Early and Middle Frasnian brachiopod faunas and turnover on the South China shelf

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The first appearance of the brachiopod *Cyrtospirifer* and related forms in the Late Devonian of South China significantly postdates the beginning of the Frasnian and the entry of the group in other parts of the world. Scattered data from different sections suggest that its first entry, associated with the emergence of other plicate spiriferids, such as theodossid and conispiriferid brachiopods, was late in the Middle Frasnian. At the same time, many rhynchonellids disappeared or became extinct locally in South China. This brachiopod faunal overturn near the *Palmatolepis punctata*–Early *Pa. hassi* zonal boundary is the most significant event in the Early–Middle Frasnian of South China, characterized by about a 35% loss of existing species and the flourishing of the plicate spiriferids, which was coeval with the end of a major biogeochemical perturbation recently recognized in the *Pa. punctata* Zone. By contrast, atrypid brachiopods do not seem to show any significant diversity change. The brachiopod faunal change was probably related to a (local?) transgressive event in South China, which also brought new pelagic faunas northwards into some intra-shelf deeper water areas, such as the Shetianqiao area in central Hunan Province. Fifteen brachiopod species are described and illustrated, which include some taxa that are first recorded or recognized in South China, e.g., the spiriferid *Pyramidaspirifer*, which is now known from both North America and South China. One new species, *Desquamatia qiziqiaoensis*, is erected.

Key words: Brachiopoda, *Cyrtospirifer*, faunal turnover, Frasnian, Devonian, South China.

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Introduction

The Devonian was a period with evolutionary innovations, for example, the flourishing of vascular plants, and emergence of amphibians on land. Invertebrates also experienced major extinctions, for example the Frasnian–Famennian mass extinction (e.g., Racki and House 2002; Baliński et al. 2002; Racki 2005). In addition, many smaller-scale events or extinctions have been recognized (e.g., House 2002). Late Devonian pelagic goniatite stratigraphy and event succession have been summarized by Becker et al. (1993), Walliser (1996), and House (2002), and tied to transgressive episodes, periods of hypoxia and deposition of black muds in specific basins. The International Subcommission on Devonian Stratigraphy (SDS) has proposed to place the base of a formal Middle Frasnian substage at the base of the MN 5 or *Palmatolepis punctata* Zone and this definition is adopted in this paper (see Ziegler and Sandberg 2001 for example).

Applying a lag-time multiple impacts hypothesis to the Frasnian–Famennian mass extinction, McGhee (2001) suggested that future searches for evidence of impact events in the Late Devonian should be concentrated in strata that occur in the Frasnian *Palmatolepis transitans* to Early *Pa. hassi* zonal interval of the so-called standard conodont zonation (Ziegler and Sandberg 1990). This period covers zones 4–8 in the more detailed, globally applicable Montagne Noire (MN) conodont zonation of Klapper (1989). There have been already some regional studies that reported various sedimentological, geochemical, and pelagic faunal signatures from that interval: Becker et al. (1993) from Western Australia, House and Kirchgasser (1993) from New York State, Morrow et al. (1998) from Nevada, House et al. (2000) from Timan, northern Russia, Becker and House (2000) from Tafilalt, SE Morocco, Becker (2002) from Boulonnais, northern France, Becker et al. (2004) from Dra Valley, SW Morocco, and Racki et al. (2004) from the Holy Cross Mountains, Poland. Currently a Timan Event in MN Zone 4 (*Pa. transitans* Zone), a Middlesex Event or basal Domanik Transgression at the base of MN Zone 5 (basal *Pa. punctata* Zone), and two pulses of the Lower Rhinestreet Event around the boundary between MN zones 6–7 (around the base of the *Palmatolepis hassi* Zone) are recognized in widely separated basins. In addition, the Middle Frasnian "*punctata* event" of Yans et al. (in press) (= *Pa. punctata* Event) corresponding to a carbon isotopic perturbation, which has also been recognized in various continents including South China.

This paper deals with faunal response during the Early and Middle Frasnian interval and reports brachiopod taxonomy and distribution from South China.

