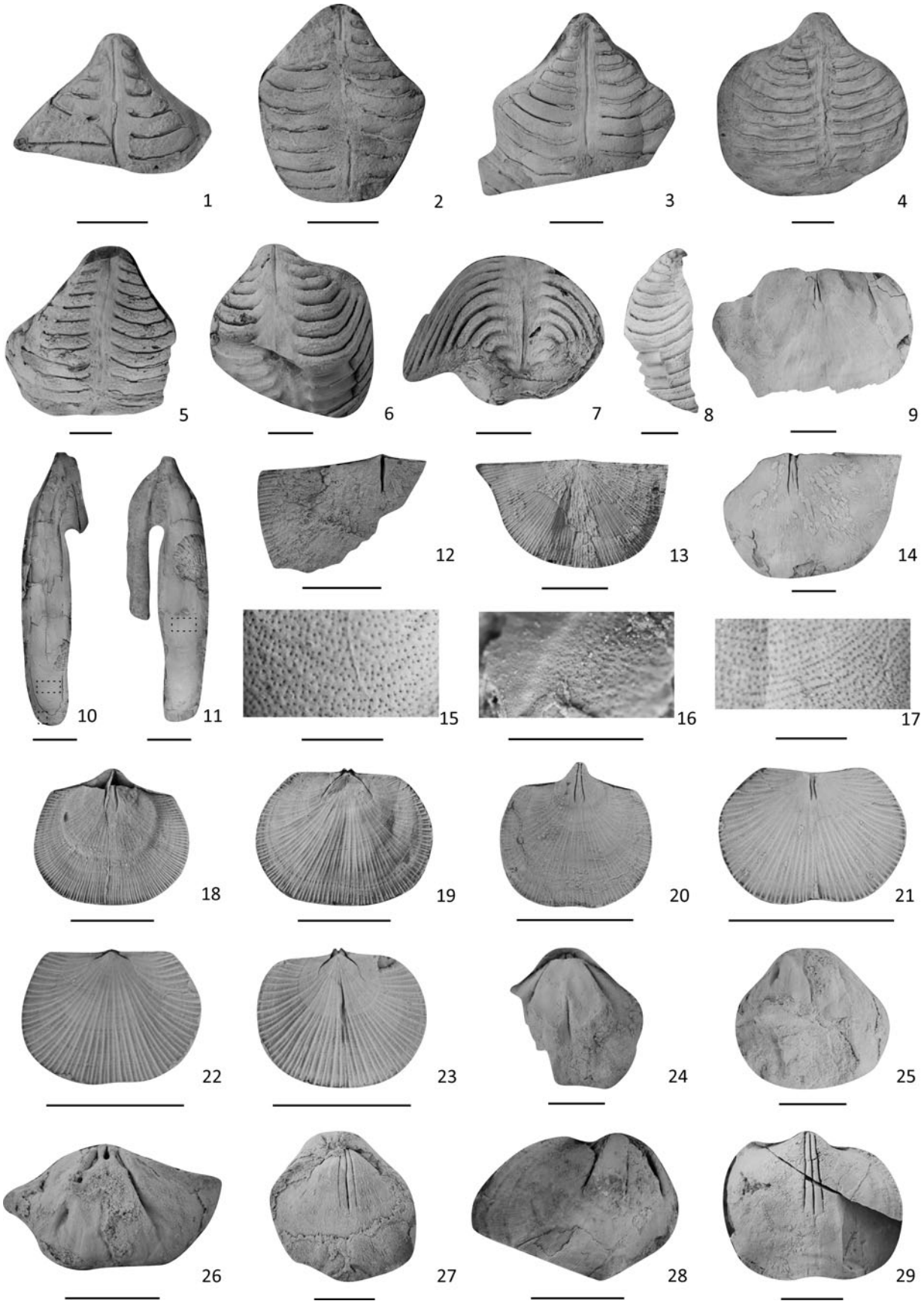

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Figure 14. Brachiopods from the Shuizhutang Formation. (**1–5**) *Leptodus lacuna*, internal molds of ventral valves: (**1**) LN262403, (**2**) LN262803, (**3**) LN262903, (**4**) LN263803, (**5**) LN268003. (**6–8**) *Oldhamina squamosa*, internal mold of a ventral valve, LN263203: (**6**) ventral view, (**7**) posterior view, (**8**) lateral view. (**9**) *Perigeyerella* sp., an internal mold of a ventral valve, LN190803. (**10, 11, 15–17**) *Permianella typica*: (**10**) an external mold of a dorsal valve with part of inner core, LN262101; (**15, 16**) respectively, enlargements of upper and lower rectangles in (**10**); (**11**) an external mold of a ventral valve, LN262201; (**17**) enlargement of rectangle in (**11**). (**12**) *Derbyia* sp., an internal mold of a ventral valve, LN177902. (**13, 14**) *Alatorthotetina derbyiformis* He and Zhu, 1985: (**13**) an internal mold of a dorsal valve, LN240102; (**14**) an internal mold of a ventral valve, LN166204. (**18–23**) *Orthothetina frechi* (Huang, 1933): (**18, 20, 21**) internal molds of ventral valves: (**18**) LN239403, (**20**) LN239203, (**21**) LN240902; (**19, 22, 23**) internal molds of dorsal valves: (**19**) LN239503, (**22**) LN241202, (**23**) LN182603. (**24–29**) *Peltichia kwangtungensis* (Zhan in Hou et al., 1979): (**24, 28**) internal molds of dorsal valves: (**24**) LN172502, (**28**) LN180101; (**25–27**) an inner core of a conjoined shell, LN172703: (**25**) dorsal view, (**26**) posterior view, (**27**) ventral view; (**29**) an internal mold of a ventral valve, LN240700. (**1–14, 18–29**) Scale bars = 1 cm; (**15–17**) scale bars = 2 mm.

and fold, and distribution patterns of concentric lamellae. The development, shape, and position of muscle scars, which have been clearly shown with sketch by Shi et al. (2002), were rarely referred to when comparing different species in the genus. Herein, the very well-preserved Liannan specimens distinctly show the different development of muscle scars.

