Brachiopods from the Middle Ordovician Shihtzupu Formation of Yunnan Province, China

RENBIN ZHAN and JISUO JIN

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The brachiopod fauna of the Middle Ordovician (upper Darriwilian) Shihtzupu Formation in the Weixin area, northeastern Yunnan Province, southwestern China, comprises 16 genera and 18 species, including one new genus (*Halirhachis*) and five new species (*Glyptorthis sarcina*, *Protoskenidioides weixinensis*, *Halirhachis leonina*, *Leptellina spatiosa*, and *Leptestiina veturna*). Cluster and principal component analyses of the latest Arenigian–mid-Caradocian faunas of the Upper Yangtze Platform with selected faunas of similar age from other palaeoplates or terranes indicate that the Weixin brachiopods have closest faunal affinities to those of the typical Shihtzupu Formation in Guizhou Province and the Naungkangyi Group of Burma (Myanmar). During latest Arenigian–mid-Caradocian times, the brachiopods of the Upper Yangtze Platform, Sibumasu, and Chu-Ili palaeogeographical regions constituted a distinct faunal province, characterized by a large number of endemic taxa as well as regionally widespread genera such as *Saucrorthis*, *Martellia*, and *Yangtzeella*. This brachiopod faunal province has very low similarity coefficients with the coeval brachiopod faunas of Laurentia and Avalonia.

Key words: Brachiopoda, taxonomy, palaeobiogeography, Ordovician, Darriwilian, southwestern China.

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Introduction

The Ordovician strata in Yunnan Province, southwestern China, are exposed in patchy outcrops in a vast area covered by thick vegetation or Mesozoic terrigenous deposits (Geological Bureau of Yunnan Province 1992). The outcrops are mainly in the northeastern and southeastern parts (South China palaeoplate) and in the western part of the province (Sibumasu palaeoplate; see Chen et al. 1995). The present study area, located in Weixin County, on the Yunnan-Guizhou Plateau of northeastern Yunnan Province, belongs to the South China Palaeoplate (Fig. 1A, B). Here, the Ordovician succession is largely continuous, conformably underlain by the Cambrian Loushankuan Group, and overlain by the Lower Silurian Lungmachi Formation at the Shizigou Valley (105°01′20″ E, 27°51′04″ N), just west of the Weixin County town (Fig. 1C). The Middle Ordovician (upper Darriwilian) Shihtzupu Formation, which is the focus of this study, contains a suite of relatively rich and diverse brachiopods. Apart from a few early reconnaissance works (e.g., Wan et al. 1979), the fossils of the Shihtzupu Formation in the Weixin area had not been systematically collected or studied until the present work. Xu et al. (1974) described some brachiopods of the Shihtzupu Formation, based on sporadic collections from the type area in Guizhou Province.

From a global perspective, brachiopods experienced a major faunal turnover at the Arenigian–Darriwilian boundary (Harper et al. 2004). In generic composition, pentamerides of Darriwilian–Caradocian age are drastically different from those of pre-Darriwilian times; rhynchonellides made their first appearance in Mid Ordovician time and rapidly became a major component of the shelly benthos during Caradocian and later Ordovician times; similarly, strophomenides (especially strophomenoids) experienced a rapid increase in abundance and diversity from Mid Ordovician time. Despite their geological importance, Darriwilian brachiopods remain poorly documented on a worldwide basis compared to the Late Ordovician, except for a few classic studies (e.g., Cooper 1956). This may have been due to the fact that the global sea level was at a lowstand during the Darriwilian and hence the general lack of shallow marine deposits in epicontinental seas and inland basins, particularly in the large cratons of Laurentia and Siberia. In North America, for example, Darriwilian brachiopods are confined to small and narrow outcrop belts along the eastern and western continental margins (Jin 1996).

South China is one of the few regions known to have rich and diverse brachiopods of Darriwilian age. In the last few years, the senior author made systematic collections of brachiopods and other fossils from the Shihtzupu Formation (Darriwilian) and coeval strata. This study, as a second installment (following the first by Zhan and Jin in press) of the systematic description of the Middle Ordovician brachiopods of South China, will focus on the brachiopods of the Shihtzupu Formation, with a preliminary discussion on their regional faunal affinities.

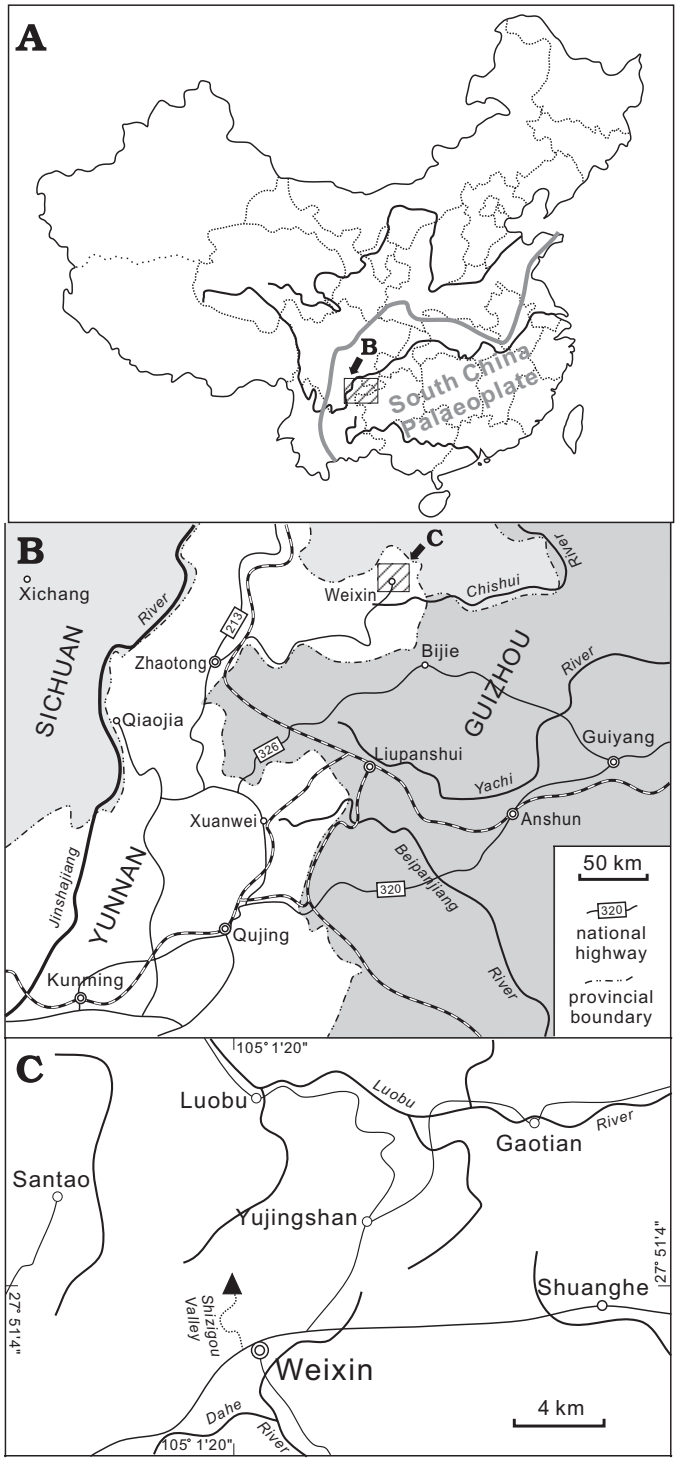


Fig. 1. Location map of the study area. **A**. Map of China, with the South China palaeoplate outlined by thick line; inset box enlarged as B. **B**. The border region between Yunnan, Guizhou and Sichuan provinces; inset enlarged as C. **C**. Detailed map of the Shizigou Valley section near the Weixin County town, with the fossil locality marked by solid triangle.

Instituional abbreviations.—Types and other figured specimens are deposited in Nanjing Institute of Geology and Palaeontology, Nanjing, China (NIGP, collection AFI1680). Topotype material is stored in the Department of Earth Sciences, University of Western Ontario, London, Canada (UWO).

Other abbreviations.—L, shell length; W, shell width; L_1, length of muscle field; W_1, width of muscle field; L_2, length of cardinalia; W_2, width of cardinalia; L_3, length of interarea; α, angle between brachiophore bases in dorsal interior; β, angle between brachiophore supports in dorsal interior.

Geological and stratigraphical setting

Palaeogeographically, the study area was in the mid-western part of the Upper Yangtze Platform (Fig. 2) where the Ordovician succession is continuous from the Tremadocian to the Hirnantian. The section is exposed along a deep mountain valley west of the Weixin County town. The section begins, at the junction of the valley with a local highway, with the Upper Cambrian dolomites of the Loushankuan Group. Northwards along the valley, the Ordovician succession comprises the Tungtzu (Tremadocian), Meitan (mainly Arenigian), Shihtzupu, Pagoda (Caradocian), Linhsiang–Wufeng (Ashgillian), and the Kuanyinchiao (Hirnantian) formations.

On the Upper Yangtze Platform, the Shihtzupu Formation is characterized by a lithofacies of calcareous to silty mudstones, confined to northern Guizhou, northeastern Yunnan, and southeastern Sichuan provinces (Wang 1981). It was first named the "Shihtzupu Shale" with the type section at Donggongsi, Zunyi, northern Guizhou (Yoh 1928), and its shelly and graptolitic fossils indicate a Llanvirnian age (Zhang 1962; Zhang et al. 1964; Wang Xiao-feng in Chen et al. 1995). Subsequent studies demonstrated that the base of the formation is diachronous, ranging from lower Llanvirnian in northern Guizhou to middle Llanvirnian in northeastern Yunnan westwards. The formation is about 12 m thick at the type section, reaching 30 m in the Meitan area, east of the type locality (Chen et al. 1995). In the study area, the Shihtzupu Formation is 8.4 m thick, largely Darriwilian in age on the basis of graptolites (Wan et al. 1979).

The contemporaneous strata of the Shihtzupu Formation on Upper Yangtze Platform include the Fengdonggang (argillaceous to concretional limestone), Kuniutan (massive, nodular limestone), Shangqiaojia (dolostone with interbeds of mudstone and sandstone), and Dashaba (silty to calcareous mudstone with minor sandstone interbeds) formations of variable thickness (Fig. 3; see also Zhang et al. 1957; Mu et al. 1978, 1979; Wang 1981; Wang et al. 1987, 1996; Zhang 1998; Wang and Chen 1994; Zhan and Jin in press). The composition of the shelly fauna varies considerably from one formation to another, although the graptolites, when present in the mudstone interbeds, are largely similar.

The fauna studied herein is from the upper part of the Shihtzupu Formation (Fig. 4), which is exposed towards the upper part of the valley. Here, the formation is divided into a lower (argillaceous limestone) and an upper (calcareous and silty mudstones) parts. Wan et al. (1979) provided the following faunal list, without any detailed stratigraphical information

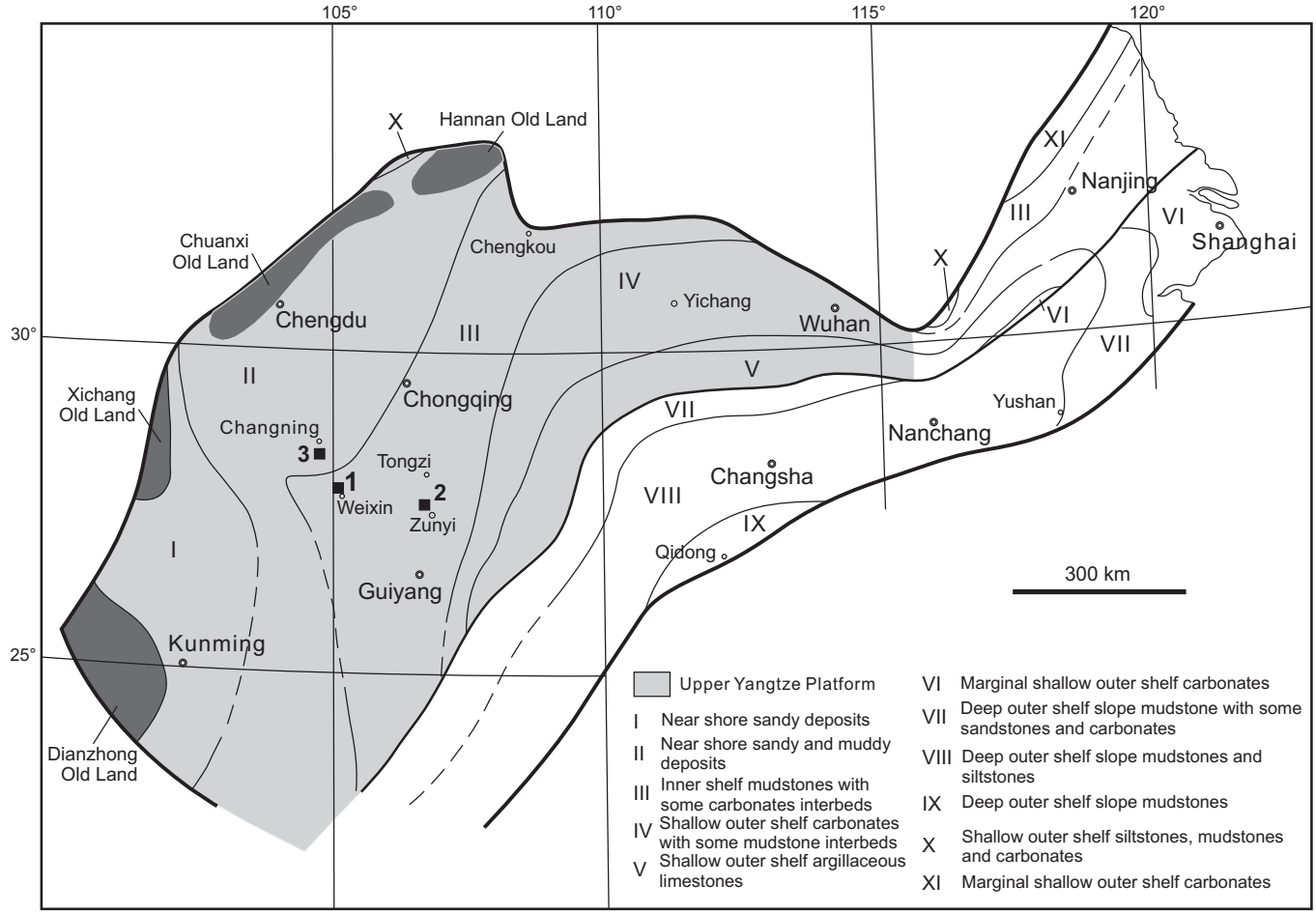


Fig. 2. Middle Ordovician sedimentary facies on the Yangtze Platform, South China palaeoplate (modified from Zhang et al. 2002), with three fossil localities discussed in the text: 1, Shihtzupu Formation at Shizigou Valley near the Weixin County town, Yunnan Province; 2, Type area of Shihtzupu Formation at Donggongsi, Zunyi, Guizhou Province; 3, Dashaba Formation at Shuanghe, Changning, Sichuan Province.

on the collection or illustrations of the fossils: graptolites (*Glyptograptus teretiusculus*, *Prolasiograptus retusus*, *Gymnograptus* sp., *Amplexograptus sanduensis*, *Pseudoclimacograptus demittoloabiosus*), trilobites (*Calymenesun tingi*, *Birmanites* cf. *hupeiensis*, *Illaenus* cf. *renhuaiensis*, *Longhodomas* cf. *yohi*), brachiopods (*Aegironetes minuta*, *Bellimurina* sp., *Peritritoechia imbricatia*, *Nicolella actoniae*, *Titanambonites* sp.) and echinoderms (such as *Sinocystis* sp.). Unfortunately, none of the original collections can be traced, and the present study is based entirely on new collections.

Age of the Weixin brachiopod fauna

On the basis of early biostratigraphical data, Wan et al. (1979) recognized a *Glyptograptus teretiusculus–Calymenesun tingi* graptolite-trilobite Zone, which would indicate a latest Llanvirnian (or latest Darriwilian) age for the Shihtzupu Formation of the Weixin area. More recently, Zhang and Chen (2003) revised the Early–Mid Ordovician graptolite zonation of the entire Upper Yangtze Platform and recognized a *Didymograptus murchisoni* Zone in the Shihtzupu Formation of the study area. They also renamed the *Glyptograptus teretiusculus* Zone of the Upper Yangtze Platform the *Gymnograptus linnarssoni* Zone. Thus, the Shihtzupu Formation of the Weixin area contains the two top graptolite zones of the Darriwilian Stage in modern stratigraphical nomenclature. In comparison, the lowest graptolite zone in the Shihtzupu Formation at the type locality (Zunyi) starts at least from the *Undulograptus intersitus* Zone (top Arenigian–lowest Llanvirnian). In terms of the brachiopods of the study area, all the samples were collected from a 3 m interval of the upper Shihtzupu Formation. It is thus reasonable to regard the Weixin brachiopod fauna to be late Darriwilian in age.

Temporal and spatial relationships of latest Arenigian–mid-Caradocian brachiopod faunas

The Weixin brachiopod fauna from the Shihtzupu Formation has strong Middle Ordovician characteristics, dominated by

Chronostratigraphy			British division		Graptolitic Zones	Weixin Yunnan	Zunyi Guizhou	Yichang Hubei	Qijiang Chongqing	Qiaojia Yunnan	Changning Sichuan
ORDOVICIAN	LATE	Caradocian	Caradocian	Lower	*Nemagraptus gracilis*	Pagoda Fm.	Pagoda Fm.	Pagoda Fm.	Pagoda Fm.	Pagoda Fm.	Pagoda Fm.
								Miaopo Fm.			
	MID	Darriwilian	Llanvirnian	Upper	*Glyptograptus teretiusculus*	Shihtzupu Fm.	Shihtzupu Fm.	Kuniutan Fm.	Fengdong-gang Fm.	Shang-qiaojia Fm.	Dashaba Fm.
					Didymograptus murchisoni						
				Middle	*Didymograptus artus*	Meitan Fm.				Xiaqiaojia Fm.	
				Lower							
			Arenigian	Upper	*Undulograptus intersitus*		Meitan Fm.	Dawan Fm.	Meitan Fm.		

Fig. 3. Stratigraphic nomenclature and correlation of Darriwilian (Middle Ordovician) strata, Upper Yangtze Platform. Data from Zhang et al. (1964), Wang et al. (1987), Wang (1981), Lai (1982), Mu et al. (1978), Chen and others (1995), Zhang and Chen (2003), and Zhan and Jin (in press).

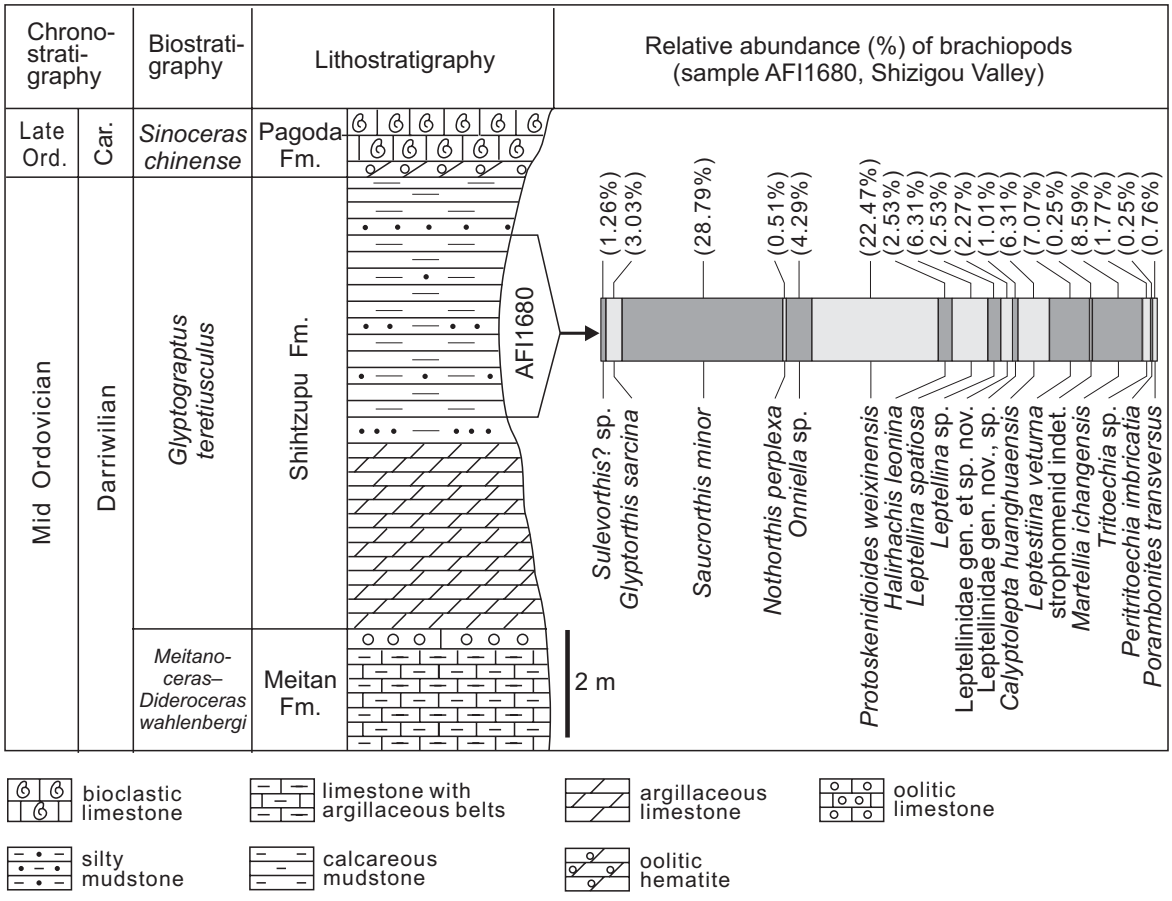


Fig. 4. Stratigraphical range and relative abundance of brachiopod species in the Shihtzupu Formation, Shizigou Valley section near the Weixin County town, Yunnan Province.