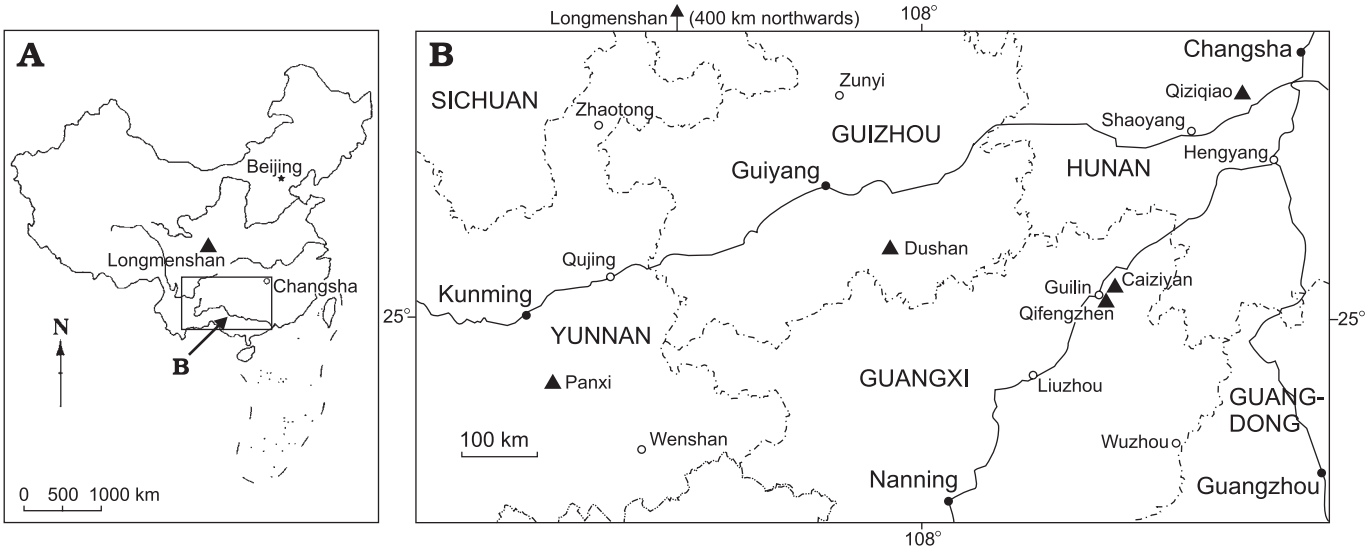


Fig. 1. Geographic map of China (**A**) and locations of the stratigraphic sections (▲) investigated in this study (**B**).

The Devonian of South China is well developed, with sediments of various settings, and with relatively well preserved neritic and pelagic faunas (e.g., Hou and Wang 1988). Some important studies that included Late Devonian brachiopod faunas are those of, e.g., Grabau (1931), Tien (1938), Wang (1956), Chen (1983, 1984), Hou (1988). Recently, a series of papers have concentrated on material from across the Frasnian–Famennian boundary, e.g., Ma et al. (2002), Ma and Day (2003), and Ma et al. (2005). However, systematic studies of Early and Middle Frasnian brachiopod faunas are still rare (see Chen 1983, 1984; Hou 1988), which deal with abundant material from the Longmenshan section of Sichuan Province. This material collected from several other important areas, including the Panxi section of Yunnan Province, Dushan section of Guizhou Province, Caiziyan section of Guangxi Zhuang Autonomous Region, and Qiziqiao section of Hunan Province (Fig. 1).

Institutional abbreviation.—PUM, the Geological Museum of Peking University.

Other abbreviations.—DS, Dushan section of Guizhou Province, China; GC, Caiziyan section in the vicinity of Guilin, China; PY, Panxi section of Yunnan Province, China; QZQ, Qiziqiao section of Hunan Province, China (see Fig. 1 for section locations); MN, Montagne Noire conodont zones of Klapper (1989).

Stratigraphy

One of the major problems in the stratigraphic study of shelly facies in South China is more accurate correlation with the "standard" faunal zones established chiefly based on pelagic conodonts and goniatites. The precise age of brachiopod faunas is a crucial question in this study. Therefore we first discuss the stratigraphy of the studied sections.

The Early Frasnian Tuqiaozi Interval and its equivalents.—Traditionally, the Middle–Late Devonian boundary in shallow water facies in South China has been defined by the disappearance of *Stringocephalus* and the appearance of *Cyrtospirifer*. However, it has also been long recognized that there is an interval between the levels of the last *Stringocephalus* and the first *Cyrtospirifer*, e.g., as represented by the Hejiazhai Member in the Dushan section of Guizhou Province (Liao et al. 1978), and the Tuqiaozi Formation (in the sense of Chen 1984) in the Longmenshan section of Sichuan Province. This interregnum, the *Stringocephalus–Cyrtospirifer* interval Zone of Ji (1989: 307), is here termed the Tuqiaozi Interval for simplicity, and can be used for the same time interval in other sections. It has been considered to be Early Frasnian in age by most workers, e.g., in Liao's (1977) work on rugose coral faunas from the Dushan section and in Chen's work (1984) on brachiopod faunas from the Longmenshan section. Conodont data in Hou (1988: 28–31) suggest that the Tuqiaozi Formation (in the sense of Chen 1984, which is different from the definition of Hou 1988 who puts the base about 84 m upwards and the top about 20 m upwards) can roughly be correlated with the earliest Frasnian (MN Zone 1) to early part of the Middle Frasnian (MN zones 5–6). As pointed out by Xiong et al. (1988: 39), the exact age of the topmost Tuqiaozi Formation in terms of conodont zonation cannot be determined because of the absence of *Palmatolepis*, and other index fossils. The early part of the Tuqiaozi Formation (Beds 2–9 of Chen 1984, approximately equal to the upper 20 m of Bed 126 and bed 127 of Hou 1988) yielded *Ancyrodella binodosa*, *A. rotundiloba*, *A. rugosa*, *A. pramosica*, *Mesotaxis ovalis*, *M. asymmetrica*, and *Playfordia primitiva*. This suggests the presence of MN zones 1–4 (Frasnian part of early *M. falsiovalis* Zone to lower part