Permophricodothyris affinis (Gemmellaro, 1899)
Figure 17.1–17.9

1899 *Reticularia affinis* Gemmellaro, p. 194, pl. 34, figs. 5–8; pl. 46, figs. 10, 11.

Holotype.—Unknown. Gemmellaro (1899) did not designate a holotype for this species.

Occurrence.—Guadalupian to Lopingian; China, Italy, Tunisia, Turkey.

Description.—Shell small to medium for genus, moderately biconvex; outline suboval, sometimes moderately transverse, greatest width normally at or posterior to midlength of ventral valve. Ventral valve moderately convex; beak thick, moderately incurved; sulcus distinct, beginning from the front of beak, deepening anteriorly; interior with heart-shaped muscle scars, including three linear adductor scars in the middle and a pair of flabellate diductor scars composed of 7–10 radial lobes on each side. Dorsal valve slightly and more evenly convex, beak blunt and short; interior with a thin and long myophragm, beginning from front of beak, extending to about three-fourths of shell length; socket elongate and wide, inner socket ridge and outer socket ridge thin. Exterior with irregularly arranged concentric lamellae, each with one or two rows of thorny spines.

Material.—An external mold of a dorsal valve (LN169403), seven internal molds of ventral valves (LN170303, LN186403, LN187103, LN250403, LN252403, LN252702, LN252903), and an internal mold of a dorsal valve (LN256303).

Remarks.—The present species can be easily separated from other species by the narrow and distinct ventral sulcus. *Permophricodothyris caroli* (Gemmellaro, 1899) also has a prominent ventral sulcus but differs by having a much higher and narrower ventral beak.

Permophricodothyris extensiformis (Chang in Yang et al., 1977)
Figure 17.10–17.21

1977 *Squamularia extensiformis* Chang in Yang et al., p. 452, pl. 180, fig. 6.

Holotype.—IV47210, Qixia Formation, Hunan Province, China (Chang in Yang et al., 1977, pl. 180, fig. 6).

Occurrence.—Permian; China.