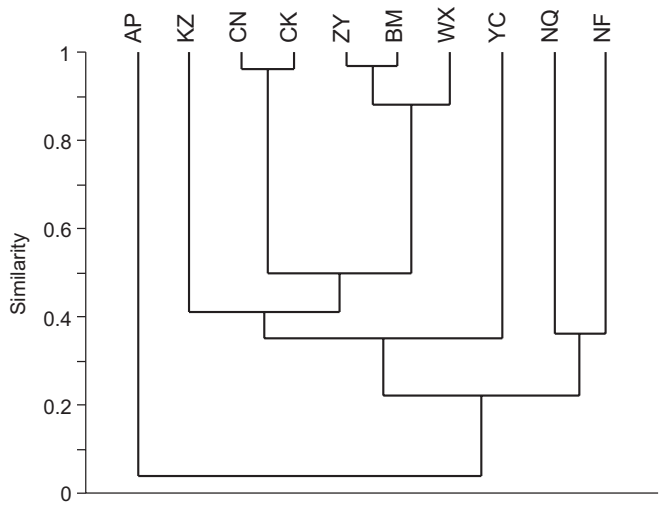


Fig. 5. Cluster analysis of 10 brachiopod faunas from uppermost Arenigian to middle Caradocian, using the algorithm of paired group and Raup-Crick similarity (PAST, Hammer et al. 2004). Abbreviations: ZY, Shihtzupu Formation, Zunyi (type locality), northern Guizhou Province; WX, Shihtzupu Formation, Weixin, northeastern Yunnan Province; CN, Dashaba Formation, Changning, southeastern Sichuan Province; YC, Miaopo Formation, Yichang, western Hubei Province; NQ, Siliangssu Formation, Ningqiang, southern Shaanxi Province; CK, Houping Formation, Chengkou, northern Chongqing; BM, Naungkangyi Group and its equivalents (Caradocian), Shan States, Burma; KZ, Uzunbulak Formation (Darriwilian), Chu-Ili Mountains, southern Kazakhstan; NF, Unnamed Ordovician tuffs (Darriwilian), Virgin Arm, Newfoundland; AP, Lenoir Formation (Darriwilian), eastern United States.

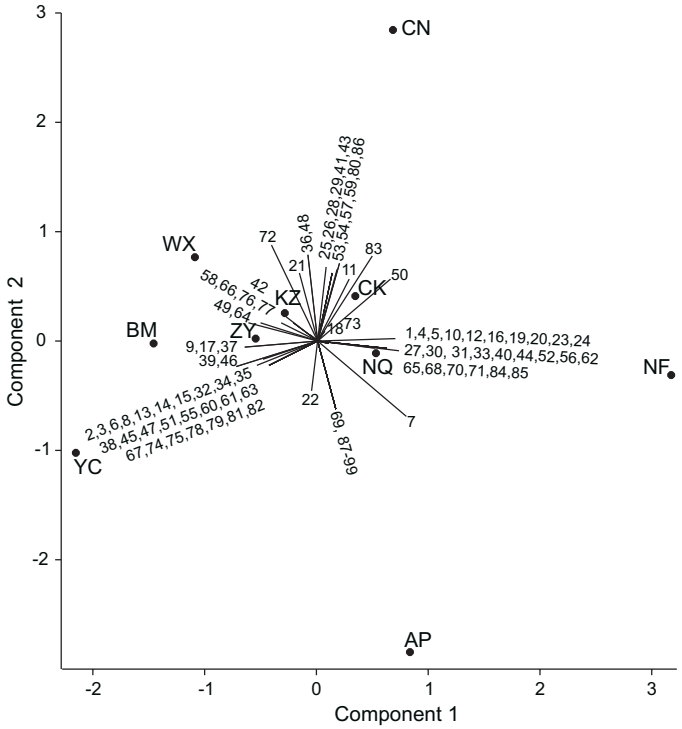


Fig. 6. Principal component analysis (PCA) of 10 selected brachiopod faunas from uppermost Arenigian–middle Caradocian of South China, Kazakhstan, Avalonia, Sibumasu, and Laurentia, performed using PAST (Hammer et al. 2004). Data matrix: variance-covariance; Algorithm: singular value decomposition (SVD). See Fig. 5 for abbreviations of the faunas and Appendix 1 for number codes.

orthides and strophomenides, which account for 14 species (12 genera) among the total of 18 species (16 genera) represented by 388 specimens. Billingsellides (3 genera and 3 species) and a pentameride (1 genus and 1 species) are relatively minor components of the fauna. In relative abundance, the small-shelled orthides *Saucrorthis minor* (116 specimens) and *Protoskenidioides weixinensis* (89 specimens) make up the bulk of the fauna. For this reason, the Weixin brachiopods can be appropriately called the *Saucrorthis–Protoskenidioides* Fauna. Similar dominance of orthides and strophomenides are common in other brachiopod faunas of Darriwilian–Caradocian age, such as those from the Dashaba Formation of Changning, Sichuan Province, SW China (*Saucrorthis–Parisorthis* Fauna; Zhan and Jin in press), the Naungkangyi Group and coeval strata of Shan States, Burma (Cocks and Zhan 1998), and the Shelve succession of Shropshire, England (Williams 1974; Harper et al. 1999).

In palaeogeographical distribution of the 16 genera in the *Saucrorthis–Protoskenidioides* Fauna, eight are cosmopolitan (known from more than four palaeoplates), four regionally widespread in two or three palaeoplates (*Calyptolepta*, *Martellia*, *Protoskenidioides*, and *Saucrorthis*), and the other four endemic to South China (*Halirhachis*, Leptellinidae gen. et sp. nov., *Peritritoechia*, and an indeterminate strophomenide).

To assess the temporal and spatial relationships (i.e., the evolutionary and palaeogeographical affinities) of the *Saucrorthis–Protoskenidioides* Fauna to other brachiopod faunas in the latest Arenigian–mid-Caradocian time slice, ten faunas of Darriwilian, pre-Darriwilian, and post-Darriwilian ages are selected for multivariate (cluster and principal component) analyses, with emphasis on the various faunas in South China (see Appendix 1).

Both cluster analysis and principal component analysis (PCA) indicate that the *Saucrorthis–Protoskenidioides* Fauna of Weixin (WX) has the highest degree of similarity with the brachiopod faunas of the typical Shihtzupu Formation (ZY) and the Naungkangyi Group of Burma (Figs. 5, 6). The close faunal affinity between WX and ZY is expected, as the two faunas are from slightly different lithofacies of the same formation and same palaeogeographical region (Upper Yangtze Platform). The Burmese fauna, however, is from a different palaeoplate (Sibumasu) and has been regarded as Caradocian in age (Cocks and Zhan 1998). The multivariate analyses suggest that WX, ZY, and BM are more closely linked as a cluster than individually with other latest Arenigian–early Caradocian brachiopod faunas of the Upper Yangtze Platform. This supports the previous interpretation of a close palaeobiogeographical link between Sibumasu and South China (Fortey and Cocks 1998) but, more interestingly, suggests that the Burmese brachiopods reported by Cocks and Zhan (1998) from the Naungkangyi Group are probably of late Darriwilian rather than Caradocian age.

Among the various brachiopod faunas of the Upper Yangtze Platform, the CN fauna from the Dashaba Formation appears to have a relatively low similarity to the WX-ZY-BM cluster, probably because CN contains some

latest Arenigian elements and several new taxa (Zhan and Jin in press). The NQ fauna also is less similar as it is a fauna from the northwestern margin of the Yangtze Platform.

By plotting a few selected brachiopod faunas (largely of Darriwilian age) from other palaeoplates, it became obvious that South China, Sibumasu, and Kazakhstan (Chu-Ili) form a palaeobiogeographical province. In contrast, the brachiopods from eastern Laurentia (AP, Appalachian basin) and Avalonia (NF, Newfoundland) have little in common with those of South China, showing distinct, global-scale provincialism. As is shown in the PCA scatter plot (Fig. 6), the South China-Sibumasu-Kazakhstan brachiopod province is characterized by a large suite of taxa divided into several main eigenvectors, which are clearly separated from those of the Laurentian (AP) or Avalonian (NF) representatives. Whereas a large number of endemic taxa define a distinct brachiopod fauna of the Upper Yangtze Platform, several regional taxa distinguish the South China-Sibumasu-Kazakhstan brachiopod province. *Saucrorthis*, for example, is widespread through the Llanvirnian strata of the Upper Yangtze Platform, being particularly abundant in offshore depositional settings (equivalent to BA3–4). Elsewhere, it is known also from the Naungkangyi Group and the Kinle Siltstone Formation of Shan States, Burma (Reed 1906; also see Cocks and Zhan 1998). *Martellia* is similarly common and widespread on the Upper Yangtze Platform and Sibumasu terrane (Reed 1917; Fang and Zhu 1974). Recently, *Martellia* have been reported from the Uzunbulak Formation (Llanvirnian) of the Chu-Ili terrane of Kazakhstan (Popov et al. 2001). Its presence in the upper San Juan Formation (lower Llanvirnian) of the Argentine Precordillera terrane (Benedetto 1987, 2003) remains to be confirmed.

Systematic palaeontology

Qualitative terms used to describe shell size: small, < 10 mm; medium, 10 to < 20 mm; large, 20 to 30 mm; very large, > 30 mm.

All material described herein came from the collection AFI1680, Shizigou Valley near the Weixin County town, northeastern Yunnan Province, southwestern China.

Order Orthida Schuchert and Cooper, 1932
Superfamily Orthoidea Woodward, 1852
Family Orthidae Woodward, 1852
Genus *Sulevorthis* Jaanusson and Bassett, 1993

Sulevorthis? sp.

Fig. 7A, B; Table 1.

Table 1. Shell measurements (mm) of *Sulevorthis*? sp.

Specimen	L	W	L/W	L_1	W_1	L_2	W_2	α
NIGP139059	2.74	3.79	0.72	0.99	0.60	–	–	–
NIGP139060	5.28	8.07	0.65	?	?	0.54	2.11	98

Material.—Two ventral internal, one dorsal internal and two external moulds.

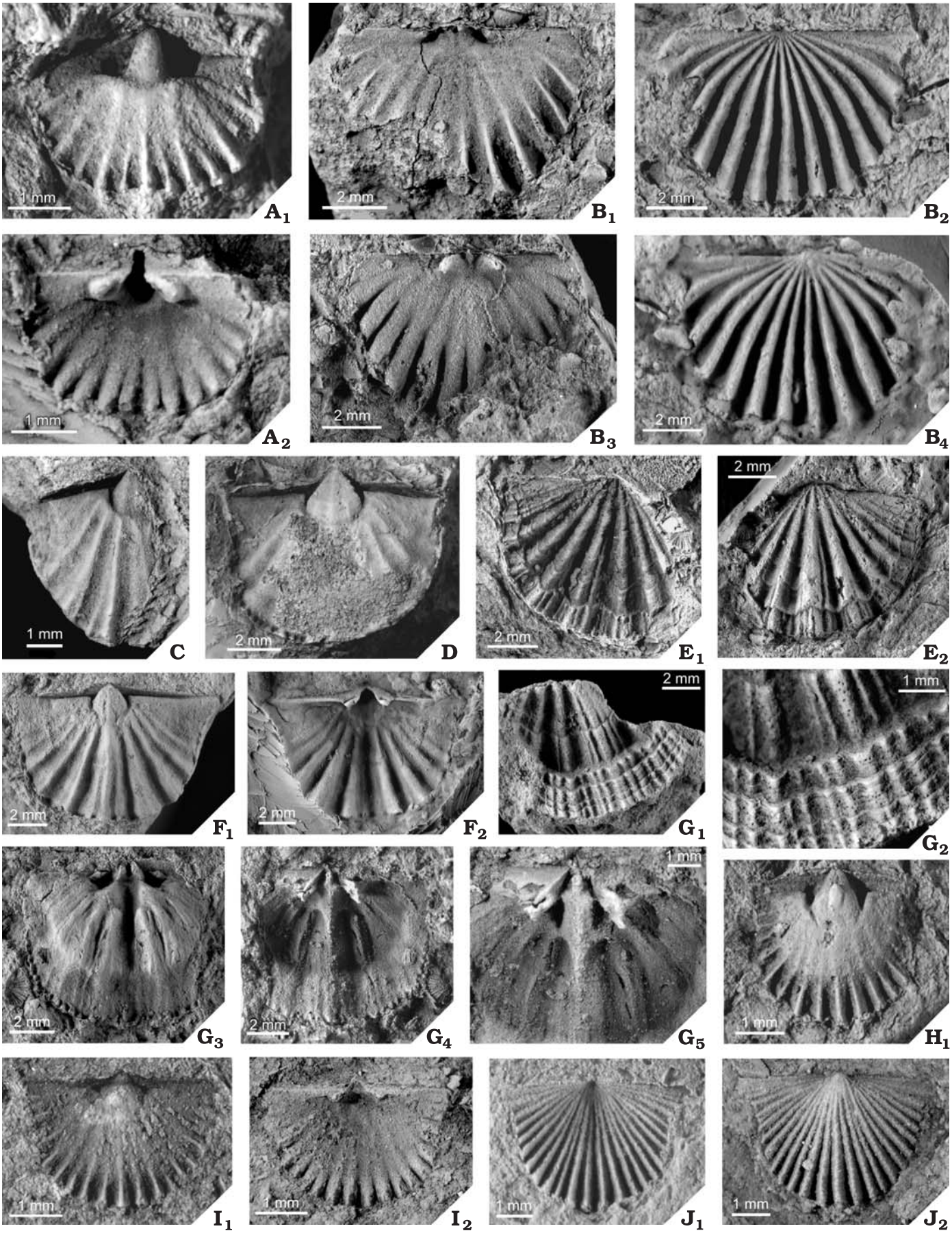
Description.—Shell small, planoconvex, subcircular with maximum width at or near hinge line. Cardinal extremities round or rectangular. Anterior commissure rectimarginate. Ventral valve moderately to strongly convex, highest around umbonal area; interarea weakly curved, about one-sixth of shell length, apsacline; delthyrium narrow, open (Fig. $7A_2$). Dorsal valve nearly flat with broad, gentle, median sulcus; interarea linear, anacline; notothyrium open. Costae simple, coarse, evenly spaced, 12–13 per valve, crests rounded, interspace of equal width as costa; concentric fila dense, evenly spaced over entire shell surface.

Teeth massive, with shallow fossetts on inner sides; dental plates absent (Fig. $7A_2$); muscle field confined to delthyrial cavity, slightly elevated anteriorly, about one-third length and one-sixth width of shell; adductor and diductor scars not clearly separated; vascula media originating just anterior to muscle field, extending parallel to two-thirds of shell length, then turning towards shell antero-lateral margins. Cardinalia about one-tenth length and one-quarter width of shell; cardinal process small, ridge-like, confined to deep and narrow notothyrial cavity (Fig. $7B_3$); brachiophores rod-like, projecting mainly ventrally, without brachiophore supports; brachiophore bases thick, divergent at 98°; sockets shallow, open antero-laterally; muscle field poorly impressed. Crenulations extending to mid-length of shell.

Discussion.—Compared with the type species of *Sulevorthis*, the Weixin material differs in having a flatter dorsal valve, weaker concentric ornamentations, smaller cardinal process, and narrower delthyrium. *Orthis* sp. reported by Williams (1974) from the Stapeley Volcanic Group (lower Llanvirnian) of Shropshire is similar to the Weixin specimens in its dorsal interior but has more coarse costae. Several Cooper's (1956) species of *Orthambonites*, subsequently assigned to *Sulevorthis* by Jaanusson and Bassett (1993), can be readily distinguished from the Weixin species in having a gently convex dorsal valve, or more densely populated costae, or thicker cardinal process.

Sulevorthis has been reported from Baltoscandinavia, British Isles and North America (Jaanusson and Bassett 1993). This is the first possible record of the genus in South China.

Fig. 7. **A**, **B**. *Sulevorthis*? sp. **A**. NIGP139059, ventral internal mould (A_1) and latex cast (A_2). **B**. NIGP139060, dorsal internal (B_1) and external (B_2) moulds of a single valve, and latex casts (B_3, B_4). **C**–**G**. *Glyptorthis sarcina* sp. nov. **C**. NIGP139061, paratype, ventral internal mould. **D**. NIGP139062, paratype, ventral internal mould. **E**. NIGP139063, paratype, dorsal external mould (E_1) and latex cast (E_2). **F**. NIGP139064, paratype, ventral internal mould (F_1) and latex cast (F_2). **G**. NIGP139065, holotype, dorsal external (G_1) and internal (G_3) moulds of a single valve, latex cast (G_4), and local enlargement showing irregularly spaced minute tubercles on shell surface (G_2) and cardinalia (G_5). **H**–**J**. *Saucrorthis minor* Xu, Rong, and Liu, 1974. **H**. NIGP139066, ventral internal mould. **I**. NIGP139067, ventral internal mould (I_1) and latex cast (I_2). **J**. NIGP139068, ventral external mould (J_1) and latex cast (J_2). →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Family Glyptorthidae Schuchert and Cooper, 1931

Genus *Glyptorthis* Foerste, 1914

Glyptorthis sarcina sp. nov.

Fig. 7C–G; Table 2.

Derivation of name: From the Latin *sarcina*, bundle, referring to the fascicostellae of the new species.

Holotype: NIGP 139065, dorsal internal and external moulds of conjoined valves.

Type locality: Shizigou Valley near the Weixin County town, northeastern Yunnan Province.

Type horizon: Upper part of Shihtzupu Formation.

Material.—Five ventral internal and two external, three dorsal internal and two external moulds.

Diagnosis.—Biconvex shell; relatively sparse, coarse costae with uncommon bifurcation in posterior half, and more intense fascicostellate branching anteriorly; ventral muscle field considerably smaller than in typical *Glyptorthis*; dorsal adductor scars marked by strong, radial ridges.

Description.—Shell small to medium, equally biconvex or dorsibiconvex, subquadrate to subsemicircular, with maximum width at or near hinge line. Cardinal extremities rounded or rectangular. Anterior commissure rectimarginate or weakly denticulate. Ventral valve moderately convex; beak erect; interarea flat or weakly concave, about one-fifth to one-seventh of shell length, apsacline; delthyrium narrow, open. Dorsal valve convex to strongly convex; sulcus narrow, starting from umbo, becoming wider and shallower anteriorly; dorsal interarea flat, anacline, less than one-tenth of shell length; notothyrium open. Costae coarse, sparse, 9–11 per valve, with rare bifurcation in posterior part of shell and intense fascicostellate branching near anterior margin of some specimens. Concentric fila dense, evenly spaced over entire shell surface; concentric lamellae irregular, best developed near anterior margin of shell. Minute tubercles dense, irregularly distributed on shell surface (Fig. 7G_2).