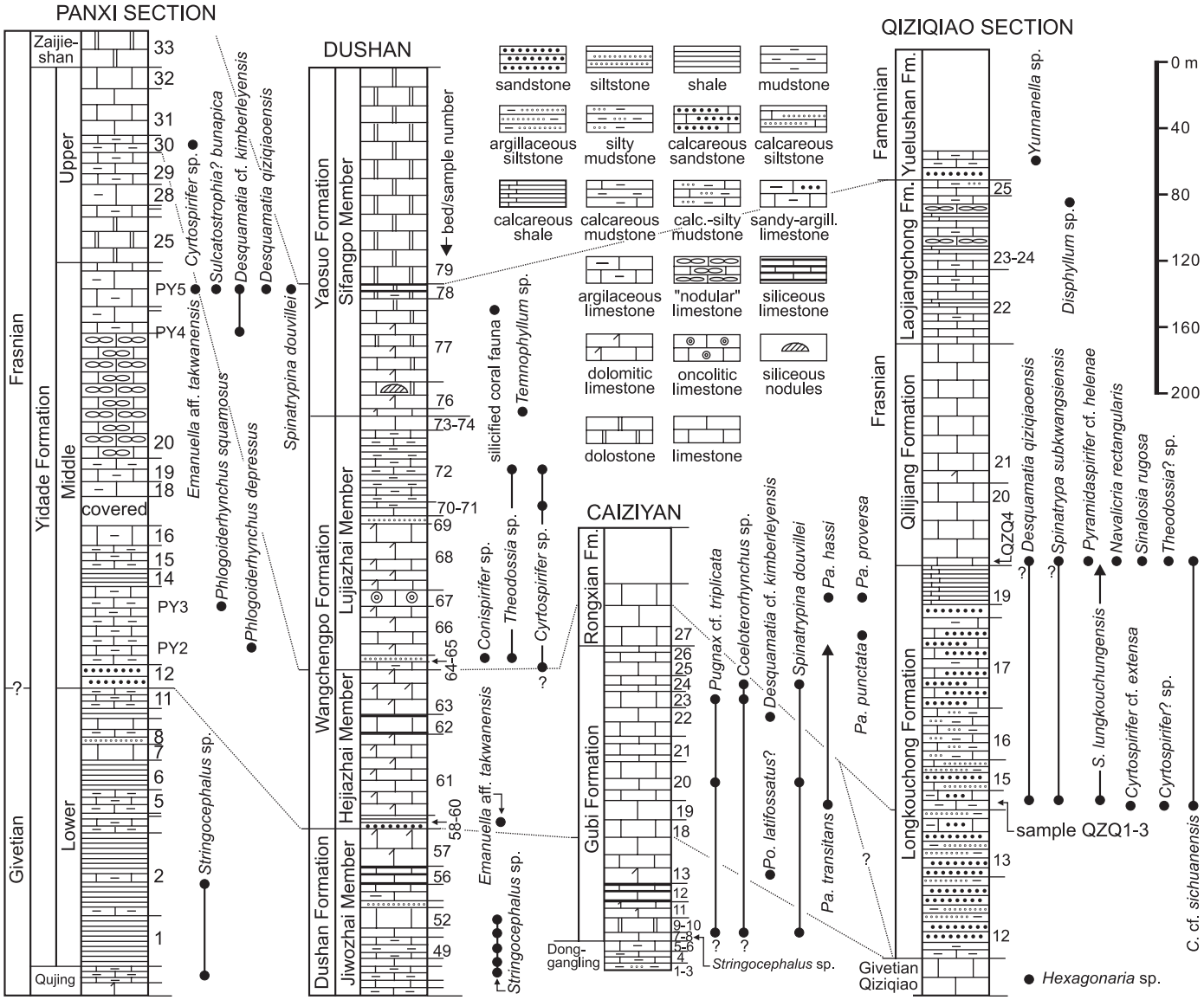


Fig. 2. Stratigraphy and distribution of Early and Middle Frasnian brachiopods in South China. Most but not all known brachiopods are described and illustrated in this paper. For the distribution of atrypids in the Dushan section, for example, see Ma et al. (2005). The stratigraphy of Panxi and the occurrence of *Cyrtospirifer* sp. are based on Yunnan compiling group (1978) and the occurrence of *Stringocephalus* in the lower part of the Yidade Formation is as in Xian et al. (1988: 148). The stratigraphy of Dushan and the occurrence of *Stringocephalus* sp. are as in Liao et al. (1979); the Caiziyan section was re-measured by Long-Ming Wei, Xue-Ping Ma, and Hua Li (personal communication 2005), with coral identifications by Wei-Hua Liao. The stratigraphy of Qiziqiao is based on data of Z.-X. Hu and Z.-Q. Deng in Tan et al. (1987), and the occurrence of *Yunnanella* sp. is based on Zu-Han Liu (personal communication 2001). Abbreviations: calc., calcareous; argill., argillaceous; *C.*, *Cyrtospirifer*; *Pa.*, *Palmatolepis*; *Po.*, *Polygnathus*; *S.*, *Spinatrypina*.

of *Palmatolepis transitans* Zone). According to brachiopod data in Chen (1984) and Hou (1988), the middle part of the Tuqiaozi Formation (Beds 10–17 of Chen 1984) is characterized by the *Pugnax triplicata–Calvinaria* spp. assemblage, including *Septalariopsis zhonghuaensis*, *Phlogoiderhynchus simplex*, and *Reticulariopsis sichuanensis* as diagnostic taxa. The disappearance of typical Early Frasnian ancyrodellids at the top of Bed 133 may indicate the Early–Middle Frasnian boundary; *Pa. punctata* has not been recorded. The upper part of the formation (Beds 18–24 of Chen 1984) is characterized by the *Yocrarhynchus orientalis*–"*Ypsilorhynchus*" *mansuyi* assemblage, including *Schizophoria orthambonita* as one of the diagnostic taxa. *Zhonghuacoelia* spp. are common throughout the middle and upper parts of the Tuqiaozi Formation and extend slightly upwards.