Description.—Medium size for genus, suboval to roundly subquadrate in outline, biconvex with ventral valve equal to or more inflated than dorsal valve; commissure rectimarginate; surface with irregularly spaced growth lamellae. Ventral beak moderately hanging over hingeline, thick and incurved; interarea small; sulcus absent; interior with large and distinct heart-shaped muscle scars, with a strong and linear adductor scar in the middle and a pair of flabellate diductor scars on each side. Dorsal valve slightly to moderately convex, maximum convexity at umbo; fold absent; interior with a thin and weak myophragm, extending about half of shell length.

Material.—Four internal molds of ventral valves (LN161903, LN168403, LN254102, LN162503) and two inner cores of two conjoined shells (LN254102, LN260702).

Remarks.—The present species is characterized by rounded outline and lateral profile, lack of sulcus and fold, and blunt umbo. It is similar to *Permophricodothyris jiangshuiensis* (Chang in Yang et al., 1977) in the lack of sulcus, fold, and outline, but the latter has a more-pointed ventral beak and more-prominent concentric lamellae. *Permophricodothyris notialasiatica* Grant, 1976 also has no sulcus and fold developed but differs by having a much lower and pointed beak.

Permophricodothyris nodosa (Chao, 1929)
Figures 17.22–17.28, 18.1–18.12

1929 *Squamularia nodosa* Chao, p. 95, pl. 11, figs. 4–6.

Syntype.—Specimens 2028, 2029, 2030, Permian coal series, Jiangxi Province, China (Chao, 1929, pl. 11, figs. 4–6).

Occurrence.—Permian; China, Thailand, United States.

Description.—Shell medium size for genus, with suboval outline; surface with regularly spaced concentric lamellae, each with two rows of thorny spines. Ventral valve moderately convex, maximum convexity at umbonal region, the remaining part of the valve becoming less convex; beak blunt and slightly incurved; sulcus slightly to moderately developed; interior with distinct heart-shaped or rhombic muscle scars, with three strong and linear adductor scars in the middle and a pair of flabellate diductor scars on both

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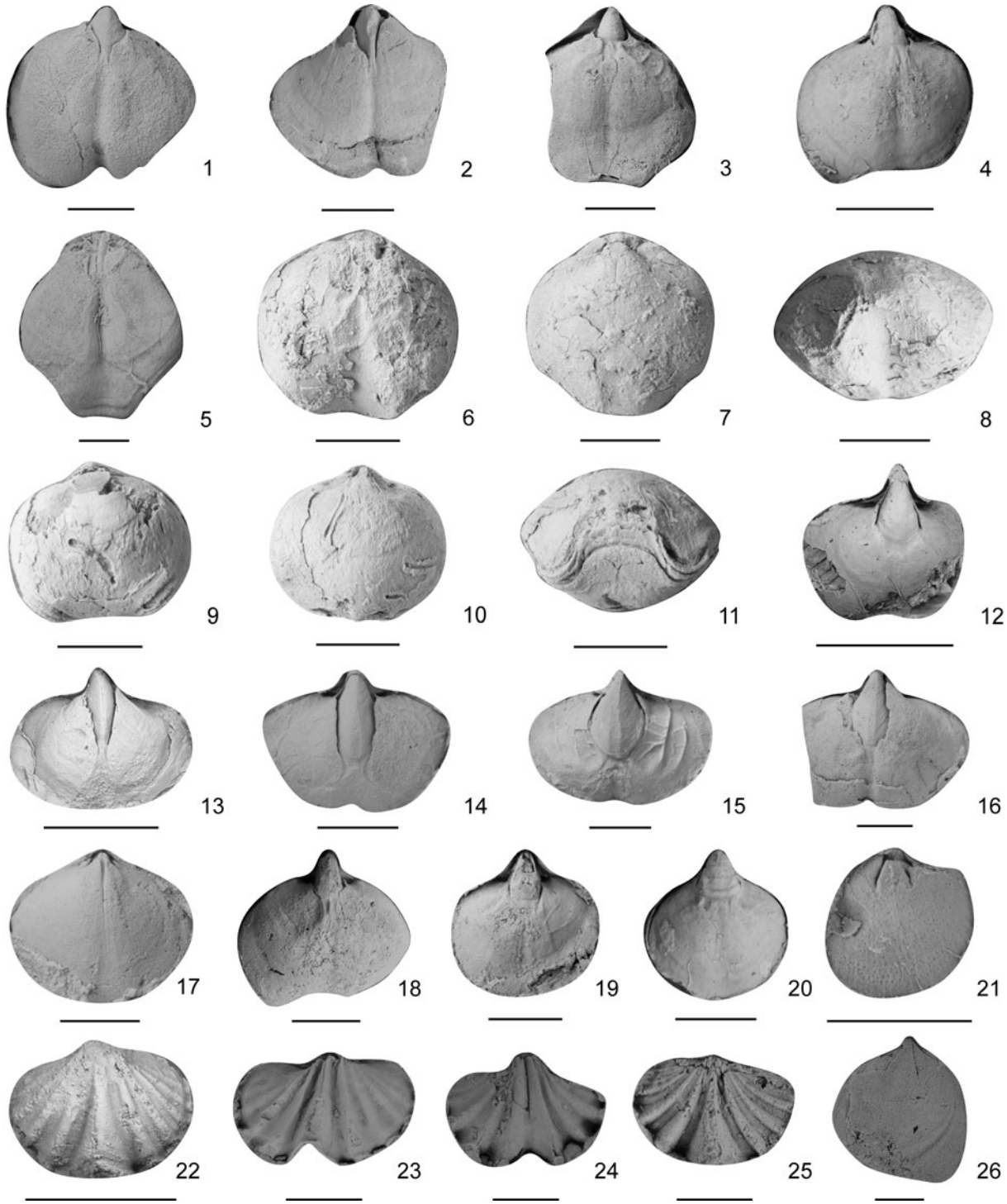