Teeth wedge-shaped; dental plates receding, subparallel; muscle field small, deeply impressed, occupying one-quarter length and one-fifth width of shell; adductor scar subtriangular, located in antero-medial part of muscle field, flanked by diductor scars; vascula media originating from anterior ends of two diductor scars, extending anteriorly to two-thirds of shell length, then diverging antero-laterally. Cardinalia about one-fifth length and one-third width of shell; cardinal process simple, ridge-like, projecting postero-ventrally, with crenulated crest; brachiophores blade-like; brachiophore bases stout, diverging from each other at 78°; notothyrial platform high, continuous anteriorly with thick median ridge; sockets large, deep; fulcral plates weak; median ridge thick, high, limited within muscle field; muscle field about half shell length or width; posterior pair of adductor scars small, located immediately anterior of notothyrial platform; anterior pair much larger, marked by strong radial ridges; mantle canal system saccate, poorly impressed.

Table 2. Shell measurements (mm) of *Glyptorthis sarcina* sp. nov.

Specimen	L	W	L/W	L_1/L	W_1/W	L_2/L	W_2/W	L_3/L	α
NIGP139062	6.58	8.03	0.82	0.33	0.26	–	–	0.17	–
NIGP139064	7.35	11.19	0.66	0.26	0.18	–	–	0.12	–
04b	3.46	4.94	0.70	–	–	–	–	0.21	–
NIGP139065	8.72	9.90	0.88	0.55	0.49	0.19	0.35	0.07	78

Discussion.—The new species is assigned to *Glyptorthis* on the basis of its prominent ventral interarea, fascicostellate branching of costae, strong concentric lamellae, and the configuration of cardinalia. This Llanvirnian species is among the oldest forms of the genus and differs from all other congeneric species in its considerably weaker concentric lamellae, smaller ventral muscle field, strong radial ridges in the dorsal muscle field, and minute tubercles on the outer shell surface. The relatively sparse primary costae of the new species are somewhat similar to those of *Glyptorthis glypta* Cooper, 1956 but the latter has strong lamellose frills. The sparse costae of *G. sarcina* are reminiscent of *Ptychopleurella* but the new species lacks the prominent, catacline to strongly apsacline, pyramidal, ventral interarea that is diagnostic of *Ptychopleurella*.

Family Productorthidae Schuchert and Cooper, 1931

Genus *Saucrorthis* Xu, Rong, and Liu, 1974

Saucrorthis minor Xu, Rong, and Liu, 1974

Figs. 7H–J, 8A–K; Table 3.

Saucrorthis minor sp. nov.; Xu et al. 1974: 151, pl. 66: 1–4.

Material.—24 ventral internal and 24 external, 31 dorsal internal and 35 external, and two internal moulds of conjoined valves respectively.

Description.—Shell small, planoconvex, subsemicircular to subcircular (e.g., Fig. 7I). Cardinal extremities rectangular to acute. Anterior commissure denticulate, rectimarginate. Ventral valve moderately to strongly convex, deepest in umbonal area; interarea moderately high, flat, apsacline; delthyrium open; beak erect. Dorsal valve plane, occasionally with gentle sulcus in antero-medial part of shell; interarea very low, anacline. Costae coarse, simple, rounded, 20–23 per valve, with rare bifurcations originating 0.5–1.0 mm from apex; minute tubercles sparse, regularly spaced on crests of costae (Fig. 8I_2).

Fig. 8. **A**–**K**. *Saucrorthis minor* Xu, Rong, and Liu, 1974. **A**. NIGP139069, ventral internal mould. **B**. NIGP139070, ventral internal mould. **C**. NIGP139071, dorsal internal mould. **D**. NIGP139072, dorsal internal mould. **E**. NIGP139073, dorsal internal mould (E_1) and latex cast (E_2) with a latex cast of *Sulevorthis*? sp. (NIGP139059) on the right side. **F**. NIGP139074, dorsal external mould (F_1) and latex cast (F_2). **G**. NIGP139075, holotype, dorsal internal mould (G_1) and latex cast (G_2) with local enlargement (G_3) showing cardinalia. **H**. NIGP139076, dorsal external mould. **I**. NIGP139077, dorsal external mould (I_1) with local enlargement (I_2) showing minute tubercles regularly dispersed on the crests of costae. **J**. NIGP139078, dorsal internal mould. **K**. NIGP139079, dorsal internal moulds. **L**, **O**. *Nothorthis perplexa* Xu and Liu, 1984. **L**. NIGP139080, dorsal internal mould (L_1) and latex cast (L_2). **O**. NIGP139081, dorsal internal mould. **M**, **N**. *Onniella* sp. **M**. NIGP139082, ventral internal mould (M_1) and latex cast (M_2). **N**. NIGP139083, dorsal internal mould. →

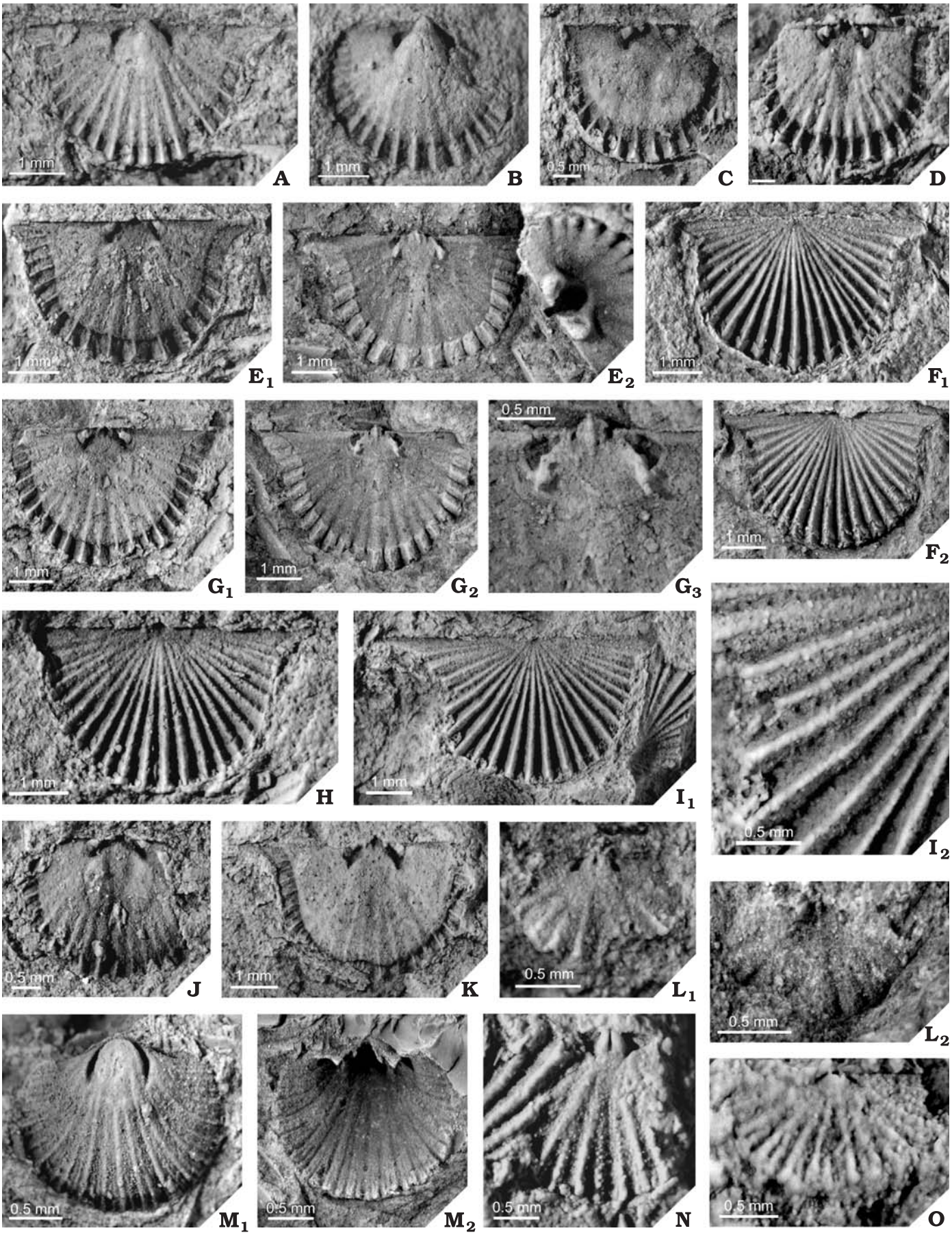
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Table 3. Shell measurements (mm) of *Saucrorthis minor* Xu, Rong, and Liu, 1974.

	L	W	L/W	L_1/L	W_1/W	L_1/W_1	L_2/L	W_2/W	α
11 dorsal valves									
AVG	2.86	4.25	0.68	0.36	0.32	0.76	0.19	0.25	82.1
STD	0.39	0.61	0.08	0.03	0.03	0.06	0.02	0.04	7.6
MIN	1.99	3.18	0.55	0.32	0.26	0.69	0.16	0.20	74
MAX	3.34	5.22	0.81	0.42	0.37	0.88	0.23	0.32	101
8 ventral valves									
AVG	3.07	4.08	0.76	0.35	0.27	0.99	–	–	–
STD	0.34	0.51	0.12	0.03	0.04	0.10	–	–	–
MIN	2.58	3.44	0.54	0.31	0.22	0.86	–	–	–
MAX	3.56	4.95	0.93	0.39	0.32	1.13	–	–	–

Table 4. Shell measurements (mm) of *Nothorthis perplexa* Xu and Liu, 1984.

Specimen	L	W	L/W	L_2	W_2	L_2/L	W_2/W	α
NIGP139081	1.07	1.70	0.63	0.14	0.41	0.13	0.24	109
NIGP139080	0.91	1.33	0.68	0.16	0.39	0.18	0.29	81

Table 5. Shell measurements (mm) of *Onniella* sp.

Specimen	L	W	L/W	L_1/L	W_1/W	L_2/L	W_2/W	L_3/L	α
NIGP139082	3.39	3.95	0.86	0.35	0.27	–	–	0.13	–
NIGP139084	2.23	3.19	0.70	0.54	0.36	0.13	0.21	0.03	56
NIGP139083	1.93	?	?	?	?	0.16	?	0.036	74
NIGP139085	1.24	1.56?	0.79	0.44	0.42	0.18	0.33	0.03	90

Concentric growth lines fine, evenly spaced, interrupted by irregular concentric lamellae towards anterior margin.

Teeth strong; dental plates thick, very short, subparallel; delthyrial platform strongly elevated; muscle field slightly elongate, bilobed anteriorly, about one-third length and one-quarter width of shell, without anterior bounding ridge; adductor scar deeply impressed, elliptical, surrounded by pair of elongate-oval diductor scars; mantle canal system saccate. Cardinalia stout, about one-fifth length and one-quarter width of shell; cardinal process swollen, occupying whole notothyrial cavity, myophore strongly projecting posteriorly and ventrally; notothyrial platform highly elevated; brachiophores blade-like, projecting antero-ventrally; brachiophore bases high, long, ridge-like, divergent at 74–101°; dorsal adductor scars clearly impressed, about one-third length or width of shell, bisected longitudinally by low and wide median ridge in most specimens; anterior pair of adductor scars subcircular, slightly larger than posterior pair. Crenulations strong around peripheral rim of each valve, becoming abruptly weaker inside rim (e.g., Fig. $8E_2$, G_2).

Discussion.—The Weixin specimens of *S. minor* may vary from elongate with rectangular cardinal extremities in some (Fig. 7H) to transverse with prominent ears in most others. The fulcral plates may be well developed (Fig. 8D, G_1–G_3) or entirely absent (Fig. $8E_1$, E_2) in half of the species population.

Among the three known species of *Saucrorthis*, *S. minor* is easily distinguished from *S. obscura* (Xu and Liu 1984; see Zhan and Jin in press) of south China and *S. irravadica* (Reed 1936) of Burma (Cocks and Zhan 1998) by having a smaller shell size and fewer, usually non-bifurcating costae. Specimens of *O. obscura* from the Dashaba Formation also have minute tubercles on the outer surface of the shell.

Superfamily Plectorthoidea Schuchert and LeVene, 1929

Family Ranorthidae Havlíček, 1949

Genus *Nothorthis* Ulrich and Cooper, 1938

Nothorthis perplexa Xu and Liu, 1984

Fig. 8L, O; Table 4.

Nothorthis? *perplexa* sp. nov.; Xu and Liu 1984: 171, pl. 11: 22–25.
Nothorthis perplexa Xu and Liu, 1984; Zhan and Jin in press.

Material.—Two dorsal internal moulds.

Discussion.—The minute, slightly transverse shells of *Nothorthis perplexa* are rare but well preserved together with the large shells of *Martellia* and *Leptellina*. The brachiophores are rod-like with widely divergent brachiophore bases (Fig. $8L_1$, L_2). The cardinal process is small, ridge- or knob-like. The multicostellae are somewhat less numerous than in other species of *Nothorthis*. These characters are essentially identical to those of the same species from the Dashaba Formation (see Zhan and Jin in press).

Superfamily Dalmanelloidea Schuchert, 1913

Family Dalmanellidae Schuchert, 1913

Genus *Onniella* Bancroft, 1928

Onniella sp.

Figs. 8M, N, 9A, B; Table 5.

Material.—Eight ventral internal and two external, six dorsal internal and one external moulds.

Description.—Shell small, subcircular, ventribiconvex, widest at about one-third length of shell. Cardinal extremities rounded. Anterior commissure rectimarginate. Ventral valve strongly and evenly convex, deepest around umbo; interarea apsacline, nearly planar, about one-eighth of shell length; beak slightly curved; delthyrium open, wide. Dorsal valve gently convex with shallow sulcus originating from umbo; interarea low, anacline, less than one-tenth of shell length; notothyrium open. Multicostellae fine, about 5–6 costellae per mm at 1 mm growth stage, with number of costellae increasing anteriorly by bifurcation (common) or intercalation (rare); first-order costae originating from apex, second-order at about one-third length, and third-order at three-quarters length of shell; concentric fila dense, evenly spaced over entire shell surface.

Teeth small, thin, triangular; dental plates thin, high, relatively long, inclined medially but subparallel at their bases. Ventral muscle field suboval, clearly impressed, about one-third length and one quarter width of shell; triangular adductor scar in middle of muscle field, slightly elevated,

elongated; two lobes of diductor scars longitudinally semielliptical. Cardinalia delicate, about one-eighth to one-sixth length, and one-fifth to one-third width of shell; cardinal process with thin shaft and swollen myophore; brachiophores rod-like, projecting strongly in ventral direction; brachiophore bases thick, divergent from each other at acute angle; brachiophore supports thin, very short, tilting basomedially; notothyrial cavity deep, slightly elevated anteriorly. Sockets small, shallow, open antero-laterally. Dorsal muscle field about one-half length and two-fifths width of shell; outer, posterior pair of adductor scars subcircular, located anterior to notothyrial cavity; inner, anterior pair much more elongated and narrow. Minute tubercles reflecting shell endopunctae dense, irregularly spaced.

Variability.—Available specimens indicate that the angle between the pair of brachiophore bases becomes smaller with larger shell size (Table 5). The brachiophore supports are commonly present and basomedially inclined, but they may be poorly developed in some shells (Fig. 9B). The dental plates are well developed and extend anteriorly to form lateral bounding ridges of the muscle field (Fig. 8M_1), but, in a few specimens, they are short and limited to the posterior part of the muscle field.

Discussion.—Williams and Wright (1963) pointed out that *Dalmanella* and *Onniella* are somewhat similar externally but *Dalmanella* can be distinguished from *Onniella* by having fulcral plates, smaller muscle scars and a more elongate ventral muscle field. On the basis of *Onniella* from the type Caradoc area of Shropshire, Hurst (1979) suggested that the differentiation of species within *Onniella* lies in the ribbing pattern, ventral muscle field, and other internal features. Most known species of *Onniella*, such as the type species, *O. broeggeri* Bancroft, 1928, from the Caradocian of Shropshire, England and those from North America (Cooper 1956) and Baltica (Hints 1975), have an unevenly convex ventral valve and a median ridge in the dorsal interior. The Weixin species has an evenly convex ventral valve but lacks a clearly defined dorsal median ridge. It probably represents a new species, but additional and better preserved specimens are needed to study all the diagnostic characters and their range of variation.

Order Protorthida Schuchert and Cooper, 1931
Superfamily Skenidioidea Kozłowski, 1929
Family Skenidiidae Kozłowski, 1929
Genus *Protoskenidioides* Williams, 1974
Protoskenidioides weixinensis sp. nov.

Fig. 9C–P; Table 6.

Derivation of name: After Weixin county, the type area of the new species.

Holotype: NIGP 139097, dorsal internal mould.

Type locality: Collection AFI 1680, Shizigou Valley near the Weixin County town, Yunnan Province.

Type horizon: Upper part of Shihtzupu Formation.

Table 6. Shell measurements (mm) of *Protoskenidioides weixinensis* sp. nov.

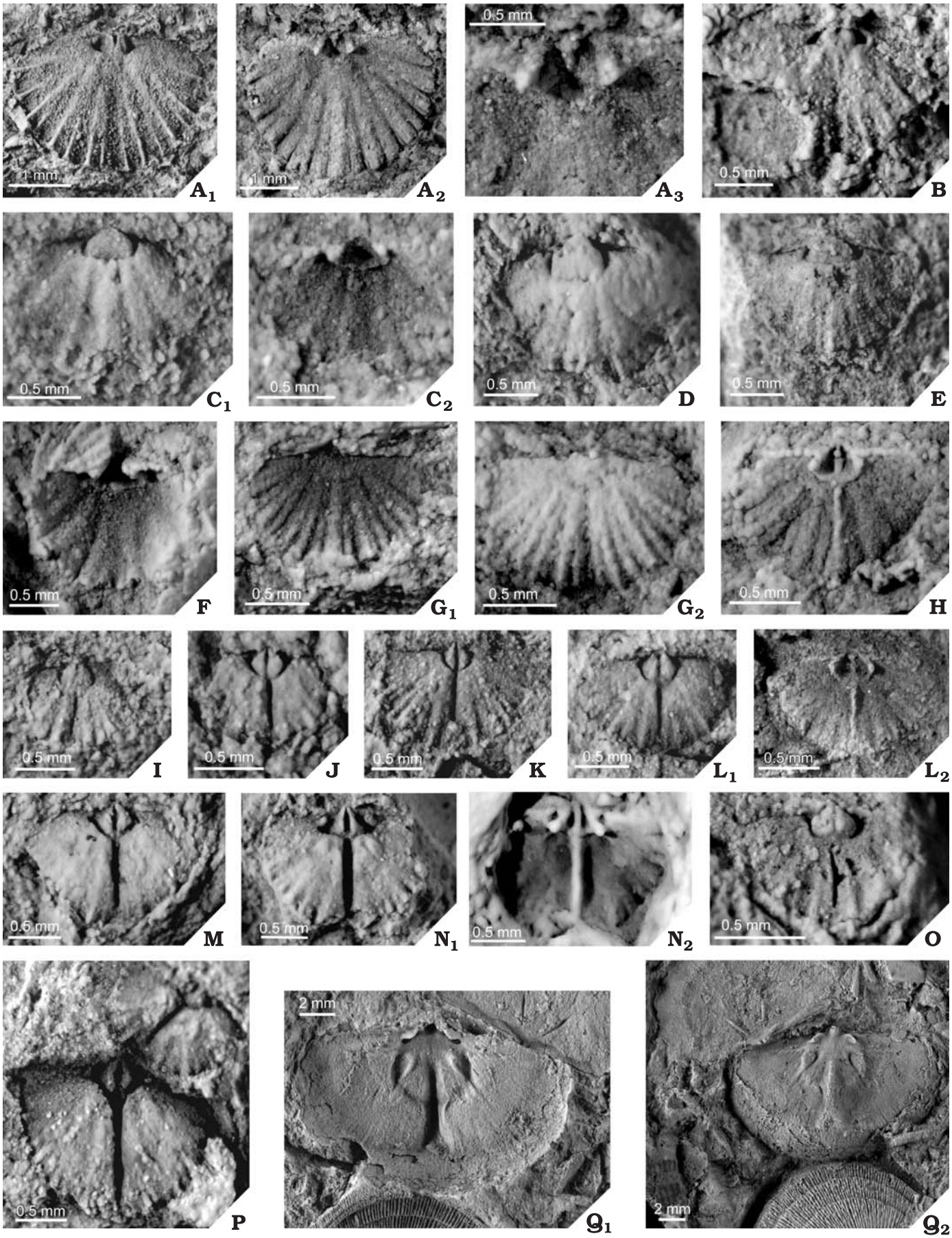
	L	W	L/W	L_1/L	W_1/W	L_1/W_1	L_2/L	W_2/W	α	β
15 dorsal valves										
AVG	1.12	1.45	0.77	0.43	0.44	0.75	0.27	0.31	74.1	93.9
STD	0.26	0.31	0.05	0.06	0.05	0.08	0.04	0.05	9.38	12.5
MIN	0.73	0.86	0.71	0.30	0.38	0.60	0.19	0.22	60	74
MAX	1.59	1.95	0.85	0.52	0.54	0.86	0.33	0.38	93	130
3 ventral valves										
AVG	1.19	1.50	0.80	0.27	0.33	0.65	–	–	–	–
STD	0.16	0.18	0.08	0.06	0.03	0.15	–	–	–	–
MIN	1.06	1.29	0.71	0.23	0.29	0.50	–	–	–	–
MAX	1.36	1.61	0.86	0.33	0.35	0.80	–	–	–	–

Material.—28 ventral internal and five external, 51 dorsal internal and 5 external moulds.