In the Caiziyan section (Fig. 2), Beds 7–8 yielded *Stringocephalus* sp., and the coral *Truncicarinulum involutum* Yu and Kuang, 1982, a nominal species for a coral zone at the top of the Givetian in the Liujing section near Nanning (Kuang and Chi 1989: 39). *Pa. transitans*, *Pa. punctata*, and *Pa. hassi* are index conodonts of respective zones. The Middle–Late Devonian boundary at Caiziyan is drawn tempo-

rarily at the base of Bed 18 (Fig. 2), pending new conodont data from the Bed 12–18 interval. According to Liao et al. (1979: 239), the beginning of the Late Devonian may be placed in the Dushan section well above the last stringocephalids (Bed 52), at the base of Bed 58.

In terms of brachiopods as shown in Fig. 2 and based on data from the Longmenshan section by Chen (1984), the Tuqiaozi Interval is characterized by the absence of both *Stringocephalus* and plicate spiriferids, such as *Cyrtospirifer*, and by the presence of a combination of brachiopods, here termed the *Yocrarhynchus–Phlogoiderhynchus* Fauna. This fauna mainly consists of *Devonoproductus*, *Schizophoria* spp., *Gypidula* spp., *Pugnax triplicata* species group, *Coeloterorhynchus* sp., "*Leiorhynchus*" spp., *Calvinaria* spp., *Costatrypa*, *Isospinatrypa*, *Spinatrypa*, *Spinatrypina*, *Desquamatia*, and smooth-shelled spiriferids *Emanuella* and *Zhonghuacoelia* spp.

First appearance of *Cyrtospirifer* (including related forms) in South China.—While it is true that the first appearance of *Cyrtospirifer* (including related similar forms) is interpreted as Late Devonian age in South China, its exact, or even approximate level of first occurrence relative to the presently recognized world-wide conodont zonation is not known. Previously a *Cyrtospirifer* brachiopod zone had been only recognized for the Frasnian in South China. Wu et al. (1992) and Ji (1989: 307) suggested that the marker genus does not occur below the Early *Palmatolepis gigas* Zone of the old conodont zonation, which would mean a level near the base of the Late Frasnian in the new substage terminology of the International Subcommission on Devonian Stratigraphy. We conclude that the lowest (earliest) occurrence of cyrtospiriferid brachiopods in South China can be correlated approximately with the Middle Frasnian. This is based on the following evidence:

(1) In the shelly facies of the Longmenshan section, the first cyrtospiriferids (including *Cyrtospirifer* of Chen 1984 and *Tenticospirifer* in Hou 1988: pl. 45: 16a–d) occur at the base of the "Shuizinwan" (= Shuijingwan) Member (Chen 1984: 98). The basal part of this member was assigned to the uppermost part of the Tuqiaozi Formation by Hou (1988) based on its uniform lithology, that is to say, the cyrtospiriferids first occur in the uppermost part of Hou's (1988) Tuqiaozi Formation, where they are associated with last *Zhonghuacoelia*. No diagnostic conodonts have been found in the "Shuijingwan" Member. However, *Mesotaxis asymmetrica* is present throughout the Tuqiaozi Formation of Chen's 1984 definition (Hou 1988), a species that does not range above MN Zone 6 (upper part of *Pa. punctata* Zone) in the Frasnian composite of Klapper (1997). This suggests that cyrtospiriferids enter in Sichuan above MN Zone 6, approximately in the Early *Pa. hassi* Zone.

(2) In other shelly facies sections, such as the Panxi and Dushan sections, a similar brachiopod sequence to that of the Longmenshan section exists: the *Stringocephalus* fauna → the *Yocrarhynchus–Phlogoiderhynchus* fauna → the plicate spiriferid fauna (including, e.g., *Cyrtospirifer*, *Theodossia*, *Conispirifer*).