Figure 15. Brachiopods from the Shuizhutang Formation. (**1–4**) *Araxathyris beipeiensis*, internal molds of ventral valves: (**1**) LN244300, (**2**) LN246503, (**3**) LN248903, (**4**) LN249101. (**5**) *A. glossexserta* Zeng et al., 1995, an internal mold of a ventral valve, LN245003. (**6–11**) *A. indentatus* Zeng et al., 1995, two inner cores of two conjoined shells: (**6–8**) LN192903: (**6**) ventral view, (**7**) dorsal view, (**8**) anterior view; (**9–11**) LN193903: (**9**) ventral view, (**10**) dorsal view, (**11**) anterior view. (**12–16**) *A. minor* n. sp., internal molds of ventral valves: (**12**) LN000101, (**13**) LN000104, (**14**) LN245200, (**15**) LN245303, (**16**) LN245903. (**17–20**) *A. undulata* Shen et al., 1992: (**17**) an internal mold of a dorsal valve, LN246802; (**18–20**) internal molds of ventral valves: (**18**) LN247501, (**19**) LN247701, (**20**) LN248701. (**21**) *Crurithyris* sp., an internal mold of a dorsal valve, LN186902. (**22–25**) *Spiriferellina nasuta* Cooper and Grant, 1976: (**22, 23, 25**) internal molds of dorsal valves: (**22**) LN001303, (**23**) LN178301, (**25**) LN180401; (**24**) an internal mold of a ventral valve, LN178401. (**26**) *Qinglongia* sp., an internal mold of a dorsal valve, LN176404. Scale bars = 5 mm.

sides, sometimes with radiate pallial muscular markings covering the whole surface. Dorsal valve slightly convex; fold slightly developed; interior with a thin myophragm, originating from the front of beak and extending about half of shell length; socket elongate rounded, inner socket ridge and outer socket ridge thin.

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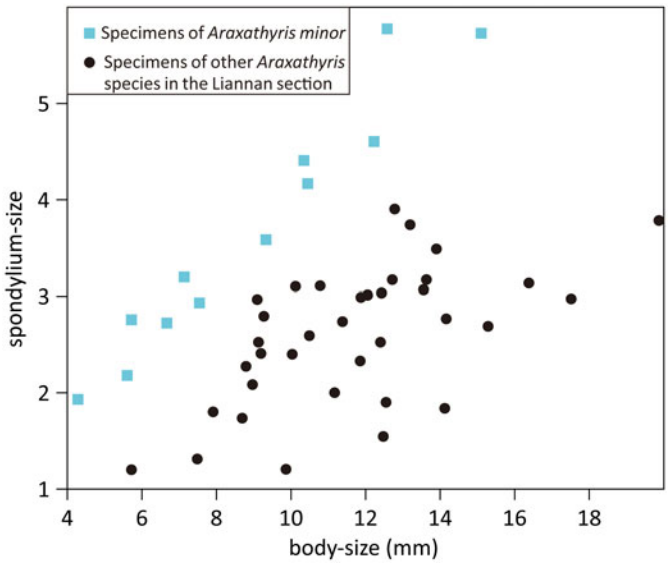