Diagnosis.—Shell very small, weakly transverse, ventribiconvex. Shell costellae increasing anteriorly through intercalation and bifurcation. Sessile spondylium undercut anteriorly. Cardinal process ridge-like, separated from median ridge by brachiophore supports; median ridge well-developed, extending to anterior margin of shell. Posterior outer pair of dorsal adductor scars larger than anterior inner pair.

Description.—Shell very small, ventribiconvex, transversely subsemicircular to subcircular, with maximum width at or slightly anterior to hinge line. Cardinal extremities rectangular to rounded. Anterior commissure rectimarginate to broadly sulcate. Ventral valve strongly convex, deepest in umbonal area; interarea high, apsacline, with planar surface; delthyrium narrow, open; beak erect. Dorsal valve gently convex, deepest around umbo; narrow sulcus starting immediately anterior of umbo; interarea low, planar, anacline; notothyrium open, relatively wide. Costellae rounded, different in size, 15–18 per valve; intercalation and bifurcation beginning about mid-length of shell. Growth lines fine, evenly spaced.

Teeth strong, wedge-shaped; dental plates thin, basolaterally divergent, becoming subparallel to medially convergent at their bases to form primitive, sessile, anteriorly undercut spondylium. Muscle field about one-quarter length and one-third width of shell. Cardinalia stout, about one-quarter length and one-third width of shell; cardinal process ridge-like, with swollen myophore, extending for whole length of notothyrial cavity in adult specimens, but limited to the posterior end in juveniles (Fig. 9I). Sockets deep, relatively large, with variously developed fulcral plates; brachiophores rod-like, projecting antero-ventrally; brachiophore bases high, thin, divergent at about 74°; brachiophore supports variously developed, meeting anteromedially to median septum at 94°, forming cruralium-like structure; notothyrial cavity deep, subrombic to subcircular in outline, bounded posteriorly by brachiophore bases and antero-aterally by brachiophore supports. Median septum very high, extending to shell anterior margin, reaching maximum height at about two-thirds length of shell. Muscle field clearly impressed, about two-fifths length or width of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2 mm
Q1
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shell, without bounding ridges; outer, posterior pair of adductor scars elliptical to longitudinally semicircular; inner, anterior pair smaller, more elongate.

Variability.—The new species shows some degrees of variation in the development and configuration of brachiophore supports, which may be strong, thick, and merging onto the median septum in some shells (Fig. 9N_1, N_2), or weak and disjunct from the median septum in others (Fig. 9L_1, L_2). The angle between the brachiophore support and the median septum varies from acute (Fig. 9M) to obtuse (Fig. 9N_1, N_2). The angle of divergence between the pair of brachiophore bases has similar variations. In shells of similar size, the dorsal median septum varies from thin and low to thick and high. Ontogenetically, small shells tend to have a weak cardinal process, a short dorsal median septum that is disjunct from the cardinal process and does not extend to the shell anterior margin (Fig. 9I, O), and a pair of subparallel brachiophore supports.

Discussion.—*Protoskenidioides weixinensis* is the youngest known species of the genus. It is characterized by a weakly transverse shell with fine costellae that increase anteriorly via bifurcation and intercalation. Despite its small shell size, the internal structures of the new species are more prominently developed than other congeneric forms, including the genotype. *Protoskenidioides revelata* Williams, 1974, the type species, from the upper Arenigian of Shropshire, England, has a larger, strongly transverse shell with less frequent intercalation of costellae. *Protoskenidioides minor* Xu and Liu, 1984 from the lower Meitan Formation (lower Arenigian) of Guizhou Province (SW China) can be distinguished by its more strongly transverse shell with notably coarser and fewer costae. Its dorsal median septum is generally absent or poorly developed. *Protoskenidioides huanghuaensis* Zeng (in Zeng et al. 1983) from the upper Dawan Formation (upper Arenigian) of Hubei Province is similar to *P. weixinensis* in ribbing style but differs in having a larger and more strongly transverse shell. Its cardinal process and median septum are absent or poorly developed.

Order Strophomenida Öpik, 1934
Superfamily Plectambonitoidea Jones, 1928
Family Taffiidae Schuchert and Cooper, 1931
Genus *Halirhachis* nov.

Derivation of name: From the Greek, *halis*, many, and *rhachis*, ridge. *Halirhachis* is a feminine noun, referring to the longitudinal ridges in the ventral interior.

Type species: *Halirhachis leonina* sp. nov.

Diagnosis.—Shell small, concavoconvex, semicircular, parvicostellate. Dental plates thin, short, low; ventral muscle field small, bilobed; a small platform immediately anterior to muscle field, undercut anteriorly, supported by high, thick median ridge limited to visceral area; pair of short, antero-laterally divergent ridges present in posterior part of shell. Cardinal process simple ridge, discrete from thick, widely divergent socket ridges; platform well-developed, tilting antero-ventrally above valve floor in medial part; median ridge high, thick.

Species included.—In addition to the genotype, the following species is probably assignable to the new genus: *Diambonia miaopoensis* Chang, 1983, Miaopo Formation, lower Caradocian, Yichang, Hubei Province.

Discussion.—The new genus differs from all other members of the superfamily Plectambonitoidea in its ventral interior. Its strong dorsal median ridge and well-developed platform are similar to those of *Bockelia* Neuman (in Neuman and Bruton 1989) and some representatives of *Leptellina* Ulrich and Cooper, 1936. Compared to the new genus, *Bockelia* differs in having a generally smaller cardinalia and *Leptellina* having a well-defined dorsal muscle field.

Halirhachis leonina sp. nov.

Fig. 10A–I; Table 7.

Sowerbyites? sp.; Wang and Yan 1978: 220, pl. 54: 5–7, 9.

Derivation of name: From the Latin, *leoninus*, of lion, referring to the type locality, Shizigou, meaning "lion's valley" in Chinese.

Holotype: NIGP 139102, ventral internal mould.

Type locality: Shizigou Valley near the Weixin County town, northeastern Yunnan, SW China.

Type horizon: Upper part of Shihtzupu Formation.

Material.—Five ventral internal, and four dorsal internal and one external moulds. Collection AFI1680.

Description.—Shell small, concavoconvex, semicircular, with maximum width along hinge line. Cardinal extremities acute, with small ears developed in some strongly transverse shells. Anterior commissure rectimarginate. Ventral valve strongly convex, deepest in central part of valve; interarea high, about one sixth of shell length, apsacline, with planar surface; beak erect; delthyrium narrow, covered by small, arched pseudodeltidium. Dorsal valve gently concave to flat in visceral area, with short, sharp geniculation; interarea low, hypercline, about one-sixteenth of shell length; notothyrium small, covered by narrow, arched chilidium. Parvicostellae mainly of two sizes; accentuated costae 7–9 in number; 4–5

← Fig. 9. **A**, **B**. *Onniella* sp. **A**. NIGP139084, dorsal internal mould (A_1) and latex cast (A_2) with local enlargement showing cardinalia (A_3). **B**. NIGP139085, dorsal internal mould. **C**–**P**. *Protoskenidioides weixinensis* sp. nov. **C**. NIGP139086, paratype, ventral internal mould (C_1) and latex cast (C_2). **D**. NIGP139087, paratype, ventral internal mould. **E**. NIGP139088, paratype, ventral internal mould. **F**. NIGP139089, paratype, latex cast of a ventral internal mould. **G**. NIGP139090, paratype, dorsal external mould (G_1) and latex cast (G_2). **H**. NIGP139091, paratype, latex cast of a dorsal internal mould. **I**. NIGP139092, paratype, dorsal internal mould of a juvenile shell. **J**. NIGP139093, paratype, dorsal internal mould. **K**. NIGP139094, paratype, dorsal internal mould. **L**. NIGP139095, paratype, dorsal internal mould (L_1) and latex cast (L_2). **M**. NIGP139096, paratype, dorsal internal mould. **N**. NIGP139097, holotype, dorsal internal mould (N_1) and latex cast (N_2). **O**. NIGP139098, paratype, dorsal internal mould of a juvenile shell. **P**. NIGP139099 and 139100, paratypes, two dorsal internal moulds. **Q**. *Leptellina spatiosa* sp. nov.; NIGP139101, paratype, dorsal internal mould (Q_1) and latex cast (Q_2) preserved together with a ventral internal mould of strophomenid gen. et sp. indet. (top right) and a dorsal external mould *Martellia ichangensis* Wang, 1956 (bottom left).

Table 7. Shell measurements (mm) of *Halirhachis leonina* gen. et sp. nov.

	L	W	L/W	L_1/L	W_1/W	L_1/W_1	L_2/L	W_2/W	L_3/L	α
4 dorsal valves										
AVG	2.09	4.57	0.46	0.57	0.48	0.56	0.20	0.30	0.06	117.5
STD	0.28	0.86	0.07	0.06	0.12	0.04	0.04	0.04	0.01	3.79
MIN	1.70	3.70	0.41	0.50	0.38	0.52	0.17	0.25	0.05	112
MAX	2.35	5.32	0.57	0.64	0.64	0.60	0.24	0.35	0.07	120
4 ventral valves										
AVG	2.78	5.67	0.49	0.22	0.18	0.62	–	–	0.17	–
STD	0.17	0.49	0.04	0.02	0.01	0.09	–	–	0.01	–
MIN	2.56	5.09	0.46	0.20	0.16	0.50	–	–	0.15	–
MAX	2.98	6.07	0.55	0.24	0.19	0.70	–	–	0.19	–

Table 8. Shell measurements (mm) of *Leptellina spatiosa* sp. nov.

	L	W	L/W	L_1/L	W_1/W	L_1/W_1	L_2/L	W_2/W	L_3/L	α
4 dorsal valves										
AVG	9.64	17.71	0.55	0.37	0.24	0.85	0.12	0.19	0.13	94.5
STD	0.87	2.90	0.05	0.05	0.02	0.11	0.03	0.02	?	0.58
MIN	8.47	14.96	0.48	0.34	0.22	0.71	0.09	0.18	?	94
MAX	10.32	21.52	0.59	0.45	0.27	0.96	0.15	0.21	?	95
4 ventral valves										
AVG	13.42	22.38	0.60	0.36	0.26	0.83	–	–	0.15	–
STD	1.01	2.53	0.04	0.08	0.02	0.20	–	–	0.02	–
MIN	11.94	19.56	0.56	0.28	0.24	0.60	–	–	0.12	–
MAX	14.20	25.19	0.65	0.46	0.28	1.09	–	–	0.17	–

finer costellae between adjacent costae at anterior margin. Concentric fila evenly spaced but usually poorly preserved.

Teeth small, wedge-shaped; dental plates short, thin; pair of blade-like plates present on both sides of teeth along hinge line, resembling accessory denticular ridges but lacking denticles. Muscle field bilobed, occupying one-fifth length and width of shell, bounded postero-laterally by dental plates; adductor scars small, slightly elevated, flanked by much larger diductor scars; small, short platform about 0.8–1 mm long, located immediately anterior to muscle field, with its surface covered by longitudinal tubercles, elevated anteriorly, supported by thick median ridge extending slightly beyond mid-length of shell. Pair of prominent ridge present in postero-lateral parts of valve, extending antero-laterally for about 1 mm, bearing anteriorly tilted, elongate tubercles; peripheral rim marked by discrete, anteriorly tilted tubercles.

Cardinalia about one-fifth length and one-third width of shell; cardinal process a simple ridge, mainly in posterior part of umbonal cavity; brachiophore processes short, rod-like; sockets small, narrow, deep, open antero-laterally; socket ridges thick, divergent from each other at about 120°; muscle field poorly impressed, about three-fifths length and one-half width of shell; outer, posterior pair of adductor scars large, longitudinally semicircular; inner, anterior pair subelliptical, less than half width of posterior pair; median ridge developed in anterior part of valve, terminating at its anterior junction with platform; platform highly raised and unsupported antero-medially (Fig 10H, I).

Discussion.—*Sowerbyites*? sp. illustrated by Wang and Yan (1978, no description) from the Miaopo Formation (lower Caradocian) of Yichang, Hubei Province, is virtually identical to the new species except for its weaker postero-lateral ridges in the ventral interior. *Diambonia miaopoensis* Chang, 1983 resembles *Halirhachis leonina* in most aspects of the ventral interior but differs in having a larger, more elongate shell and lacking accessory denticular ridges along the ventral hinge line.

Family Leptellinidae Ulrich and Cooper, 1936

Genus *Leptellina* Ulrich and Cooper, 1936

Leptellina spatiosa sp. nov.

Figs. 9Q, 10J–O, 11A–C; Table 8.

Derivation of name: From the Latin, *spatiosus*, large, spacious, referring to the large shell size of the new species.

Holotype: NIGP 139113, ventral internal and external moulds.

Type locality: Shizigou Valley near the Weixin County town, Yunnan Province, SW China.

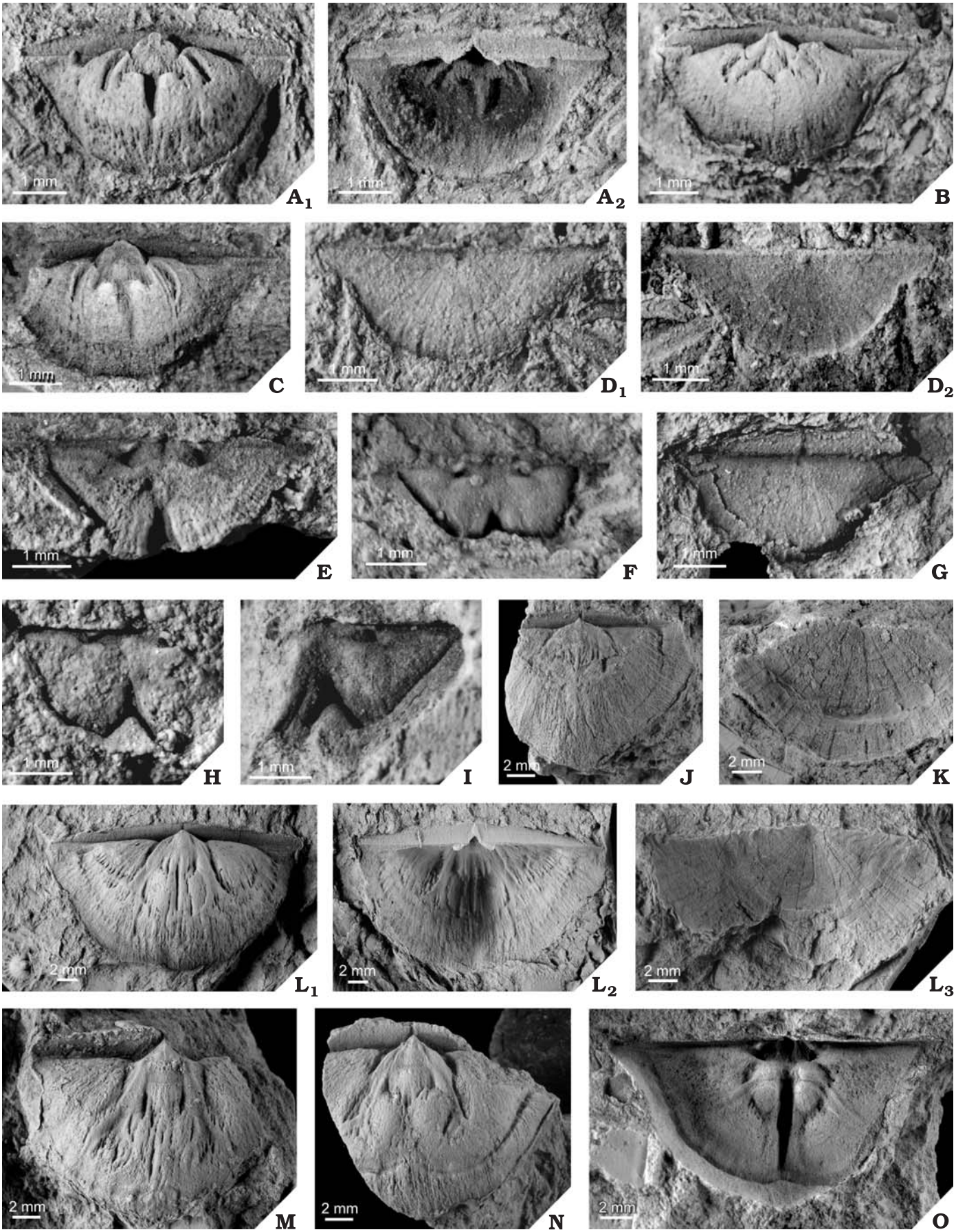
Type horizon: Upper part of Shihtzupu Formation.

Material.—Six ventral internal and three external, nine dorsal internal and seven external moulds. Collection AFI1680.

Diagnosis.—Shell medium to large, transverse, concavo-convex, with short dorsal geniculation; ventral muscle field comprising two widely separated lobes; cardinal process simple; dorsal muscle bounding ridges prominent; median ridge terminating at junction with platform margin.

Description.—Shell medium to large, concavoconvex, subsemicircular, with maximum width along hinge line. Cardinal extremities acute, with short ears in some shells (Figs. 10O, 11C). Anterior commissure rectimarginate. Ventral valve strongly convex, about three-fifths as long as wide; interarea high, about one-seventh of shell length, apsacline, with planar to weakly concave surface; delthyrium narrow, covered by arched pseudodeltidium. Dorsal valve about half as long as wide, unevenly concave, with short, sharp geniculation; interarea about one-eighth of shell length, planar,

Fig. 10. **A–I**. *Halirhachis leonina* gen. et sp. nov. **A**. NIGP139102, holotype, ventral internal mould (A_1) and latex cast (A_2). **B**. NIGP139103, paratype, ventral internal mould. **C**. NIGP139104, paratype, ventral internal mould. **D**. NIGP139105, paratype, dorsal external mould (D_1) and latex cast (D_2). **E**. NIGP139106, paratype, dorsal internal mould. **F**. NIGP139107, paratype, dorsal internal mould of a juvenile. **G**. NIGP139108, paratype, dorsal external mould. **H**. NIGP139109, paratype, dorsal internal mould. **I**. NIGP139110, paratype, dorsal internal mould. **J–O**. *Leptellina spatiosa* sp. nov. **J**. NIGP139111, paratype, ventral internal mould. **K**. NIGP139112, paratype, ventral external mould. **L**. NIGP139113, holotype, ventral internal (L_1) and external (L_3) moulds of a single valve, and latex cast (L_2) showing interior. **M**. NIGP139114, paratype, ventral internal mould. **N**. NIGP139115, paratype, ventral internal mould. **O**. NIGP139116, paratype, dorsal internal mould. →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hypercline; notothyrium small, covered by strongly convex chilidium. Unequal parvicostellae; 7–9 accentuated costae, with accentuated costellae inserting at one-third and two-thirds shell length respectively; 3–4 finer costellae between two adjacent accentuated costae or costellae. Concentric fila dense, evenly spaced; weak concentric rugae present in some specimens, especially in postero-lateral parts of shell.