(3) In platform margin to pelagic facies sections in South China, the first cyrtospiriferids occur high in the Middle Frasnian. In the Caiziyan section, Beds 19–26 (Fig. 2) yielded conodonts *Mesotaxis asymmetrica*, and *Pa. transitans* among others; the lower part of Bed 27 yielded *Ancyrodella gigas* and *Pa. punctata*; the upper part of Bed 27 yielded *Pa. hassi* and *Palmatolepis proversa*. Therefore, the 19–26 interval may be roughly assigned to the *Palmatolepis transitans* Zone (MN Zone 4), whereas Bed 27 includes approximately the *Pa. punctata* and Early *Pa. hassi* zones (MN zones 5–8). Unfortunately, no cyrtospiriferid brachiopods have yet been found in Bed 27, or below, although other brachiopods, such as atrypids and rhynchonellids, are common to abundant in some layers. In the Yangdi (= Fuhe) section, a plicate spiriferid (possibly *Pyramidaspirifer*) first occurred in the uppermost part of the Baqi Formation (= bed 6 of Ji 1994: 84; X.-P. Ma's new field observation), which was assigned to the Early *Pa. hassi* Zone by Ji (1994). In the Ma'anshan section of Xiangzhou County, Guangxi, *Cyrtospirifer* seems first to occur in the *Pa. jamieae* Zone, whereas the *Pa. punctata–Pa. hassi* Zone strata are characterized by the "*Leiorhynchus*"–"*Atrypa*" fauna (Ji 1994: 89–90; taxonomy of brachiopods not studied in details). However, *Pa. foliacea*, an index species of MN Zone 12 (later parts of the Early *Pa. rhenana* Zone) occurs about 9 m above the base of the Guilin Formation (Ji 1986), which suggests that *Cyrtospirifer* entered much later in the Early *Pa. rhenana* Zone. It is probably natural that first occurrences of cyrtospiriferids are different in horizons because benthic brachiopods are generally rare.

One exception is the Liujing section, where *Tenticospirifer* was mentioned to occur first in the latest part of the Early *Polygnathus asymmetricus* Zone (correlated with middle *Pa. transitans* Zone, MN Zone 4), about 12–14 m from the base of the Gubi Formation (Kuang 1989: 72–73, fig. 14); unfortunately no illustrations of "*Tenticospirifer*" were shown, and the taxon is not even mentioned for the Gubi Formation by Zhao (1989).

Age of the Longkouchong Formation of Hunan Province.—This formation has long been considered as Early Frasnian by most workers since Tien (1938). Tan et al. (1987: 89) considered that the Hejiazhai Member and the Tuqiaozi Formation should mostly or entirely be Givetian, being older than the Longkouchong Formation because of the absence of *Cyrtospirifer* in the former two units. The presence of *Cyrtospirifer* has now been confirmed by our recent re-sampling in the Qiziqiao section (type locality of the Longkouchong Fm.). In addition, the Longkouchong Formation does not yield ambocoelid brachiopods though these are very common in the middle part of the Yidade Formation in the Panxi section, in the Hejiazhai Member in the Dushan section (Fig. 2), and in the Tuqiaozi Formation in the Longmenshan section. The Longkouchong Formation hosts cyrtospiriferid brachiopods and abundant atrypids (*Desquamatia qiziqiaoensis*). Therefore, the Longkouchong Formation should be different in age

from the Tuqiaozi Formation and the Hejiazhai Member, and we agree with Tan et al. (1987) that it should be younger. Our previous analysis of the first *Cyrtospirifer* appearance in South China suggests that most of the Longkouchong Formation should be Middle Frasnian. Lacking fossil evidence, the basal part of this formation (Beds 12 and 13 in Fig. 2: 89 m thick) is correlated tentatively with the Tuqiaozi Formation (and its equivalents). It cannot be ruled out that a hiatus exists between the Givetian Qiziqiao Formation and the Frasnian Longkouchong Formation, and that Beds 12 and 13 could be correlated with any stratigraphic position in the Early Frasnian to early Middle Frasnian. The Qilijiang Formation may be correlated with the upper part of the Zhengshuihe Formation of the Shetianqiao section (about 90 km south-west of the Qiziqiao section), and correlates with the *Pa. jamieae* through the Early *Pa. rhenana* zones. The overlying Laojiangchong Formation is correlated with the Late *Pa. rhenana* and *Pa. linguiformis* zones (Ma, Sun, et al. 2004).

Age of the Yidade Formation.—The Yidade Formation is here subdivided into lower, middle, and upper parts (Fig. 2). The lower unit bears *Leiorhynchus* brachiopods and rare plant fossils (Yunnan compiling group 1978) and *Stringocephalus* was mentioned to be present at about 50 m above the base (Xian et al. 1988: 148, no illustration). Generally in South China, the position of the last disappearance of *Stringocephalus* is well below the Middle–Late Devonian boundary, in the *Schmidtognathus hermanni* Zone (Bai et al. 1994: 193). Wang and Yu (1962: 89) considered the lower and middle parts (beds 24–27 of Ku 1949) to be of Givetian age because of the presence of *Ambocoelia sinensis* (assigned in *Zhonghuacoelia* by Chen 1984), *Schizophoria macfarlanii*, "*Atrypa desquamata*", and "*Hypothyridina parallelepipeda*". Taxonomic lists in old literature (without description and illustrations) may not be adequate and we have made some changes in their taxonomic status. The *Phlogoiderhynchus* Zone of Sartenaer (1980) occurs from latest Givetian through early Frasnian strata (Earliest to Middle *Mesotaxis asymmetrica* zones = *M. falsiovalis* to *Palmatolepis punctata* zones or *Skeletognathus norrisi* Zone to MN 5 Zone: Sartenaer 1985). Becker collected from Western Australia the *Spinatrypina–Phlogoiderhynchus–Devonoproductus–Ladjia* brachiopod fauna associated with goniatites of the *Koenenites* Zone (see Becker et al. 1993: MN Zone 2 within the Late *Mesotaxis falsiovalis* Zone of Ziegler and Sandberg 1990). The Middle–Late Devonian boundary is placed tentatively at the top of the lower part, with a 14 m thick brownish gray thick-bedded fine sandstone layer (Bed 12) as the base of the Frasnian.