Figure 16. Graph of spondylium size to body size of all *Araxathyris* specimens from the Liannan section.

Material.—Fourteen internal molds of ventral valves (LN166403, LN171703, LN183103, LN183503, LN253303, LN249803, LN250003, LN250203, LN250702, LN250903, LN251403, LN251603, LN251803, LN259203), three internal molds of dorsal valves (LN179503, LN181603, LN185203), and two external molds of ventral valves (LN182503, LN255603).

Remarks.—The present species is most like *Permophricodothyris elegantula* (Waagen, 1883), with low convexity of both valves and a weak sulcus and fold, but the latter has very delicate and small beaks. *Permophricodothyris incerta* Zhan in Li et al., 1989 also has moderately convex shells but differs by hav9ng a much more elongate outline.

Permophricodothyris ovata Pavlova, 1965
Figure 18.13–18.15

1965 *Permophricodothyris ovata* Pavlova, p. 86, fig. 4.

Holotype.—Specimen 2071/181, Dorasham II, Azerbaijan (Pavlova, 1965, fig. 4A–D).

Occurrence.—Wordian to Changhsingian; Armenia, Azerbaijan, Iran, China.

Description.—Shell about medium size, elongated ovate in outline. Ventral valve strongly convex, very regularly curved in both directions; beak moderately wide and pointed; sulcus slightly developed; interior with weak muscle scars, with a linear adductor scar in the middle and flabellate diductor scars on both sides; external surface with regularly distributed concentric lamellae.

Material.—Three internal molds of ventral valves (LN170700, LN251003, LN255101).

Remarks.—The present species is characterized by the very regular elliptical outline of the shell, strongly convex valve, and weak sulcus. *Permophricodothyris globosa* (Feng in Feng and Jiang, 1978) is similar to *P. ovata* in outline and development of the sulcus, but *P. globosa* differs by having a much more inflated ventral valve. It is similar to *Permophricodothyris grandis* (Chao, 1929) in Shi et al. (2002) in outline and convexity, but the latter has much larger size and stronger muscle scars.

Permophricodothyris flata new species
Figure 18.20–18.31

Type specimens.—Holotype, an internal mold of a ventral valve (LN253103); paratype, an inner core of two conjoined shells (LN259302).

Diagnosis.—Medium to large *Permophricodothyris* with slightly convex to nearly flattened shells, a low and slightly inflated ventral beak, and a suboval to subcircular outline.

Occurrence.—Wuchiapingian; China.

Description.—Medium to large size for genus, outline suboval to subcircular, greatest width normally around midlength of ventral valve; commissure rectimarginate; concentric lamellae numbering about 4–5 per 5 mm at middle to posterior part, about 12–13 per 5 mm at anterior part, each with a row of thorny spines. Ventral valve flat to slightly and evenly convex; beak low and blunt, slightly or not curved; interarea small; delthyrium bounded by deltidial flange on each side, partly occupied by dorsal beak. Interior with distinct and strong muscle scars, heart shaped or diamond shaped, bisected by a short median ridge, sometimes located at almost the middle of valve (Fig. 18.24); three linear adductor muscle marks strong in the middle, flabellate diductor scars on each side.

Dorsal valve slightly convex; beak short and more pointed; ears slightly concave. Interior with deep and elongate sockets, thin and long socket ridges; myophragm weak and long, beginning from umbonal region and extending to anterior part; muscle marks weakly impressed.

Etymology.—Named for its nearly flat profile.

Other material.—Five internal molds of ventral valves (LN183904, LN251104, LN252503, LN253703, LN175804) and an inner core of two conjoined shells (LN259802).