Teeth small; dental plates absent; ventral muscle field bilobed, about one-third length and one-quarter width of shell; adductor scars subtriangular, deeply impressed, located in postero-medial part of muscle field, flanked by larger, much longer, antero-laterally divergent diductor scars; mantle canal system saccate; vascula media originating from anterior ends of diductor scars, extending antero-laterally for a short distance, then bifurcating into antero-medial and lateral branches and further into numerous branches; vascula genitalia located on both sides of muscle field, antero-laterally bounded by anteriorly pointed coarse tubercles; ventral platform variously developed, with its margin marked by low ridge or discrete septules.

Cardinalia stout, about one-eighth length and one-fifth width of shell; cardinal process simple, thick, ridge- or rod-like, projecting ventrally; sockets small, deep, open antero-laterally; inner socket ridges high, discrete from cardinal process, divergent from each other at 94–95°, terminating into rod-like processes. Muscle field elevated, about one-third length and one-quarter width of shell, with high, thick, postero-lateral bounding ridges and weak antero-lateral ridges; anterior pair of adductor scars slightly larger and more elongate than posterior pair. Median ridge thick, highest at anterior end of muscle field, terminating at junction with anterior margin of platform. Platform semicircular in outline, with its marginal ridge ranging from low to relatively high and tilted towards shell margin. Vascula media beginning from anterior ends of adductor scars, extending along median ridge to platform margin, then turning postero-laterally to form many branches; vascula myaria originating from junction of two pairs of adductor scars, extending and branching antero-laterally.

Variability.—The margin of the ventral platform is usually marked by a row of anteriorly projecting septules but, in some specimens, it is a low, continuous ridge (Fig. 10N). The ventral muscle bounding ridges are typically weak but may become high and thick, particularly in specimens with a well-developed ventral platform margin. In some ventral interior a median septum is present in the central part of the valve but in some others it is absent. The margin of the dorsal platform is normally a simple ridge tilted towards shell margin, but rarely the platform is poorly defined (Fig. 9Q). The irregular concentric rugae are visible only in some specimens.

Discussion.—Most of the known species of *Leptellina* are Darriwilian in age (Cocks and Rong 1989), but none of these have the large, bilobed ventral muscle field and the prominent bounding ridges of dorsal muscle field (resembling a bema) of the new species. Various species of *Leptellina* from North America (Cooper 1956) and Scotland (Williams 1962), as well as those from Bohemia (lower Caradocian, Havlíček 1967), for example, have a comparatively smaller ventral muscle field. *Leptellina qianjiangensis* (Liang in Liu et al. 1983) from the Changwu Formation (middle Ashgillian) of western Zhejiang Province (Cocks and Rong, 1989) is similar to *L. spatiosa*, especially in its large and bilobed ventral muscle field, but differs in having a more elongate and convex ventral valve, more numerous accentuated costae and costellae, and a much stronger dorsal platform. *Lepidomena pulchra* Laurie (1991) from the base of the Lower Limestone Member of the Benjamin Limestone (Caradocian) of Tasmania has a similar ventral muscle field and mantle canal system, but it has a less transverse shell, more numerous accentuated costae, and a high and blade-like cardinal process, and lacks dorsal muscle bounding ridges.

Leptellina sp.

Fig. 11D–J; Table 9.

Material.—Five ventral internal, and three dorsal internal and two external moulds.

Diagnosis.—Similar to *L. spatiosa* sp. nov., but subcircular in outline. Ventral muscle field subtriangular to subpentagonal; two trunks of vascula media long, parallel; pair of crescent-shaped knobs near mid-length of ventral valve. Dorsal valve gently concave with short, sharp geniculation.

Description.—Shell medium-sized, concavoconvex, subcircular, with maximum width along hinge line. Cardinal extremities rounded to subrectangular. Ventral valve nearly three-quarters as long as wide; interarea apsacline, about one-seventh of shell length; delthyrium narrow, covered by arched pseudodeltidium. Visceral area of dorsal valve gently concave; geniculation short, sharp; dorsal interarea low, planar, hypercline, less than one-tenth of shell length. Unequal parvicostellae.

Teeth stout, projecting anteriorly from hingeline as wedge-shaped knobs, with crenulated upper surfaces; dental plates absent; muscle field deeply impressed, subtriangular to subpentagonal, about one-quarter length and width of shell; adductor scars triangular, elevated, flanked by elongate diductor scars; mantle canal system saccate (Fig.

→

Fig. 11. **A**–**C**. *Leptellina spatiosa* sp. nov. **A**. NIGP139117, paratype, dorsal internal mould (A_1) and latex cast (A_2). **B**. NIGP139118, paratype, dorsal internal mould. **C**. NIGP139119, paratype, dorsal external mould. **D**–**J**. *Leptellina* sp. **D**. NIGP139120, ventral internal mould. **E**. NIGP139121, ventral internal mould. **F**. NIGP139122, ventral internal mould (F_1) and latex cast (F_2). **G**. NIGP139123, ventral internal mould. **H**. NIGP139124, dorsal internal mould. **I**. NIGP139125, dorsal internal mould. **J**. NIGP139126, dorsal external mould. **K**–**N**. Leptellinidae gen. et sp. nov. (to be erected by Zhan and Jin in press). **K**. NIGP139127, ventral internal (K_1) and external (K_2) moulds. **L**. NIGP139128, dorsal internal mould. **M**. NIGP139129, ventral internal mould. **N**. NIGP139130, ventral internal mould preserved together with a dorsal internal mould of *Protoskenidioides weixinensis* sp. nov. (top).

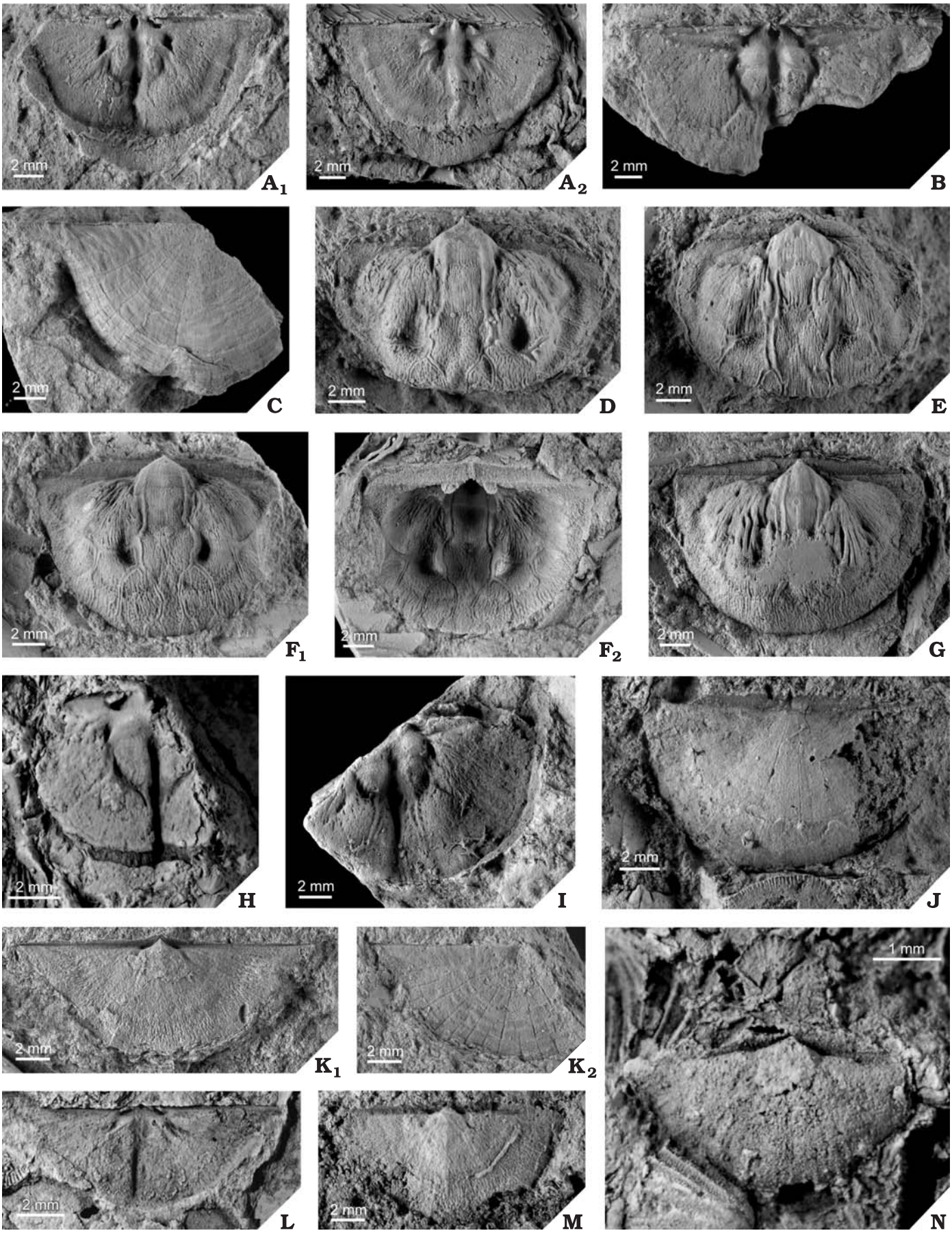
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Table 9. Shell measurements (mm) of *Leptellina* sp.

	L	W	L/W	L_1/L	W_1/W	L_1/W_1	L_2/L	W_2/W	L_3/L	α
2 dorsal valves										
AVG	9.39	13.77	0.69	0.38	0.32	0.82	0.13	0.28	?	100
STD	1.61	3.75	0.07	0.01	0.01	0.10	0.01	0.01	?	?
MIN	8.25	11.11	0.64	0.37	0.31	0.75	0.12	0.27	?	?
MAX	10.52	16.42	0.74	0.38	0.33	0.89	0.14	0.28	?	?
4 ventral valves										
AVG	11.11	15.18	0.73	0.25	0.27	0.68	–	–	0.14	–
STD	0.52	1.14	0.05	0.05	0.02	0.12	–	–	0.03	–
MIN	10.66	14.32	0.70	0.19	0.24	0.56	–	–	0.11	–
MAX	11.67	16.75	0.80	0.29	0.28	0.79	–	–	0.17	–

Table 10. Shell measurements (mm) of Leptellinidae gen. et sp. nov. (to be erected by Zhan and Jin in press).

	L	W	L/W	L_1/L	W_1/W	L_1/W_1	L_2/L	W_2/W	L_3/L	α
1 dorsal valve										
NIGP 139128	4.49	11.73	0.38	0.45	0.24	0.70	0.10	0.16	0.04	127
5 ventral valves										
AVG	5.10	10.82	0.48	0.24	0.19	0.63	–	–	0.12	–
STD	2.20	5.30	0.06	0.02	0.03	0.02	–	–	0.02	–
MIN	2.39	4.79	0.39	0.21	0.15	0.61	–	–	0.10	–
MAX	7.32	17.80	0.53	0.27	0.22	0.65	–	–	0.14	–

11D–F), clearly impressed; vascula media beginning from anterior ends of diductor scars, extending anteriorly parallel to each other for 3–4 mm, then bifurcating in anterior and lateral directions, with each branch producing numerous fine branchlets towards shell margins; vascula genitalia in postero-lateral parts of valve marked by antero-laterally directed ridges and striae. Two cresent or droplet-shaped knobs developed near mid-length of shell, immediately outside main trunks of vascula media (Fig. 11D, F).

Cardinalia about one-eighth length and one-quarter width of shell; cardinal process thick, ridge- or rod-like, projecting ventrally. Inner socket ridges divergent from each other at about 100°, terminating in rod-like processes. Muscle bounding ridges well-developed, comprising two segments on each side, forming bema-like structure; muscle field subelliptical in outline, about two-fifths length and one-third width of shell; posterior pair of adductor scars circular; anterior pair more elongated; median ridge originating immediately anterior of notothyrial platform, highest at anterior part of muscle field, and terminating at junction with anterior margin of platform; margin of platform marked by thick ridge perpendicular to valve floor.

Discussion.—*Leptellina* sp. from Weixin is similar to *L. qianjiangensis* (Liang in Liu et al. 1983) in shell outline and convexity, but the latter has weaker muscle bounding ridges in the dorsal valve, a much stronger platform, a bilobed ventral muscle field, and much shorter main trunks of ventral vascula media. The pair of knobs have not been observed in other species of *Leptellina*, and their morphological function is unknown. *Davidsonia* Bouchard-Chantereaux, 1849 has a pair of similar structures called "ventral cones" (Copper 1978, 1996; Havlíček 1967, 1998), which commonly bear spiralial grooves. No such grooves are associated with the knobs of *Leptellina* sp. The taxonomic position of this species cannot be determined until more specimens become available for studying the intra-population variation, particularly regarding the development of the pair of ventral knobs.

Leptellinidae gen. et sp. nov. (to be erected by Zhan and Jin in press)

Figs. 11K–N, 12A; Table 10.

Material.—Five ventral internal and two external, and two dorsal internal moulds.

Discussion.—Compared to type material from Changning, southeastern Sichuan Province (Zhan and Jin in press), the Weixin shells are more transverse, and have a weaker but longer dorsal median septum (Fig. 11L), and more weakly impressed ventral muscle field without bounding ridges (Fig. 11K_1, M). All the other internal and external characters of the specimens from both localities are identical (see Zhan and Jin in press for detailed description).

Leptellinidae gen. nov. (to be erected by Zhan and Jin in press), sp.

Fig. 12B–D; Table 11.

Material.—Three ventral external, and one dorsal internal moulds.

Description.—Shell small to medium, concavoconvex, subsemicircular, with maximum width along hinge line. Cardinal extremities acute to subrectangular. Anterior commissure rectimarginate. Ventral valve gently convex, deepest around umbo. Dorsal valve unevenly concave with greatest concavity at junction between visceral and marginal area of shell; interarea low, hypercline. Unequal parvicostellae; 7–9 accentuated costae, with fine costellae inserting at 2.5 mm and 5 mm growth stage respectively; 4–5 fine costellae between

Fig. 12. **A**. Leptellinidae gen. et sp. nov. (to be erected by Zhan and Jin in press); NIGP139131, ventral internal mould (A_1) and latex cast (A_2) preserved together with a bryozoan colony (top left). **B**–**D**. Leptellinidae gen. nov., sp. **B**. NIGP139132, dorsal internal mould (B_1) and latex cast (B_2). **C**. NIGP139133, ventral external mould (C_1) and latex cast (C_2). **D**. NIGP139134, ventral external mould. **E**–**M**. *Calyptolepta huanghuaensis* (Chang, 1983). **E**. NIGP139135, ventral internal mould. **F**. NIGP139136, broken ventral internal mould. **G**. NIGP139137, dorsal internal mould. **H**. NIGP139138, holotype, dorsal internal mould (H_1) and latex cast (H_2) with local enlargement (H_3) showing cardinalia and bema. **I**. NIGP139139, dorsal external mould. **J**. NIGP139140, dorsal internal mould of a juvenile shell. **K**. NIGP139141, dorsal internal mould. **L**. NIGP139142, two dorsal internal moulds. **M**. NIGP139143, dorsal internal mould. **N**. *Leptestiina veturna* sp. nov.; NIGP139144, paratype, ventral internal mould. →

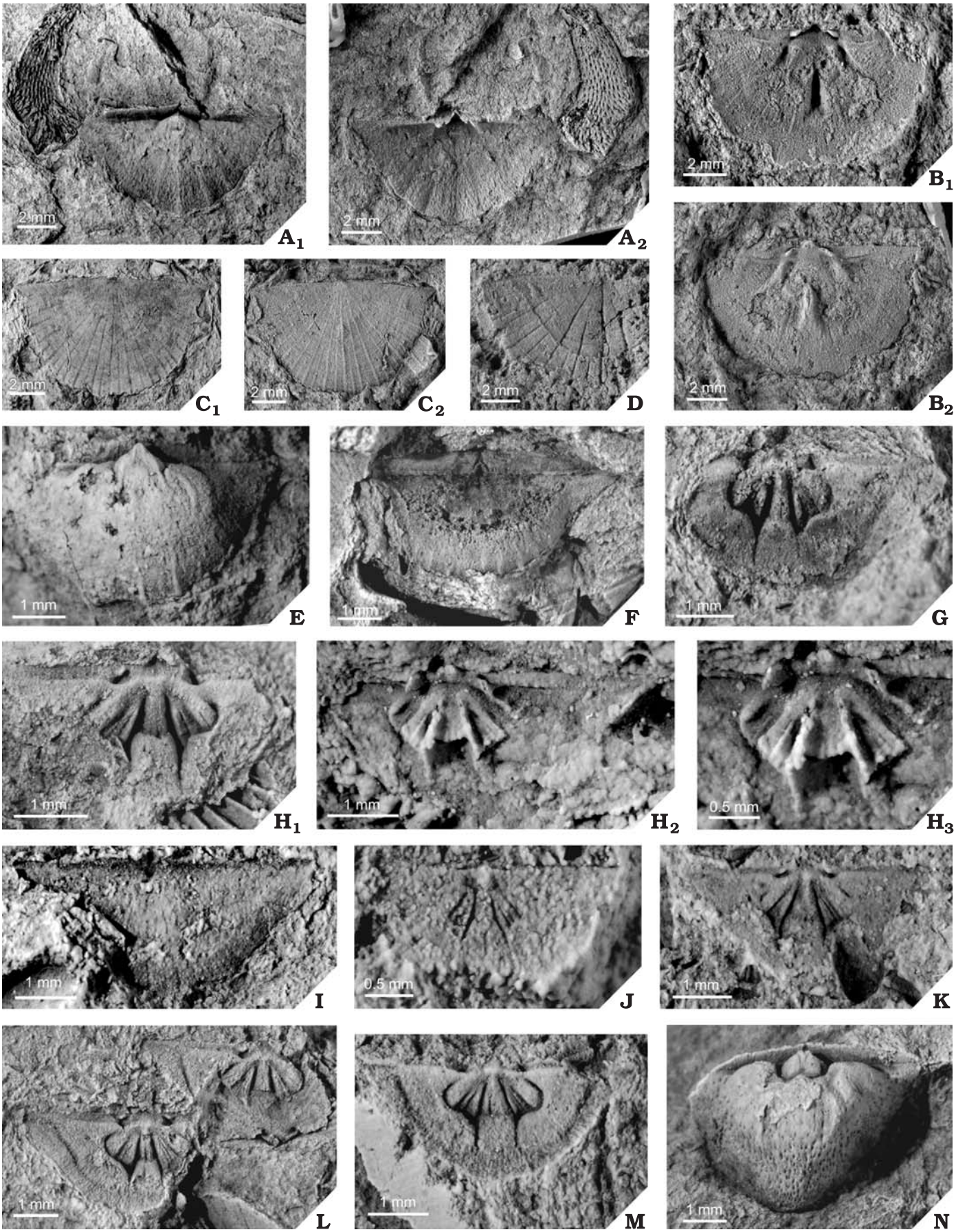
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Table 11. Shell measurements (mm) of Leptellinidae gen. nov., sp.

	L	W	L/W	L_1/L	W_1/W	L_1/W_1	L_2/L	W_2/W	L_3/L	α
1 dorsal valve										
NIGP 139132	6.58	10.68	0.62	0.35	0.26	0.82	0.11	0.21	0.04	120
2 ventral valves										
NIGP 139133	6.72	10.95	0.61	?	?	?	–	–	?	–
07b	3.48	5.08	0.69	?	?	?	–	–	?	–

Table 12. Shell measurements (mm) of *Calyptolepta huanghuaensis* (Chang 1983).