To summarize, the Tuqiaozi Formation and its equivalents have some similarities in common: the presence of smooth spiriferids and the absence of *Stringocephalus* and plicate spiriferid brachiopods (cyrtospiriferids and theodossids), for example, in the Panxi, Dushan, and Caiziyan sections (Fig. 2). Therefore as in the Longmenshan section, this interval is assigned to the base of the Frasnian through the Middle Frasnian (in the *Palmatolepis hassi* Zone).

Brachiopod distribution

The largest brachiopod turnover occurs in the Middle Frasnian *Palmatolepis punctata*–Early *Pa. hassi* zonal transition interval. About 35% of brachiopod species (including those long-ranging species not shown in Fig. 3) of the *Ancyrodella rotundiloba pristina* Zone (*sensu* Sandberg et al. 1989) through to the *Pa. punctata* Zone disappeared by the end of the *Pa. punctata* Zone. Most brachiopod species in the *Pa. hassi* Zone are new, at the beginning of the Early *Pa. hassi* Zone. This turnover is characterized by loss of most rhynchonellids, and the sudden regional emergence of plicate spiriferids, probably related to a deepening event in South China, which also brought new pelagic faunas northwards into some intra-shelf deeper water areas, such as the Shetianqiao area in central Hunan Province that was dominated by shelf carbonate facies. These new pelagic faunas include ostracods and ammonoids (Ma, Sun, et al. 2004; Ma, Bai, et al. 2004). By comparison with rhynchonellids and spiriferids, atrypids only show minor changes (Fig. 3).

The *Palmatolepis transitans–Pa. punctata* Zone (MN Zone 4–5) boundary represents a smaller scale faunal change interpreted as background turnover. The faunal changes at the Middle–Late Devonian boundary, and the *Palmatolepis hassi–Pa. jamieae* Zone boundary are not discussed here as insufficient material has been studied.

Systematic paleontology

(by Xueping Ma)

In the present paper, "cf." is used when the labeled differences between the studied specimens and the taxon in comparison may prove to be intraspecific variations when more specimens available; "aff." means the studied specimens are significantly different from the taxon in comparison and should represent a different species.

Order Strophomenida Öpik, 1934
Superfamily Strophomenoidea King, 1846
Family Douvillinidae Caster, 1939
Subfamily Leptodontellinae Williams, 1965
Genus *Sulcatostrophia* Caster, 1939
Sulcatostrophia? *bunapica* Veevers, 1959a

Fig. 4A.

1912 ?*Orthothetes crenistria* Phillips; Mansuy 1912: 66–67, pl. 12: 3.
1931 ?*Shellwienella crenistria* (Phillips); Grabau 1931: 20, pl. 1: 2 (Mansuy's specimen re-illustrated, with English translation of original description).
1959 *Nervostrophia bunapica* sp. nov.; Veevers 1959a: 65–69, text-figs. 36, 37, pl. 7: 1–8.

Material.—One poorly preserved specimen, with broken margins, sample PY5 (see Fig. 2).