Remarks.—It can be easily distinguished from most of its counterparts by shell convexity. Compared with most species in the genus, *P. incerta* and *P. nodosa* have much less convex shells but still have more inflated shells than the present species. Moreover, *P. incerta* differs by having a more elongated outline, and *P. nodosa* differs by having a higher and more pointed ventral beak.

Permophricodothyris sp.
Figure 18.16–18.19

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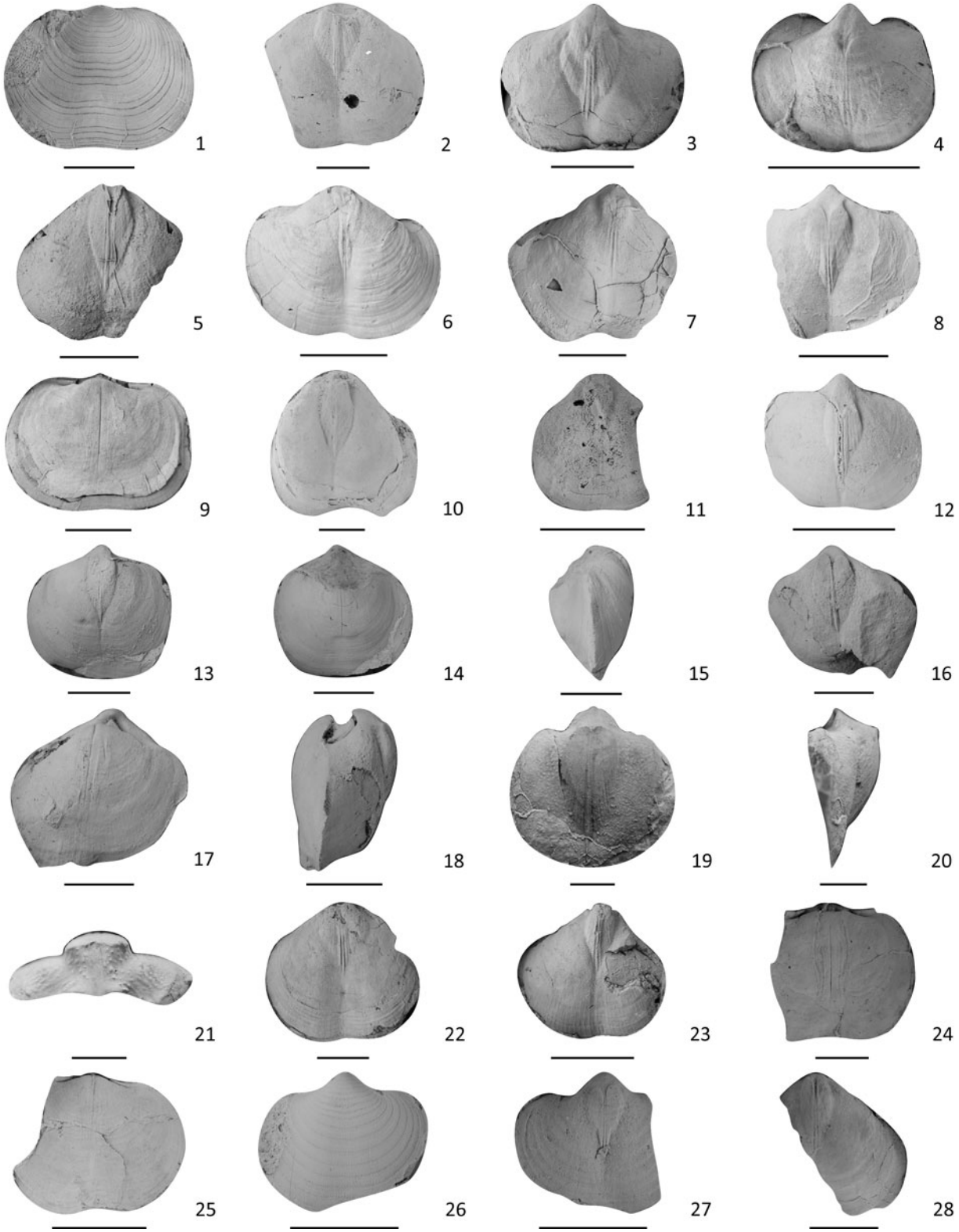