	L	W	L/W	L_1/L	W_1/W	L_1/W_1	L_2/L	W_2/W	L_3/L	α
6 dorsal valves										
AVG	2.10	4.40	0.48	0.45	0.36	0.60	0.15	0.24	0.11	104.7
STD	0.42	0.98	0.04	0.04	0.06	0.09	0.04	0.04	0.04	29.04
MIN	1.38	2.91	0.41	0.38	0.30	0.50	0.09	0.19	0.06	82
MAX	2.66	5.60	0.54	0.47	0.46	0.72	0.18	0.30	0.16	157
2 ventral valves										
AVG	3.00	4.73	0.59	0.23	0.20	0.68	–	–	0.19	–
STD	0.30	0.78	0.02	0.02	0.02	0.02	–	–	0.04	–
MIN	2.78	4.18	0.57	0.21	0.19	0.66	–	–	0.16	–
MAX	3.21	5.28	0.61	0.24	0.21	0.69	–	–	0.21	–

two adjacent coarse costae or costellae. Concentric fila evenly spaced, about 11–12 per mm.

Cardinalia about one-ninth length and one-fifth width of shell; cardinal process a simple knob, projecting mainly ventrally; sockets small, narrow, deep, open antero-laterally; socket ridges thick, discrete from cardinal process, divergent from each other at about 120°, and terminating as short, rod-like processes. Muscle field slightly elevated, about one-third length and one-quarter width of shell; outer, posterior pair of adductor scars elliptical, with thick, high lateral bounding ridges; inner, anterior pair smaller, subcircular. Median ridge originating between anterior pair of adductor scars, limited to central part of shell. Platform marked by weak, discrete, anteriorly or antero-laterally tilted small septules.

Discussion.—This species differs from Leptellinidae gen. et sp. nov. (to be erected by Zhan and Jin in press) in having a much less transverse and more gently concavoconvex shell. More specimens, particularly ventral valves, are needed for identification to species level.

Family Grorudiidae Cocks and Rong, 1989

Genus *Calyptolepta* Neuman, 1976

Calyptolepta huanghuaensis (Chang, 1983)

Fig. 12E–M; Table 12.

Bilobia huanghuaensis sp. nov.; Chang 1983: 477, pl. 1: 22.

Material.—Two ventral internal and three external, 10 dorsal internal and 10 external moulds.

Description.—Shell small, concavoconvex, subsemicircular; maximum width along hinge line. Cardinal extremities acute, with long, narrow ears. Anterior commissure rectimarginate. Ventral valve evenly, strongly convex, deepest at mid-length of shell; interarea relatively high, about one-fifth length of shell, apsacline, with planar or slightly curved surface (Fig. 12E, F); delthyrium narrow; pseudodeltidium arched. Dorsal valve about half as long as wide; unevenly concave, deepest centrally (Fig. 12G, L, M); interarea about one-tenth length of shell, catacline to hypercline; notothyrium small; chilidium convex. Unequal parvicostellae; 9–11 accentuated costae, bifurcating twice at about 1.0 mm and 1.5 mm growth stages respectively.

Teeth small, wedge-shaped; dental plates thin, short. Muscle field clearly impressed, bilobed, about one-fifth length and width of shell; adductor scars small, subtriangular, slightly elevated, located in postero-medial part of muscle field; diductor scars elongate, widely divergent from each other. Vascula media saccate, originating from anterior ends of diductor scars.

Cardinalia stout, about one-seventh length and one-quarter width of shell; cardinal process undercut, simple knob or trifid, projecting ventrally (Fig. 12H_1–H_3); sockets small, narrow, open antero-laterally; socket ridges thick, discrete from cardinal process, terminating as blade-like processes. Bema well-developed, elevated, undercut anteriorly, about one-half length and one-third width of shell; central side septa beginning in front of notothyrial cavity, highest at anterior margin of bema; one or two pairs of longitudinal transmuscle ridges weak, short, developed mainly in anterior half of adductor scars; inner pair of adductor scars slightly smaller but higher than outer pair; connecting plate between central side septa variously developed, confined to bema, undercut (Fig. 12H_2, H_3). Platform marked by closely arranged but discrete longitudinal septules, particularly on both sides (Fig. 12L, M). Shell marginal area strongly curved dorsally, covered by dense crenulations and pseudopunctae.

Variability.—The species shows a number of ontogenetic variations. With increasing shell size, the bema becomes stronger and more elevated, the ratio of dorsal interarea height to shell length increases, and the angle between the pair of socket ridges decreases. The connecting plate between central side septa is absent in juveniles (e.g., Fig. 12J) but well-developed in most adults (Fig. 12H_3). There are also some intrapopulation variations in the present collection. The central side septa, for example, may change from poorly developed (Fig. 12K) to prominent (Fig. 12H, L, M) in shells of similar sizes. The length of central side septa is similarly variable. The number and strength of transmuscle ridges on bema are different from one individual to another or even from one side to another in a single valve (e.g., Fig. 12K, L).

Discussion.—The holotype of this species from the Miaopo Formation (lower Caradocian) of Yichang, western Hubei Province, is about 9 mm long and 12 mm wide, nearly three

or four times as large as the Weixin material, but all the external and internal characters of the specimens from both localities are identical. The dorsal internal structures, particularly the undercut cardinal process and the strong central side septa, are different from those of *Bilobia* Cooper, 1956. Some specimens of *Calyptolepta rarum* (Neuman 1976) are similar to the Weixin shells of *C. huanghuaensis* in having an undercut cardinal process, a pair of strong side septa, and a highly elevated and undercut connecting plate.

The type species, *C. diaphragma* Neuman, 1976 from the Middle Ordovician (Darriwilian) tuffs of Newfoundland, can be distinguished from *C. huanghuaensis* by having a more prominent dorsal platform and more numerous costellae. *Calyptolepta chengkouensis* (Xu, Rong, and Liu 1974) reported from various Middle Ordovician rocks of South China (Xu and Liu 1984; Zhan and Jin in press) is different from *C. huanghuaensis* in its more numerous costellae, smaller dorsal platform, and stronger ventral platform.

Family Leptestiidae Öpik, 1933

Genus *Leptestiina* Havlíček, 1952

Leptestiina veturna sp. nov.

Figs. 12N, 13A–I; Table 13.

Derivation of name: From the Latin *veturnus*, old, referring to the lowest known range of the genus represented by the new species.

Holotype: NIGP 139147 (Fig. 13C), ventral internal mould.

Type locality: Shizigou Valley near the Weixin County town, Yunnan Province.

Type horizon: Upper part of Shihtzupu Formation.

Material.—Thirteen ventral internal and four external, two dorsal internal and nine external moulds. Collection AFI1680.

Diagnosis.—Small, weakly transverse, strongly concavoconvex shells of *Leptestiina*, with relatively sparse accentuated costae.

Description.—Shell small, concavoconvex, subsemicircular to subcircular; maximum width along hinge line. Cardinal extremities acute to rounded. Anterior commissure rectimarginate. Ventral valve about three-quarters as long as wide, strongly convex, deepest in central part; visceral area more convex than marginal area of shell; interarea high, about one-eighth length of shell, apsacline with planar or slightly curved surface; delthyrium relatively wide, covered by weakly arched pseudodeltidium in its posterior two-thirds (Fig. $13C_2$). Dorsal valve about three-fifths as long as wide, deeply concave, with greatest concavity at junction between visceral area and geniculation; interarea low, shorter than one-tenth length of shell, anacline; notothyrium narrow, short, covered by arched chilidium (Fig. $13H_2$). Unequal parvicostellae; 7–9 accentuated costae, with finer costellae inserting three times; about 9–11 fine costellae between two adjacent costae at shell anterior margin. Concentric fila evenly spaced, about 15–16 per mm.

Teeth small, wedge-shaped; dental plates short, high, subparallel, continuous with anterior bounding ridge of muscle field. Muscle field subtriangular to subpentagonal, about one-fifth length and width of shell, elevated anteriorly; adductor scars small, narrow, mainly in posteromedial part of muscle field, separated from diductor scars by pair of thin plates in some shells (Fig. 13D); diductor scars much larger, subcircular, surrounding adductor scars laterally and anteriorly. Mantle canal system saccate; vascula media originating from anterior ends of diductor scars, with long, straight, weakly divergent main trunks. Bema relatively large, well-developed; dorsal platform marked by weak, discrete septules.

Table 13. Shell measurements (mm) of *Leptestiina veturna* sp. nov.

	L	W	L/W	L_1/L	W_1/W	L_1/W_1	L_3/L
4 dorsal valves							
AVG	3.54	5.69	0.62	?	?	?	0.06
STD	0.18	0.40	0.06	?	?	?	0.02
MIN	3.42	5.24	0.55	?	?	?	0.05
MAX	3.80	6.21	0.68	?	?	?	0.08
8 ventral valves							
AVG	3.74	5.15	0.72	0.20	0.22	0.65	0.13
STD	0.63	0.69	0.04	0.02	0.02	0.05	0.02
MIN	2.71	4.15	0.65	0.16	0.20	0.57	0.11
MAX	4.79	6.26	0.77	0.23	0.25	0.72	0.16

Discussion.—The convexity of ventral valves has a certain degree of variation: the visceral area is usually much more convex than the shell marginal area, giving the valve a galeate shape (e.g., Fig. $13E_1$), but some shells are almost evenly convex (Figs. 12N, $13C_1$).

There are seven species assigned to *Leptestiina*, ranging from early Caradocian to mid-Ashgillian (Cocks and Rong 1989, 2000). In China, previously known forms of the genus are associated with the *Foliomena* fauna in the upper Pingliang (upper Caradocian) and the Linhsiang (lower Ashgillian) formations (Fu 1982; Rong et al. 1994). The new species of late Darriwilian age is probably the oldest known of the genus. In comparison, the type species, *L. prantli* Havlíček, 1952 from the Králův Dvůr Formation (middle Ashgillian) of Bohemia, can be distinguished by its more transverse shell, more numerous costae, and lower shell convexity. *Leptestiina* cf. *prantli* from the Linhsiang Formation of western Guizhou Province (Rong et al. 1994) has a strongly transverse shell.

Superfamily Strophomenoidea King, 1846

Family Strophomenidae King, 1846

Strophomenid gen. et sp. indet.

Fig. 13J; Table 14.

Material.—One dorsal internal mould.

Description.—Shell medium-sized, subsemicircular, gently concave with nearly planar visceral area. Interarea low, catacline. Notothyrium relatively wide, covered by thin, arched chilidium (Fig. $13J_2$). Cardinalia about one-tenth length and one-third width of shell; two lobes of cardinal pro-

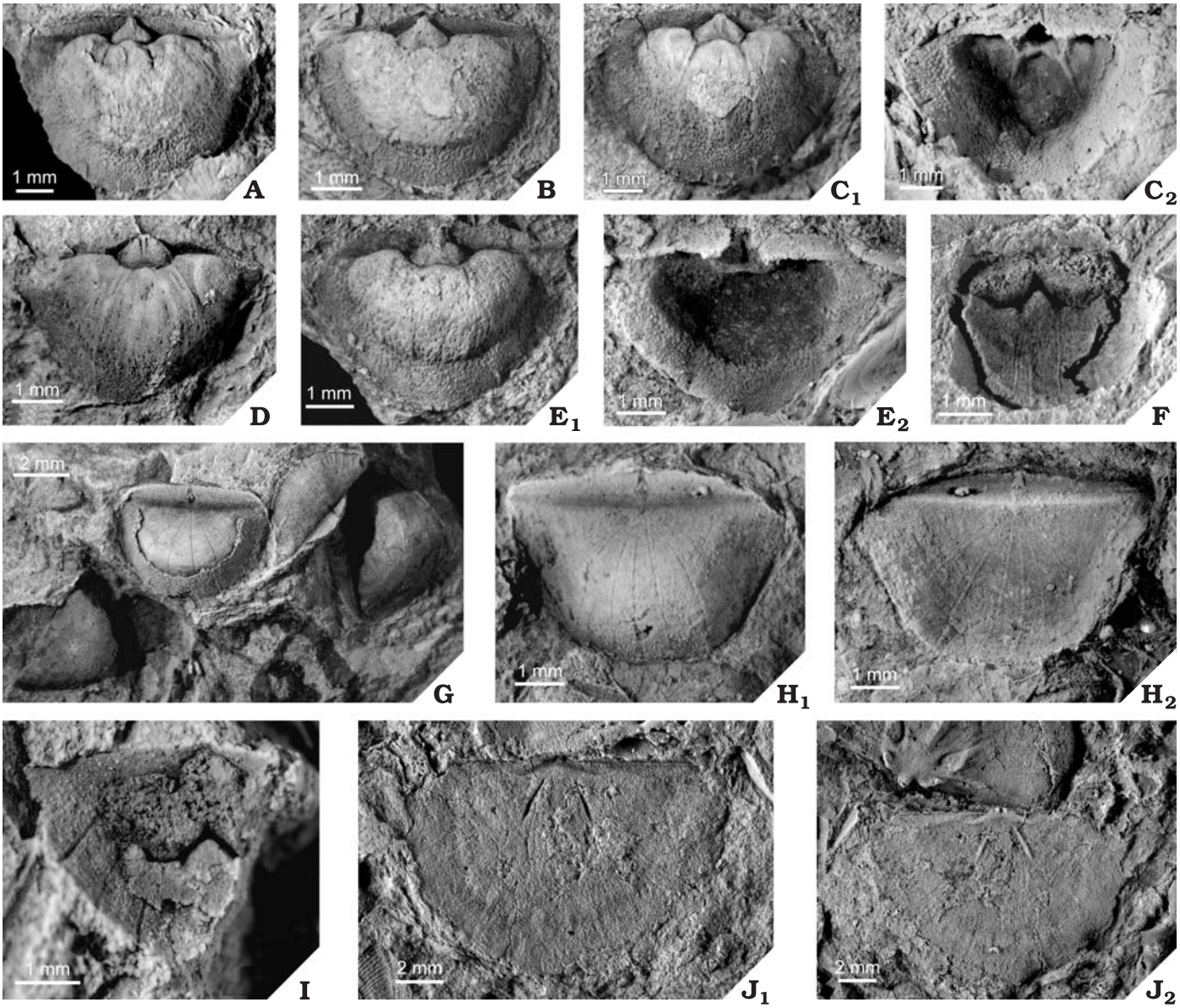


Fig. 13. **A**–**I**. *Leptestiina veturna* sp. nov. **A**. NIGP139145, paratype, ventral internal mould. **B**. NIGP139146, paratype, ventral internal mould. **C**. NIGP139147, holotype, ventral internal mould (C_1) and latex cast (C_2). **D**. NIGP139148, paratype, ventral internal mould. **E**. NIGP139149, paratype, ventral internal mould (E_1) and latex cast (E_2). **F**. NIGP139150, paratype, dorsal internal mould. **G**. NIGP139151, paratype, three dorsal external moulds, with dorsal external mould of Leptellinidae gen. et sp. nov. (to be erected by Zhan and Jin in press) (second from right). **H**. NIGP139152, paratype, dorsal external mould (H_1) and latex cast (H_2); note also ventral interarea. **I**. NIGP139153, paratype, broken dorsal internal mould. **J**. Strophomenid gen. et sp. indeterminate; NIGP139154, dorsal internal mould (J_1) and latex cast (J_2), together with a dorsal internal mould of *Leptellina spatiosa* sp. nov. (top).

cess small, discrete, rod-like, sitting on highly elevated notothyrial platform, projecting ventrally and posteriorly; sockets shallow, open antero-laterally; socket ridges thick, low, divergent from each other at 129 degrees, curving postero-laterally. Muscle field weakly impressed, bounded postero-laterally by pair of thin side septa.

Discussion.—The only dorsal valve available has Type A cardinalia (Rong and Cocks 1994; Cocks and Rong 2000) and weak transmuscle ridges, which confirm its affinity to Strophomenidae. *Platymena*? *mutabilis* Xu, Rong, and Liu, 1974 from the Shihtzupu Formation of northern Guizhou Province is similar to the Weixin specimen in its nearly flat dorsal valve with similar cardinalia and postero-lateral muscle bounding ridges, but differs in having a semicircular outline and a low, thin, dorsal median septum.

Order Billingsellida Schuchert, 1893
Suborder Clitambonitidina Öpik, 1934
Superfamily Polytoechioidea Öpik, 1934
Family Polytoechiidae Öpik, 1934
Genus *Martellia* Wirth, 1936
Martellia ichangensis Wang, 1956

Fig. 14A–J; Table 15.

Table 14. Shell measurements (mm) of strophomenid gen. et sp. indet.

Specimen	L	W	L/W	L_1/L	W_1/W	L_1/W_1	L_2/L	W_2/W	L_3/L	α
NIGP 139154	9.13	13.38	0.68	?	?	?	0.09	0.29	?	129

Table 15. Shell measurements (mm) of *Martellia ichangensis* Wang, 1956.

	L	W	L/W	L_1/L	W_1/W	L_1/W_1	L_2/L	W_2/W	L_3/L	α
7 dorsal valves										
AVG	13.32	15.97	0.83	0.54	0.50	0.89	0.26	0.63	0.11	114.7
STD	1.89	2.01	0.02	0.04	0.03	0.09	0.02	0.03	0.02	3.25
MIN	11.09	13.85	0.80	0.48	0.45	0.79	0.24	0.58	0.10	111
MAX	16.28	18.58	0.88	0.60	0.53	1.07	0.29	0.66	0.15	119
2 ventral valves										
AVG	15.80	17.05	0.93	0.43	0.24	1.68	–	–	0.36	–
STD	1.00	0.64	0.02	0.03	0.003	0.07	–	–	0.01	–
MIN	15.09	16.59	0.91	0.40	0.23	1.63	–	–	0.35	–
MAX	16.50	17.50	0.94	0.45	0.24	1.73	–	–	0.37	–

Martellia ichangensis sp. nov.; Wang 1956: 11, pl. 2: 1–5.
Martellia ichangensis Wang, 1956; Xu et al. 1974: 148, pl. 65: 5–7.
Martellia ichangensis Wang, 1956; Zeng 1977: 47, pl. 15: 7, 8.
Martellia orbicularis sp. nov.; Zeng 1977: 47, pl. 15: 10–12.
Martellia ichangensis Wang, 1956; Xu et al. 1978: 296, pl. 116: 14.
Martellia ichangensis Wang, 1956; Xu and Liu 1984: 196, pl. 12: 27–29, 31; text-fig. 12.

Material.—Seven ventral internal and four external, 16 dorsal internal and seven external moulds.

Description.—Shell medium-sized, subcircular, ventribiconvex, with maximum width near one-third shell length; cardinal extremities rectangular to rounded; anterior commissure rectimarginate to weakly uniplicate. Ventral valve nearly as long as wide, strongly convex, deepest in umbonal area; interarea very high, slightly greater than one-third length of shell, apsacline, with planar surface bearing fine striae parallel to hinge line; beak erect; delthyrium small, covered by thick, arched deltidium; sulcus weak, narrow, developed in anterior third of shell. Dorsal valve evenly convex, deepest around umbo; interarea low, about one-tenth of shell length, anacline, with planar to gently concave surface; notothyrium narrow, covered by thick and strongly arched chilidium; fold low, narrow, present in anterior third of valve. Costellae equal-sized, dense, hollow, increasing anteriorly by bifurcation and intercalation, about 5 per mm at 5 mm growth stage; concentric fila dense, evenly spaced, interrupting costellae; 5–7 concentric lamellae unevenly spaced.

Teeth stout; dental plates high, thin, inclined basomedially, becoming subparallel at their bases, extending anteriorly slightly beyond muscle field; delthyrial chamber large, deep. Muscle field strongly elongate, about two-fifths length and one-quarter width of shell, slightly elevated; pair of elongate-oval adductor scars located in posterior part of muscle field, enclosed laterally and anteriorly by larger and more elongate-oval diductor scars. Median ridge low, extending through muscle field and beyond for two-thirds of shell length. Mantle canal system saccate, clearly impressed; vascula media originating from anterior ends of diductor scars, extending parallelly for short distance before dividing into many branches medially and laterally.

Cardinalia large, about one-quarter length and three-fifths width of shell; cardinal process thick, ridge-like, projecting posteriorly; notothyrial platform strongly elevated, transversely continuous with thick socket ridges to form free-hanging transverse plate supported by strong median ridge (Fig. 14F_2); sockets deep, narrow, open laterally; socket ridges divergent at about 115°. Muscle field clearly defined, about one-half length and width of shell; outer, posterior pair of adductor scars elongate, subtriangular, strongly divergent, separated from inner, anterior pair by two thin, long side septa; anterior, inner pair of adductor scars much larger, more elongate, subtriangular, bearing two weak, longitudinal transmuscle ridges. Median ridge (myophragm) high, thick. Mantle canal system apocopate; vascula media dividing into many branches shortly after originating from anterior end of muscle field.