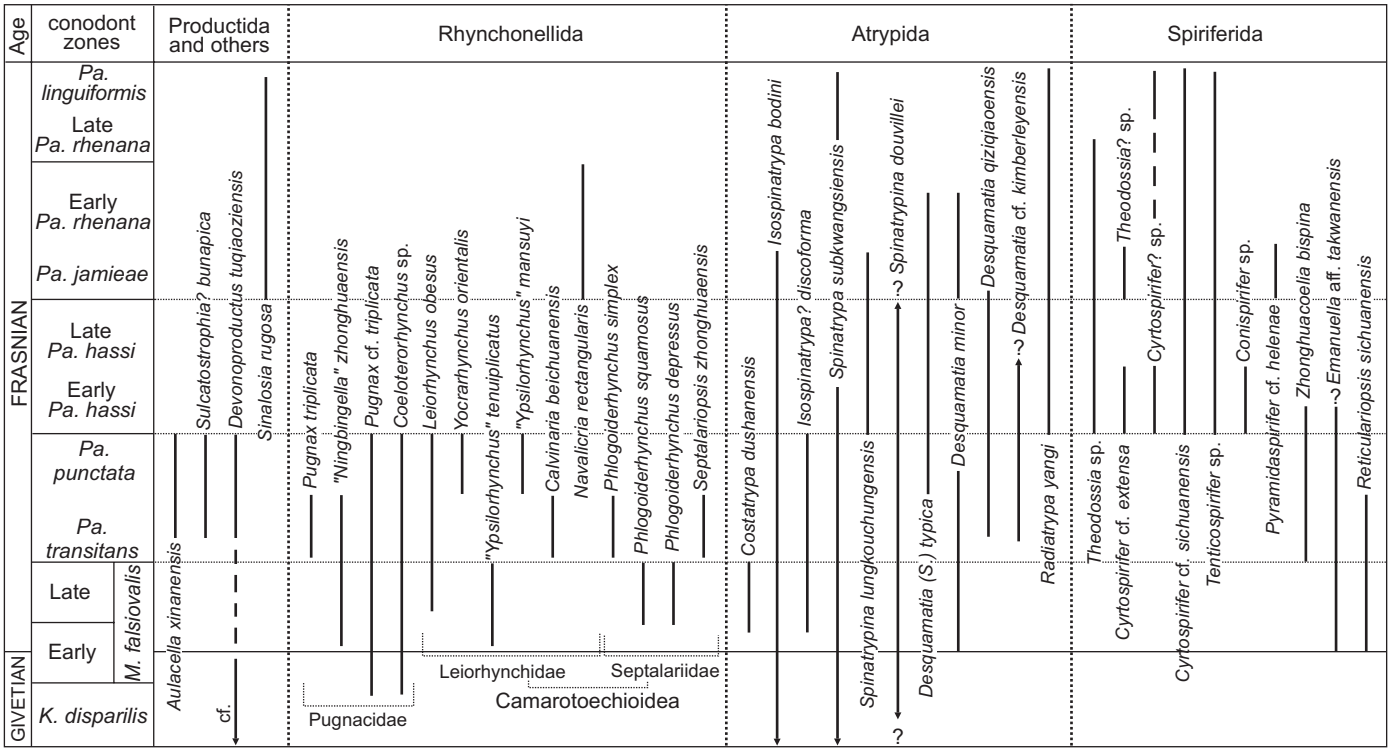


Fig. 3. Brachiopod distribution in the Early and Middle Frasnian of South China. (from Chen 1983; 1984; Hou 1988; Sartenaer and Xu 1991; Ma et al. 2005; this study, and our unpublished data). Species of "*Ningbingella*" and "*Ypsilorhynchus*" needs confirmation of their generic status. Abbreviations: *K*., *Klapperina*; *M*. *Mesotaxis*; *Pa*., *Palmatolepis*.

Discussion.—This shell has an unequally parvicostellate ornament, with about 6 to 12 radial striae between adjacent costae or costellae. Other features include: hinge entirely denticulate; ventral interarea with 18 vertical ridges per 5 mm; dorsal interarea about 1/2 to 2/5 height of ventral interarea, and chilidium convex and semi-cylindrical, covering entire notothyrium. *Nervostrophia* has intermittently discontinuous, tear-drop shaped, radial costellae (Cocks and Rong 2000: 286), which does not allow the assignment of the present species in the genus. The present species is similar in outline and ornament to members of *Parapholidostrophia* Johnson, 1971, but differs in having dense radial striae. Internal differences in Veevers' (1959a) type specimens are the absence of a dorsal median septum and the presence of a longitudinally grooved, bifid cardinal process. Veevers (1959a) equated *Sulcatostrophia*? *bunapica* with "*Orthothetes crenistria*" (Phillips, 1836), described by Mansuy (1912) from eastern Yunnan. Mansuy's shell is a ventral valve on a slab that does not allow complete comparisons. The studied specimen can be distinguished from Middle Devonian (Givetian) *Nervostrophia guanwushanensis* Chen in Xu et al. 1978 by its larger size and more numerous striae between adjacent costae or costellae (6–12 *versus* 3–6). It also differs from *Douvillina* cf. *interstrialis* (Phillips, 1841) described from the Early Frasnian by Xu et al. (1978: 302–307) in that the latter species has a much more transversely oval outline and fewer striae (2–3 in number) between adjacent costae or costellae.

Occurrence.—This species was first described by Veevers (1959a) from the Frasnian Sadler Formation of the Fitzroy Basin, western Australia. The studied specimen is from the Panxi section of eastern Yunnan Province; middle part of the Yidade Formation (approximately the Frasnian *Mesotaxis falsiovalis–Palmatolepis punctata* zones).

Order Rhynchonellida Kuhn, 1949
Superfamily Camarotoechioidea Schuchert, 1929 (in Schuchert and LeVene 1929)
Family Septalariidae Havlíček, 1960
Genus *Phlogoiderhynchus* Sartenaer, 1970
Phlogoiderhynchus squamosus (Wang, 1956)

Fig. 4B.

1956 *Paurorhyncha squamosa* Wang (sp. nov.); Wang 1956: 171–172, pl. 4: D1–D5.

Material.—One almost complete, exfoliated specimen, sample PY3 (see Fig. 2).

Discussion.—Major features include: surface with about 35 plications, including 8 on fold; flank plications rarely bifurcating or intercalating; plications low and flat topped, with narrow interspaces; with 0–1 parietal plication; internally, dorsal median septum long, extending to about midlength.