Figure 17. Brachiopods from the Shuizhutang Formation. (**1–9**) *Permophricodothyris affinis*: (**1**) an external mold of a dorsal valve, LN169403; (**2–8**) internal molds of ventral valves: (**2**) LN170303, (**3**) LN186403, (**4**) LN187103, (**5**) LN250403, (**6**) LN252403, (**7**) LN252702, (**8**) LN252903; (**9**) an internal mold of a dorsal valve, LN256303. (**10–21**) *P. extensiformis*: (**10–12, 19**) internal molds of ventral valves: (**10**) LN161903, (**11**) LN168403, (**12**) LN254102, (**19**) LN162503; (**20, 21**) lateral and posterior views of (**19**), respectively; (**13–18**) two inner cores of two conjoined shells: (**13–15**) LN254102: (**13**) ventral view, (**14**) dorsal view, (**15**) anterior view; (**16–18**) LN260702: (**16**) ventral view, (**17**) dorsal view, (**18**) anterior view. (**22–28**) *P. nodosa*: (**22, 23, 27, 28**) internal molds of ventral valves: (**22**) LN166403, (**23**) LN171703, (**27**) LN183103, (**28**) LN183503; (**24, 25**) internal molds of dorsal valves: (**24**) LN179503, (**25**) LN181603; (**26**) an external mold of a ventral valve, LN182503. Scale bars = 1 cm.

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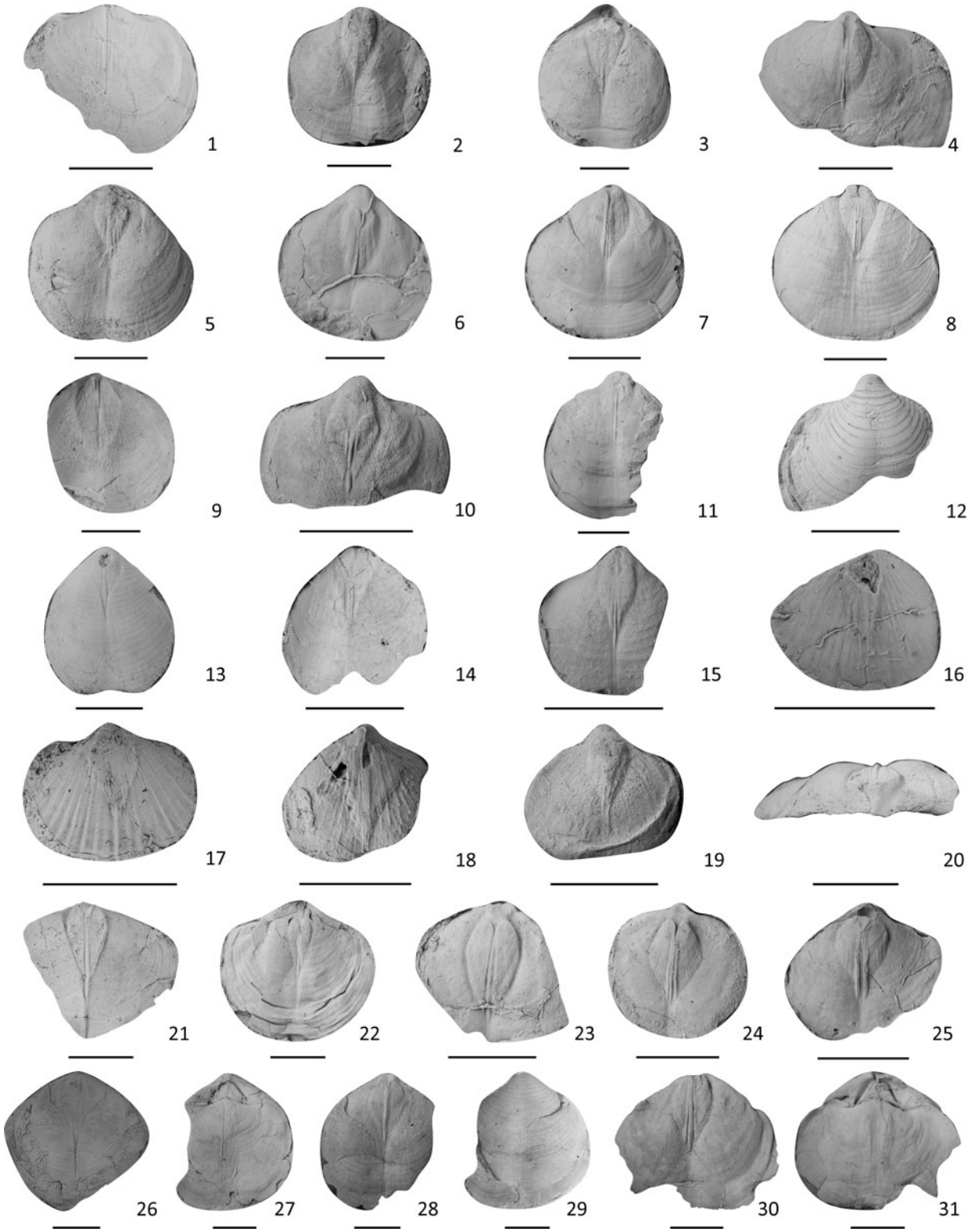