Discussion.—This species has been reported from the upper Dawan and Meitan formations (upper Arenigian) at many localities on the Upper Yangtze Platform from central to southwestern China (e.g., Zeng 1977; Xu et al. 1978; Xu and Liu 1984). It is characterized by a subcircular shell outline and weak anterior fold and sulcus. *Martellia fenxiangensis* Zeng (1977: pl. 15: 4–6) from the upper Dawan Formation (upper Arenigian) of Yichang, Hubei Province, has a weak fold and sulcus, but its shell is elongate. *Martellia orbicularis* Zeng (1977), from the same type locality and horizon as *M. ichangensis* and *M. fenxiangensis*, was established on the basis of its nearly circular shell outline without fold and sulcus, but Zeng's (1977: pl. 15: 10–12) illustrated ventral valve clearly has a weak and narrow sulcus and its internal structures are identical to those of *M. ichangensis*. This implies that *M. orbicularis* is a junior synonym of *M. ichangensis*.

During ontogeny, the shells of *M. ichangensis* tend to become less transverse due to accelerated longitudinal allometric growth. The two relatively small ventral internal moulds (Fig. 14I, J), for example, are somewhat more transverse than other ventral valves in the same population (e.g., Fig. 14A, B).

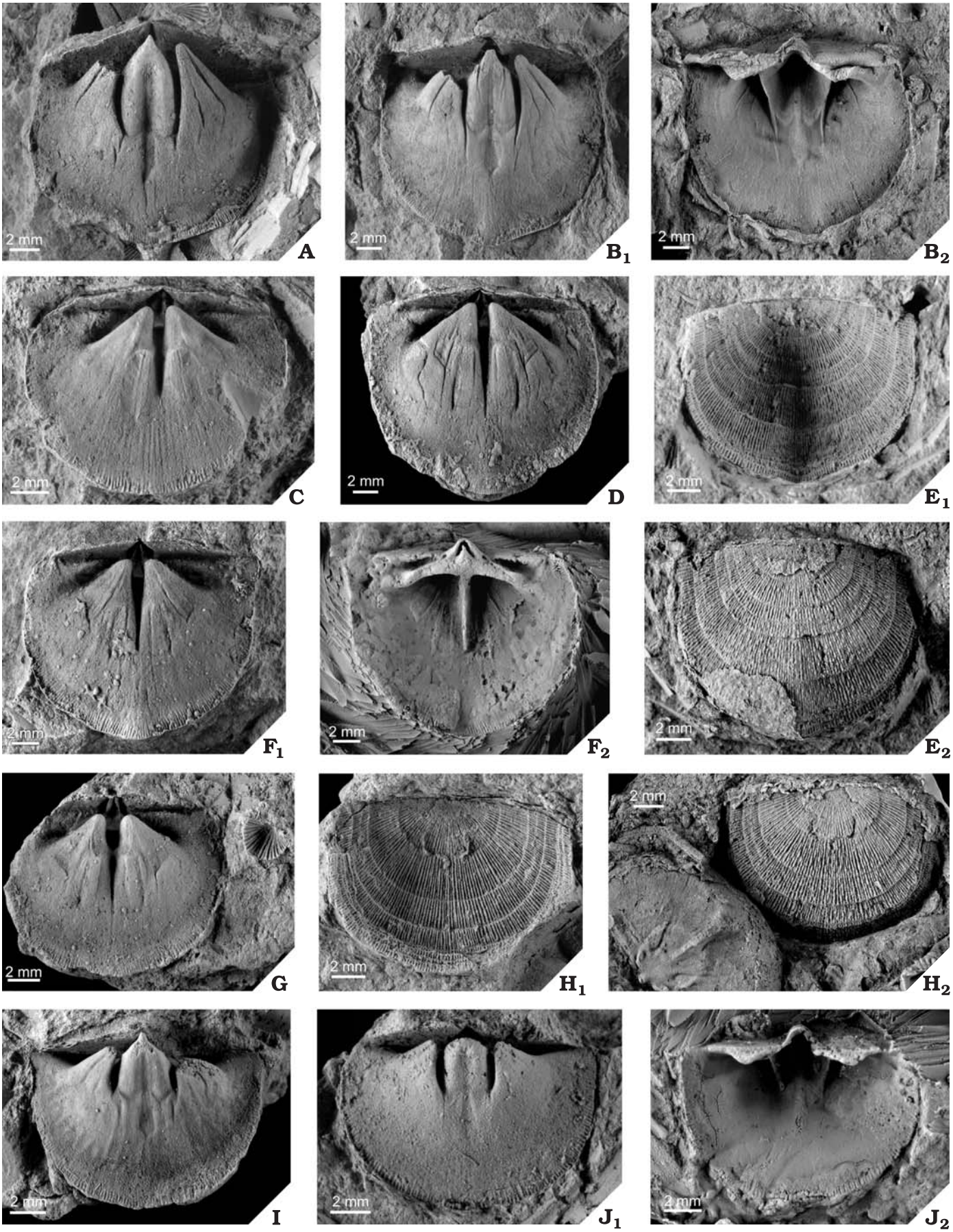
Genus *Tritoechia* Ulrich and Cooper, 1936

Tritoechia sp.

Fig. 15A–C; Table 16.

Material.—Four ventral internal and three dorsal internal moulds.

Description.—Shell small, ventribiconvex, subsemicircular (about three-fifths as long as wide), with maximum width along hinge line; cardinal extremities acute to rectangular; anterior commissure rectimarginate. Ventral valve strongly convex, deepest in umbonal area; interarea relatively high, about one-sixth length of valve, apsacline; beak erect; noto-


2 mm
A
2 mm
B1
2 mm
B2
2 mm
C
2 mm
D
2 mm
E1
2 mm
F1
2 mm
F2
2 mm
E2
2 mm
G
2 mm
H1
2 mm
H2
2 mm
I
2 mm
J1
2 mm
J2

thyrium small, covered by a thick, strongly arched deltidium. Dorsal valve gently convex; interarea low, about one-tenth length of valve, anacline; notothyrium narrow, completely covered by thin, strongly convex chilidium. Ornament of roughly equal-sized costellae, about 7 per mm along anterior margin of shell.

Teeth relatively strong; dental plates high, thick, subparallel, extending to anterior margin of muscle field; delthyrial chamber wide, deep. Muscle field clearly impressed, confined to delthyrial chamber; adductor scar narrow, elevated; diductor scars wider, longitudinally rectangular. Mantle canal system saccate, weakly impressed; vascula media originating from anterior ends of diductor scars, divergent, extending and branching anteriorly and laterally.

Cardinalia about one-fifth length and one-half width of shell; cardinal process small, thin, ridge-like, projecting posteriorly; notothyrial platform strongly elevated, continuous laterally with prominent socket ridges to form arched, free-hanging, transverse plate; sockets deep, narrow, open laterally; socket ridges diverging strongly. Muscle field poorly impressed, with weak myophragm.

Discussion.—Various species of *Tritoechia* of Tremadocian to Arenigian age commonly have a weakly transverse to equidimentional shell, a weak cardinalia and a variously developed median ridge. The Weixin material of Darriwilian age is one of the youngest representatives of the genus, and differs from other congeneric species in having a more transverse shell, stronger cardinalia and lacking a median ridge. The shells of *Tritoechia dawanensis* Zeng (1977: pl. 13: 8, length/width ratio 0.84) and *T. gaoluoensis* Zeng (1977: pl. 13: 9, ratio at 0.74) from the lower Dawan Formation (lower Arenigian) of western Hubei Province, for example, are less transverse than those from Weixin.

Table 16. Shell measurements (mm) of *Tritoechia* sp.

	L	W	L/W	L_1/L	W_1/W	L_1/W_1	L_2/L	W_2/W	L_3/L	α
2 dorsal valve										
NIGP 139166	2.35	3.87?	0.61	?	?	?	0.17	0.55	0.06	148
NIGP 139165	4.18	6.97	0.60	?	?	?	0.24	0.47	0.10	130
2 ventral valves										
NIGP 139167	4.88	7.76	0.63	0.35	0.25	0.86	–	–	0.18	–

Table 17. Shell measurements (mm) of *Peritritoechia imbricatia*? Xu, Rong, and Liu, 1974.

Specimen	L	W	L/W	L_1	W_1	L_1/L	W_1/W	L_1/W_1	L_3	L_3/L
NIGP 139168	2.77	4.28	0.65	1.10	1.27	0.40	0.30	0.87	0.58?	0.21

Genus *Peritritoechia* Xu, Rong, and Liu, 1974

Peritritoechia imbricatia? Xu, Rong, and Liu, 1974

Fig. 15D; Table 17.

Peritritoechia imbricatia sp. nov.; Xu et al. 1974: 152, pl. 66: 25–27.

Material.—One ventral internal mould.

Description.—Ventral valve small, about two-thirds as long as wide, strongly convex, deepest in postero-medial part; cardinal extremities subrectangular; maximum width along hinge line; interarea high, about one-fifth length of shell, apsacline, with planar surface; delthyrium small, covered by gently convex deltidium; pedicle foramen submesothyridid; pedicle epithelium thick, well preserved, 0.47 mm in diameter (Fig. $15D_2$).

Teeth small, wedge-shaped; dental plates thin, high, tilting medially, extending anteriorly to serve as lateral muscle bounding ridges; delthyrial chamber deep. Muscle field clearly impressed, subtriangular, about two-fifths length and two-sevenths width of shell; adductor scars minute, elongate-oval, located at posterior end of muscle field; diductor scars much larger, subtriangular; myophragm low.

Discussion.—The outline and internal characters of the ventral valve are similar to those of *Peritritoechia imbricatia* illustrated by Xu et al. (1974) from the Shihtzupu Formation (Mid Ordovician) of Meitan, northern Guizhou Province, but the latter differs somewhat from the present specimen by having a pair of subparallel dental plates and a long ventral median ridge extending anteriorly beyond the ventral muscle field. The uncertain species-level identification of the Weixin specimen is denoted here by a question mark.

Order Pentamerida Schuchert and Cooper, 1931

Superfamily Porambonitoidea Davidson, 1853

Family Porambonitidae Davidson, 1853

Genus *Porambonites* Pander, 1830

Porambonites transversus Xu, Rong, and Liu, 1974

Fig. 15E.

Porambonites transversus sp. nov.; Xu et al. 1974: 153, pl. 66: 32, 33, 36.

Material.—One internal mould of conjoined shell, one ventral internal and one external mould.

Description.—Shell very large (up to 27.9 mm long, 40.1 mm wide), dorsibiconvex, transversely elliptical, with maximum width near mid-length of shell (hinge line about two-thirds as wide as shell). Lateral parts of shell flattened to gently deflected in ventral direction. Cardinal extremities rounded. Anterior commissure broadly uniplicate. Ventral valve gently convex posteriorly, planar antero-laterally;

← Fig. 14. *Martellia ichangensis* Wang, 1956. **A**. NIGP139155, ventral internal mould. **B**. NIGP139156, ventral internal mould (B_1) and latex cast (B_2). **C**. NIGP139157, dorsal internal mould. **D**. NIGP139158, dorsal internal mould. **E**. NIGP139159, dorsal external mould (E_1) and latex cast (E_2). **F**. NIGP139160, dorsal internal mould (F_1) and latex cast (F_2). **G**. NIGP139161, dorsal internal mould. **H**. NIGP139162, dorsal external mould (H_1) and latex cast (H_2). **I**. NIGP139163, ventral internal mould. **J**. NIGP139164, ventral internal mould (J_1) and latex cast (J_2).

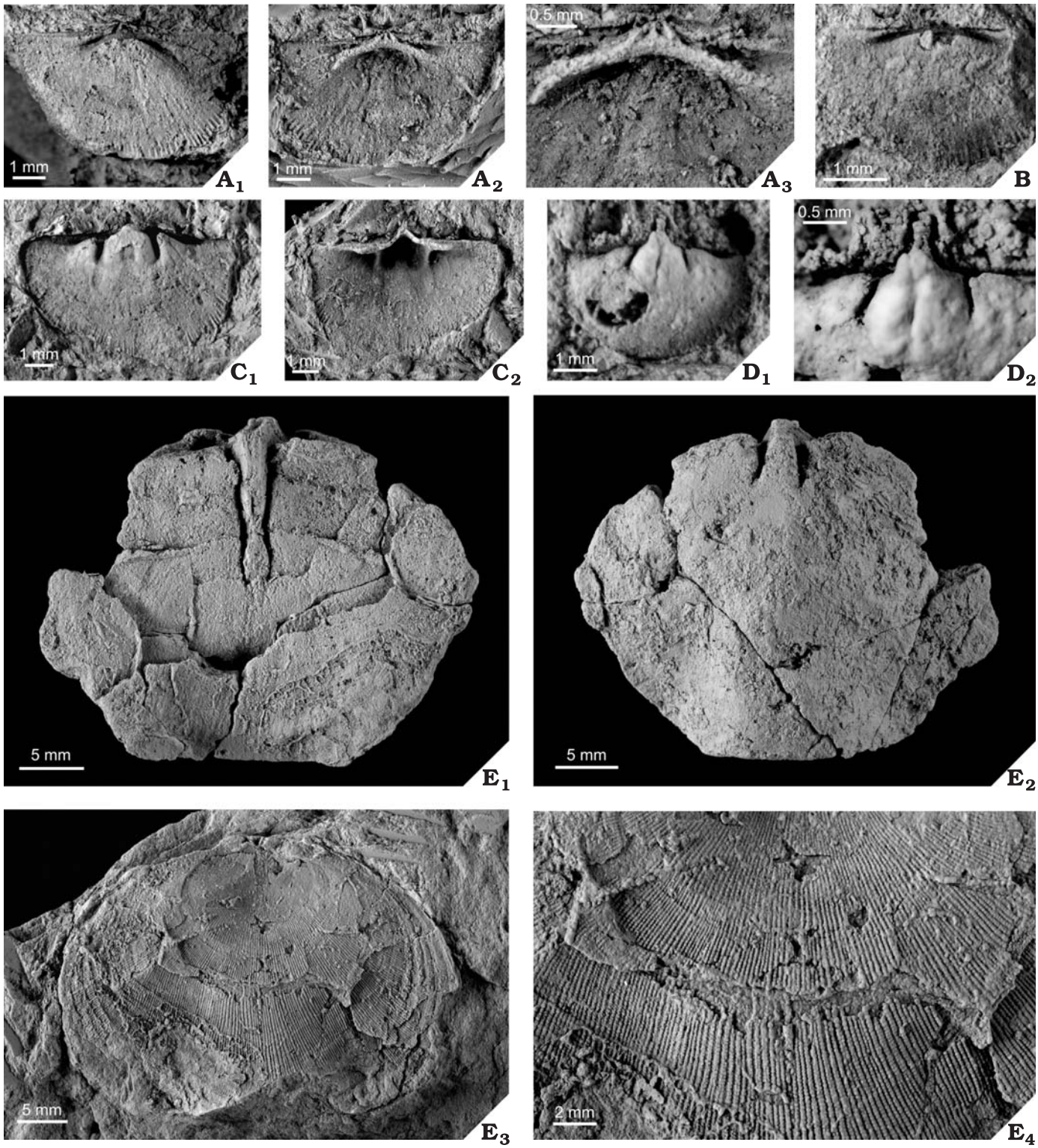


Fig. 15. **A–C**. *Tritoechia* sp. **A**. NIGP139165, dorsal internal mould (A_1) and latex cast (A_2) with enlarged view of cardinalia (A_3). **B**. NIGP139166, dorsal internal mould. **C**. NIGP139167, ventral internal (C_1) and latex cast (C_2). **D**. *Peritritoechia imbricatia*? Xu, Rong, and Liu, 1974; NIGP139168, ventral internal mould (D_1) with local enlargement (D_2) showing muscle field and pedicle epithelium. **E**. *Porambonites transversus* Xu, Rong, and Liu, 1974; NIGP139169, ventral and dorsal views (E_1, E_2) of internal mould, ventral external mould (E_3) and enlarged view of beaded costellae (E_4).

sulcus beginning immediately in front of umbo, widening and deepening rapidly to reach two-fifths width of shell at anterior margin; interarea low, apsacline; delthyrium open. Dorsal valve strongly convex, deepest at about one-third length of shell; fold originating in front of umbo; interarea anacline; notothyrium open. Costellae dense, evenly spaced,

equal-sized, increasing anteriorly by intercalation, about 4 per mm at 5 mm growth stage. Growth lines evenly spaced, 6–7 per mm, showing "string of beads" along interspaces over entire shell surface.

Teeth stout, massive; dental plates long, about one-half length of shell, thin, high, tilting medially, becoming subparallel in their bases, fusing at their ends to form sessile spondylium. Muscle field well defined, not clearly differentiated into adductor and diductor scars. Cardinalia (7.2 mm long, 10.0 mm wide) about one-quarter length and width of shell; cardinal process absent; crura short, rod-like. Outer hinge plates thick, high, divergent from each other at 115°; inner hinge plates parallel, thick, high posteriorly.

Discussion.—The holotype (NIGP 22246) of *Porambonites transversus* from the Shihtzupu Formation of Fenggang, northeastern Guizhou Province is smaller and less transverse (L/W ratio 0.77) than the Weixin material, otherwise their external and internal characters are identical. One ventral internal mould of *Porambonites* spp. Cocks and Zhan (1998: 128, pl. 5: 8) from the Naungkangyi Group of Northern Shan States (Burma) is similar to the Weixin specimen in outline and internal structures but is of smaller size. The Naungkangyi material is likely assignable to *P. transversus*, considering the close faunal relationship between the Sibumasu and South China palaeoplates during late Middle Ordovician time (Fortey and Cocks 1998, 2003).

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References

Bancroft, B.B. 1928. On the notational representation of the rib-system in Orthacea. *Manchester Literary and Philosophical Society, Memoirs and Proceedings* 72: 53–90.

Benedetto, J.L. 1987. Braquiopodos clitambonitaceos de la Formacion San Juan (Ordovicico temprano), Precordillera de San Juan, Argentina. *Ameghiniana* 24: 95–108.

Benedetto, J.L. 2003. Brachiopods. *In*: J.L. Benedetto (ed.), *Ordovician fossils of Argentina*, 91–109. Secretaría de Ciencia y Tecnología, Universidad Nacional de Córdoba, Córdoba, Argentina.

Bouchard-Chantereaux, M. 1849. Mémoire sur un nouveau genre de brachiopods formant le passage des formes articulées à celles qui ne le sont pas. *Annales des Sciences Naturelles, 3, Zoologie* 12: 84–95.

Chang Mei-li 1983. Brachiopods from the Miaopo Formation in Huanghuachang of Yichang, Hubei Province [in Chinese with English abstract]. *Acta Palaeontologica Sinica* 22: 474–481.

Chen Xu, Rong Jia-yu, Wang Xiao-feng, Wang Zhi-hao, Zhang Yuan-dong, and Zhan Ren-bin 1995. Correlation of Ordovician Rocks of China. *International Union of Geological Sciences Publication* 31: 1–104.

Cocks, L.R.M. and Rong Jia-yu 1989. Classification and review of the brachiopod superfamily Plectambonitacea. *Bulletin of the British Museum (Natural History), Geology* 45: 77–163.

Cocks, L.R.M. and Rong Jia-yu 2000. Strophomenida. *In*: R.L. Kaesler (ed.), *Treatise on Invertebrate Paleontology, Part H. Brachiopoda (revised), Vol. 2*, 216–349. Geological Society of America and University of Kansas Press, Lawrence.

Cocks, L.R.M. and Zhan Ren-bin 1998. Caradoc brachiopods from the Shan States, Burma (Myanmar). *Bulletin of the Natural History Museum London, Geology* 54: 109–130.

Cooper, G.A. 1956. Chazyan and related brachiopods. *Smithsonian Miscellaneous Collections* 127 (2 vols): 1–1245.

Copper, P. 1978. Devonian atrypoids from western and northern Canada. *Special Papers of Geological Association of Canada* 18: 289–331.

Copper, P. 1996. *Davidsonia* and *Rugodavidsonia* (new genus), cryptic Devonian atrypid brachiopods from Europe and South China. *Journal of Paleontology* 70: 588–602.