Figure 18. Brachiopods from the Shuizhutang Formation. (**1–12**) *Permophricodothyris nodosa*: (**1**) an internal mold of a dorsal valve, LN185203; (**2–11**) internal molds of ventral valves: (**2**) LN253303, (**3**) LN249803, (**4**) LN250003, (**5**) LN250203, (**6**) LN250702, (**7**) LN250903, (**8**) LN251403, (**9**) LN251603, (**10**) LN251803, (**11**) LN259203; (**12**) an external mold of a ventral valve, LN255603. (**13–15**) *P. ovata*: internal molds of ventral valves: (**13**) LN170700, (**14**) LN251003, (**15**) LN255101. (**16–19**) *Permophricodothyris* sp., internal molds of ventral valves: (**16**) LN176901, (**17**) LN183301, (**18**) LN188704, (**19**) LN253901. (**20–31**) *P. flata* n. sp.: (**21–26**) internal molds of ventral valves: (**21**) LN183904, (**22**) LN251104, (**23**) LN252503, (**24**) LN253103, (**25**) LN253703, (**26**) LN175804; (**20**) posterior view of (**21**); (**27, 28, 30, 31**) two inner cores of two conjoined shells: (**27, 28**) LN259302: (**27**) ventral view, (**28**) dorsal view; (**30, 31**) LN259802: (**30**) ventral view, (**31**) dorsal view; (**29**) the external mold of the ventral valve of (**28**). Scale bars = 1 cm.

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Occurrence.—Wuchiapingian; China.

Description.—Shell small for genus, with suboval outline. Ventral valve moderately convex; beak moderately high and pointed, with an apical angle of 90°–110°; sulcus absent; interior with strong and relatively large muscle scars, linear adductor scars strong in the middle, and diductor scars flabellate on each side; coarse and strong pustules radially arranged around muscle platform margins. In some specimens, strong linear impressions of external laminae evenly and radially distributed and covering the whole shell surface (Fig. 18.17).

Material.—Four internal molds of ventral valves (LN176901, LN183301, LN188704, LN253901).

Remarks.—The present species is very different from all known species in the genus. Although with small size, it has strong and relatively large muscle scars ($0.51 <$ muscle scar length/shell length < 0.69) and very strong pustules around the muscle scars covering most parts of the inner surface.

Conclusions

A late Wuchiapingian brachiopod fauna, which contains 57 species of 28 genera and is much more diversified than all reported contemporaneous brachiopod faunas from South China, is described. Four new species, *Tyloplecta liannanensis*, *Linoproductus huananensis*, *Araxathyris minor*, and *Permophricodothyris flata* are proposed. Comparison of the Douling fauna and the Shuizhutang fauna reveals that the brachiopod fauna shows a recovery mainly on the generic level during the survival stage and a rapid radiation on both generic and specific levels during the late Wuchiapingian.

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Declaration of competing interests

The authors declare none.

Data availability statement

Data available from the Dryad Digital Repository: http://doi.org/10.5061/dryad.gxd2547q2

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