Davidson, T. 1853. *British Fossil Brachiopoda, vol. I. Introduction*. 136 pp. Monographs of the Palaeontographical Society, London.

Fang Ren-sen and Zhu Xiang-shui 1974. Brachiopods [in Chinese]. *In*: Geological Bureau of Yunnan Province (ed.), *Palaeontological Atlas of Yunnan Province*, 287–479. People's Publishing House of Yunnan Province, Kunming.

Foerste, A.F. 1914. Lorraine faunas of New York and Quebec. *Scientific Laboratory of Denison University, Bulletin* 17: 247–339.

Fortey, R.A. and Cocks, L.R.M. 1998. Biogeography and palaeogeography of the Sibumasu terrane in the Ordovician: a review. *In*: R. Hall and J.D. Holloway (eds.), *Biogeography and Geological Evolution of SE Asia*, 43–56. Backhuys Publishers, Leiden.

Fortey, R.A. and Cocks, L.R.M. 2003. Palaeontological evidence bearing on global Ordovician–Silurian continental reconstructions. *Earth-Science Reviews* 61: 245–307.

Fu Li-pu 1982. Brachiopoda [in Chinese]. *In*: Xian Institute of Geology and Mineral Resources (ed.), *Paleontological Atlas of Northwest China, Shaanxi-Gansu-Ningxia Volume, pt. 1, Precambrian and Early Palaeozoic*, 95–178. Geological Publishing House, Beijing.

Geological Bureau of Yunnan Province 1992. Regional Geology of Yunnan Province [in Chinese]. *Geological Memoirs* 1 (21): 1–647.

Hammer, Ø., Harper, D.A.T., and Ryan, P.D. 2004. PAST—PAlaeontological STatistics, ver. 1.21. http://folk.uio.no/ohammer/past.

Harper, D.A.T., Cocks, L.R.M., Popov, L.E., Sheehan, P.M., Bassett, M.G., Copper, P., Holmer, L.E., Jin, J., and Rong Jia-yu 2004. Brachiopods. *In*: B.D. Webby, F. Paris, M.L. Droser, and I.G. Percival (eds.), *The Great Ordovician Biodiversification Event*, 157–178. Columbia University Press, New York.

Harper, D.A.T., Rong Jia-yu, and Sheehan, P.M. 1999. Ordovician diversity patterns in early rhynchonelliform (protorthide, orthide and strophomenide) brachiopods. *Acta Universitatis Carolinae, Geologia* 43: 325–327.

Havlíček, V. 1949. The Orthacea of the Komarov Beds (Brachiopoda). *Věstník Státního Geologického ústavu Československé Republiky* 24: 249–256.

Havlíček, V. 1952. On the Ordovician representatives of the family Plectambonitidae (Brachiopoda). *Sborník Ústředního ústavu geologického* 19: 397–428.

Havlíček, V. 1967. Brachiopoda of the suborder Strophomenidina in Czechoslovakia. *Rozpravy Ústředního ústavu geologického* 33: 1–235.

Havlíček, V. 1998. *Davidsonia* (Brachiopoda, Middle Devonian) in Moravia and its peculiar characters. *Věstník Českého geologického ústavu* 73: 219–222.

Hints, L. 1975. *Brahiopody Enteletacea ordovika Pribaltiki*. 117 pp. Eesti NSV Teaduste Akadeemia Geoloogia Intituut, Tallinn.

Hurst, J.M. 1979. The stratigraphy and brachiopods of the upper part of the

type Caradoc of south Salop. *Bulletin of the British Museum (Natural History), Geology* 32: 183–304.

Jaanusson, V., and Bassett, M.G. 1993. *Orthambonites* and related Ordovician brachiopod genera. *Palaeontology* 36: 21–63.

Jin, J. 1996. Ordovician (Llanvirn–Ashgill) rhynchonellid brachiopod biogeography. *In*: P. Copper and J. Jin (eds.), *Brachiopods*, 123–132. Balkema, Rotterdam.

Jones, O.T. 1928. *Plectambonites* and some allied genera. *Memoirs of the Geological Survey of Great Britain, Palaeontology* 1: 367–527.

King, W. 1846. Remarks on certain genera belonging to the class Palliobranchiata. *Annals and Magazine of Natural History* 18: 26–42.

Kozłowski, R. 1929. Les brachiopodes gothlandiens de la Podolie Polonaise. *Palaeontologia Polonica* 1: 1–245.

Lai Cai-gen 1982. *Ordovician of China* [in Chinese]. 297 pp. Geological Publishing House, Beijing.

Laurie, J.R. 1991. Articulate brachiopods from the Ordovician and Lower Silurian of Tasmania. *Association of Australasian Palaeontologists, Memoir* 11: 1–106.

Liu Di-yong, Xu Han-kui, and Liang Wen-ping 1983. Phylum Brachiopoda [in Chinese]. *In*: Nanjing Institute of Geology and Mineral Resources (ed.), *Palaeontological Atlas of East China (1), Early Palaeozoic Volume*, 254–286. Geological Publishing House, Beijing.

Mu En-zhi, Zhu Zhao-ling, Chen Jun-yuan, and Rong Jia-yu 1978. Ordovician near Shuanghe, Changning, Sichuan [in Chinese]. *Journal of Stratigraphy* (Nanjing) 2: 105–122.

Mu En-zhi, Zhu Zhao-ling, Chen Jun-yuan, and Rong Jia-yu 1979. The Ordovician System of Southwest China [in Chinese]. *In*: Nanjing Institute of Geology and Palaeontology (ed.), *Carbonate Biostratigraphy of Southwest China*, 108–154. Science Press, Beijing.

Neuman, R.B. 1976. Early Ordovician (late Arenig) brachiopods from Virgin Arm, New World Island, Newfoundland. *Geological Survey of Canada, Bulletin* 261: 11–61.

Neuman, R.B. and Bruton, D.L. 1989. Brachiopods and trilobites from the Ordovician Lower Hovin Group (Arenig/Llanvirn), Hølonda area, Thondheim region, Norway: new and revised taxa and paleogeographic interpretation. *Norges Geologiske Undersøkelse, Bulletin* 414: 49–89.

Öpik, A.A. 1933. Über Plectamboniten. *Acta et Commentationes Universitatis Tartuensis (Dorpatensis), Series A* 24: 1–79.

Öpik, A.A. 1934. Über Klitamboniten. *Acta et Commentationes Universitatis Tartuensis (Dorpatensis), Series A* 26: 1–239.

Pander, C.H. 1830. *Beiträge zur Geognosie des Russichen Reiches*. xx + 165 pp. K. Kray, St. Petersburg.

Popov, L.E., Vinn, O., and Nikitina, O.I. 2001. Brachiopods of the redefined family Tritoeciidae from the Ordovician of Kazakhstan and South Urals. *Geobios* 34: 131–155.

Reed, F.R.C. 1906. The Lower Palaeozoic fossils of the northern Shan States, Burma. *Palaeontologia Indica* 2: 1–154.

Reed, F.R.C. 1917. Ordovician and Silurian fossils from Yunnan. *Palaeontologia Indica* 6 (3): 1–85.

Reed, F.R.C. 1936. The Lower Palaeozoic faunas of the Southern Shan States. *Memoirs of Geological Survey of India, Palaeontologia Indica* 21: 1–130.

Rong Jia-yu and Cocks, L.R.M. 1994. True *Strophomena* and a revision of the classification and evolution of strophomenoid and "strophodontoid" brachiopods. *Palaeontology* 37: 651–694.

Rong Jia-yu, Harper, D.A.T., Zhan Ren-bin, and Li Rong-yu 1994. *Kassinella–Christiania* Association in the early Ashgill *Foliomena* brachiopod fauna of South China. *Lethaia* 27: 19–28.

Schuchert, C. 1893. A classification of the Brachiopoda. *American Geologist* 11: 141–167.

Schuchert, C. 1913. Class 2, Brachiopoda. *In*: K.A. von Zittel, *Textbook of Palaeontology 1,* 2nd Edition (translated and edited by C.R. Eastman), 355–420. MacMillan and 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* 22: 241–251.

Schuchert, C. and Cooper, G.A. 1932. Brachiopod genera of the Suborders Orthoidea and Pentameroidea. *Peabody Museum of Natural History, Memoir* 4: 1–270.

Schuchert, C. and LeVene, C.M. 1929. New names for brachiopod homonyms. *American Journal of Science* 17: 119–122.

Ulrich, E.O. and Cooper, G.A. 1936. New genera and species of Ozarkian and Canadian brachiopods. *Journal of Paleontology* 10: 616–631.

Ulrich, E.O. and Cooper, G.A. 1938. Ozarkian and Canadian Brachiopoda. *Geological Society of America, Special Paper* 13: 1–323.

Wan Chao-yuan, Liu Yu-zhou, Chen Wen-yi, Zhao Xing-long, and Wang Lai-xing 1979. *Reports on the Regional Geological Survey: Weixin District: Ordovician*, 15–47 [in Chinese]. Geological Survey of Guizhou Province, Guiyang (unpublished report).

Wang Gang and Chen Xu 1994. Llanvirn graptolites from the border areas of Sichuan, Yunnan and Guizhou. *In*: Chen Xu, B.-D. Erdtmann, and Ni Yu-nan (eds.), *Graptolite Research Today*, 81–86. Nanjing University Press, Nanjing.

Wang Ru-zhi 1981. *Stratigraphic Review of Southwest China: Ordovician* [in Chinese]. 115 pp. Chengdu Institute of Geology and Mineral Resource, Chengdu (unpublished report).

Wang Shu-min and Yan Guo-shun 1978. Ordovician brachiopods [in Chinese]. *In*: Stratigraphic Research Group on Three Gorges of Hubei Geological Bureau (ed.), *Sinian to Permian Stratigraphy and Palaeontology of Eastern Yangtze Gorges*, 210–228. Geological Publishing House, Beijing.

Wang Xiao-feng, Chen Xu, Chen Xiao-hong, and Zhu Ci-ying 1996. *Stratigraphic Lexicon of China, Ordovician Volume* [in Chinese]. 126 pp. Geological Publishing House, Beijing.

Wang Xiao-feng, Ni Shi-zhao, Zeng Qing-luan, Xu Guang-hong, Zhou Tian-mei, Li Zhi-hong, Xiang Li-wen, and Lai Cai-gen 1987. *Biostratigraphy of the Yangtze Gorge area (2), Early Palaeozoic Era* [in Chinese with English summary]. 641 pp. Geological Publishing House, Beijing.

Wang Yu 1956. New species of brachiopods (Part 1). *Scientia Sinica* 5: 157–176.

Williams, A. 1962. The Barr and Lower Ardmillan Series (Caradoc) of the Girvan District, South-west Ayrshire, with descriptions of the Brachiopoda. *Geological Society of London, Memoir* 3: 1–267.

Williams, A. 1974. Ordovician Brachiopoda from the Shelve district Shropshire. *Bulletin of the British Museum (Natural History), Geology, Supplement* 11: 1–163.

Williams A. and Wright, A.D. 1963. The classification of the "*Orthis testudinaria* Dalman" group of brachiopods. *Journal of Paleontology* 37: 1–32.

Wirth, E. 1936. Über "*Clitambonites*" *Giraldii* Martelli und *Yangtzeella Poloi* Martelli aus dem Ordoviz Chinas. *Palaeontologische Zeitschrift* 18: 292–302.

Woodward, S.P. 1852. *A Manual of the Mollusca; or, a Rudimentary Treatise of Recent and Fossil Shells*. xvi + 486 pp. John Weale, London.

Xu Han-kui and Liu Di-yong 1984. Late Lower Ordovician brachiopods of Southwest China [in Chinese with English summary]. *Bulletin of Nanjing Institute of Geology and Palaeontology* 8: 147–235.

Xu Han-kui, Rong Jia-yu, and Liu Di-yong 1974. Ordovician brachiopods [in Chinese]. *In*: Nanjing Institute of Geology and Palaeontology (ed.), *Handbook of Stratigraphy and Palaeontology in Southwest China*, 144–154. Science Press, Beijing.

Xu Qing-Jian, Wan Zheng-quan, and Chen Yuan-ren 1978. Brachiopoda [in Chinese]. *In*: Geological Bureau of Sichuan Province (ed.), *Paleontological Atlas of Southwest China, Sichuan Volume, part 1, Sinian–Devonian*, 284–381. Geological Publishing House, Beijing.

Yoh, S.S. 1928. A geological reconnaissance from Chungching, Sechuan Province to Kueiyang, Kueichou Province. *Bulletin of Geological Survey of China* 11: 31–36.

Zeng Qing-luan 1977. Phylum Brachiopoda [in Chinese]. *In*: Hubei Institute of Geological Sciences (ed.), *Palaeontological Atlas of South-central Region (1), Early Palaeozoic*, 27–69. Geological Publishing House, Beijing.

Zeng Qing-luan, Ni Shi-zhao, Xu Guang-hong, Zhou Tian-mei, Wang

Xiao-feng, Li Zhi-hong, Lai Cai-gen, and Xiang Li-wen 1983. Subdivision and correlation on the Ordovician in the eastern Yangtze Gorges, China [in Chinese with English summary]. *Bulletin of Yichang Institute of Geology and Mineral Resources* 6: 1–68.

Zhan Ren-bin and Jisuo Jin (in press). Brachiopods from the Dashaba Formation (Middle Ordovician) of Sichuan Province, Southwest China. *Special Papers in Palaeontology* 74.

Zhang Jia-hua 1998. Conodonts from the Guniutan Formation (Llanvirn) in Hubei and Hunan provinces, southcentral China. *Acta Universitatis Stockholmiensis, Stockholm Contributions in Geology* 46: 1–161.

Zhang Wen-tang 1962. *Ordovician of China* [in Chinese]. 161 pp. Science Press, Beijing.

Zhang Wen-tang, Li Ji-jin, Qian Yi-yuan, Zhu Zhao-ling, Chen Chu-zhen, and Zhang Shou-xin 1957. Cambrian and Ordovician strata of East Gorges, Hubei [in Chinese]. *Bulletin of Science* (Beijing) 1957 (5): 145–146.

Zhang Wen-tang, Xu Han-kui, Chen Xu, Chen Jun-yuan, Yuan Ke-xing, Lin Yao-kun, and Wang Jun-geng 1964. Ordovician of Northern Guizhou [in Chinese]. *In*: Nanjing Institute of Geology and Palaeontology (ed.), *Palaeozoic Rocks from Northern Guizhou*, 33–78. Nanjing Institute of Geology and Palaeontology, Nanjing.

Zhang Yuan-dong and Chen Xu 2003. The Early-Middle Ordovician graptolite sequence of the Upper Yangtze region, South China. *In*: G.L. Albanesi, M.S. Beresi, and S.H. Peralta (eds.), Ordovician from the Andes. *INSUGEO, Serie Correlación Geológica* 17: 173–180.

Zhang Yun-bai, Zhou Zhi-yi, and Zhang Jun-ming 2002. Sedimentary differentiation during the latest Early Ordovician–earliest Darriwilian in the Yangtze Block [in Chinese with English abstract]. *Journal of Stratigraphy* (Nanjing) 26: 302–314.

Zhu Zhao-ling, Ge Mei-yu, Xu Han-kui, Yuan Ke-xing, Liu Ying-kai, Li Yu-zhong, Su Liang-you, He Ting-gui, Wang Zhao-xi, Li Xi-zhang, Miao Zuo-gui, Ma Chun-fa, and Li Cai-shun 1977. Early Palaeozoic rocks of Chengkou district, Sichuan Province [in Chinese]. *In*: Nanjing Institute of Geology and Palaeontology (ed.), *Stratigraphy and Palaeontology* 5: 1–64.

Appendix 1

Generic faunal list and abbreviations used in multivariate analyses in Figs. 5 and 6. The number in the brackets after each genus is the code used in Fig. 6.

ZY: Shihtzupu Formation, Zunyi (type locality), northern Guizhou Province (Xu et al. 1974; Zhan and Jin in press); *Saucrorthis* (72), *Leptaena* (35), *Aegironetes* (3), *Leptellina* (37), *Bellimurina* (9), *Platymena* (61), *Peritritoechia* (58), *Orthambonites* (50), *Porambonites* (64), *Porambonites* (64), *Gonambonites* (23).

WX: Shihtzupu Formation, Weixin, northeastern Yunnan Province (this paper).

CN: Dashaba Formation, Changning, southeastern Sichuan Province (Zhan and Jin in press); *Orthambonites* (50), *Paralenorthis* (53), *Saucrorthis* (72), *Parisorthis* (54), *Phragmorthis* (59), *Nothorthis* (48), *Horderleyella*? (26), *Tarfaya*? (80), *Tritoechia* (83), *Calyptolepta* (11), Leptellinidae gen. nov. (40), *Longvillia*? (41), indet. strophomenid sp. 1 (28), indet. strophomenid sp. 2 (29), *Pentagomena* (57), *Heteromena* (25), *Glyptomena* (21), *Maydenella* (43), *Yangtzeella* (86).

YC: Miaopo Formation, Yichang, western Hubei Province (Chang 1983 with some revisions in this paper); *Pseudolingula* (67), *Paterula* (55), *Acrotreta* (2), *Torynelasma*? (82), *Taphrorthis* (79), *Nicolella* (47), *Skenidioides* (74), *Leptellina* (37), *Leptelloidea* (38), *Calyptolepta* (11), *Halirhachis* (46), *Leptestiina* (39), *Mezounica* (45), *Sowerbyella* (75), *Kozlowskites* (34), *Aegironetes* (3), *Chonetoidea* (13), *Christiania* (14).

NQ: Siliangssu Formation, Ningqiang, southern Shaanxi Province (Fu 1982; Chen et al. 1995); *Orthis* (52), *Metorthis* (44), *Paurorthis* (56), *Calyptolepta* (11), *Ptychoglyptus* (68), *Rafinesquina* (70), *Vellamo* (84), *Yangtzeella* (86), *Idiostrophia* (27).

CK: Houping Formation, Chengkou, northern Chongqing (Zhu et al. 1977; Chen et al. 1995); *Saucrorthis* (72), *Parisorthis* (54), *Eodiorthelasma* (18), *Virgoria* (85), *Phragmorthis* (59), *Calyptolepta* (11), *Schedophyla* (73).

BM: Naungkangyi Group and its equivalents (Caradocian), Shan States, Burma (Cocks and Zhan 1998); *Plaesiomys* (60), *Nicolella* (47), *Saucrorthis* (72), *Onniella* (49), *Skenidioides* (74), *Leptellina* (37), *Bekkerella* (8), *Ishimia* (32), *Bellimurina* (9), *Dirafinesquina* (17), *Glyptomena* (21), *Porambonites* (64), *Cyclospira* (15).

KZ: Uzunbulak Formation (Darriwilian), Chu-Ili Mountains, southern Kazakhstan (Popov et al. 2001); *Orthidium* (51), *Paralenorthis* (53), *Taphrodonta* (78), *Leptellina* (37), *Aporthophyla* (6), *Toquimia* (81), *Christiania* (14), *Tritoechia* (83), *Pomatotrema* (63), *Martellia* (42), *Yangtzeella* (86).

NF: Unnamed Ordovician tuffs (Darriwilian), Virgin Arm, Newfoundland (Neuman 1976); *Orthambonites* (50), *Productorthis* (65), *Glyptorina* (20), *Plectorthis* (62), *Acanthorthis* (1), *Paurorthis* (56), *Virgoria* (85), *Ingria* (30), *Ahtiella* (4), *Guttasella* (24), *Inversella* (31), *Calyptolepta* (11), *Bimuria* (10), *Tritoechia* (83), *Atelelasma* (7), *Jaanussonites* (33), *Antigonambonites* (5), *Gonambonites* (23), *Rugostrophia* (71), *Camerella* (12).

AP: Lenoir Formation (Darriwilian), eastern United States (Cooper 1956); *Onychoplecia* (87), *Sphenotreta* (88), *Ancistrorhyncha* (89), *Hesperorthis* (90), *Rostricellula* (91), *Mimella* (92), *Multicostella* (93), *Glyptorthis* (22), *Valcourea* (94), *Macrocoelia* (95), *Dactylogonia* (96), *Atelelasma* (7), *Dorytreta* (97), *Titanambonites* (98), *Ptychopleurella* (69), *Stenocamara* (99).