Differences between the studied specimen and the type specimen from the same section are in slightly fewer and coarser plications on the fold. The species is assigned to

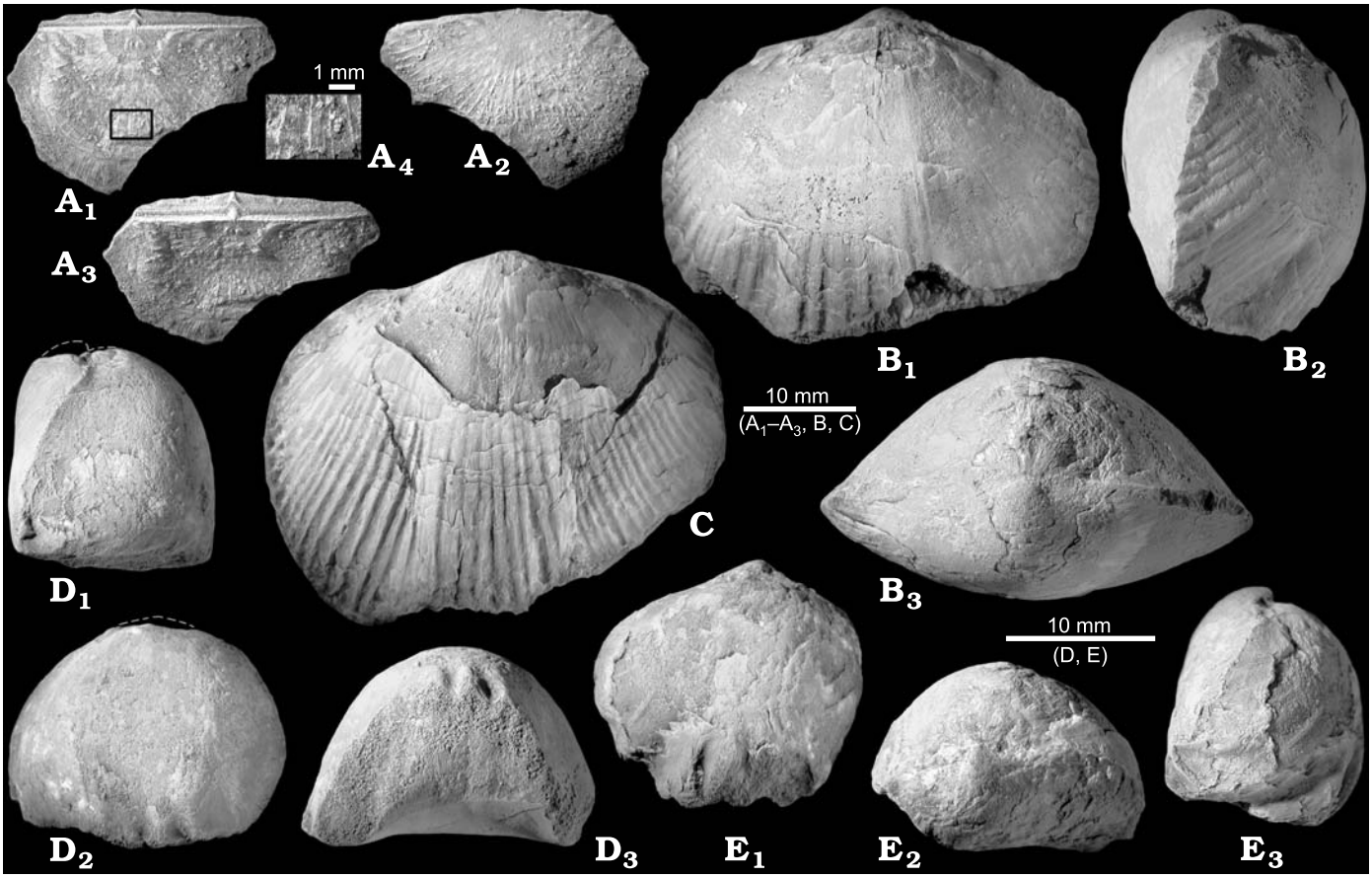


Fig. 4. Strophomenid and rhynchonellid brachiopods from the Early and Middle Frasnian of the Panxi and Caiziyan sections. **A**. *Sulcatostrophia*? *bunapica* Veevers, 1959a, PUM05001, sample PY5, Panxi section, Middle Frasnian, dorsal (A_1), ventral (A_2), area (A_3) views, and enlargement of framed area in image A_1 (A_4). **B**. *Phlogoiderhynchus squamosus* (Wang, 1956), PUM05002, sample PY3, Panxi section, Early Frasnian, dorsal (B_1), lateral (B_2), and posterior (B_3) views. **C**. *Phlogoiderhynchus depressus* (Wang, 1956), PUM05003, sample PY2, Panxi section, Early Frasnian, dorsal view. **D**. *Pugnax* cf. *triplicata* (Chen in Xu et al. 1978), PUM05004, sample GC20, Caiziyan section, Early Frasnian, lateral (D_1: ventral beak broken), dorsal (D_2), and anterior (D_3: left anterior broken, right lateral anterior slightly broken) views. **E**. *Coeloterorhynchus* sp., PUM05005, sample GC21-24, Caiziyan section, Early Frasnian, dorsal (E_1: right anterior and right lateral broken), posterior (E_2), and lateral (E_3) views.

Phlogoiderhynchus by its external morphology (e.g., large size: 37.4 mm wide, ≥29.4 mm long, and 20.7 mm thick for the figured specimen; wider than long, incurved or adpressed ventral beak, fold and sinus morphology, and biconvex profile). No detailed internal structures are available. It differs from the type species—*Phlogoiderhynchus arefactus* (Veevers, 1959a) in its larger size, more convex dorsal valve, and stronger and more numerous flank plications. *Calvinaria simplex* Chen in Xu et al. (1978) from the Tuqiaozi Formation of the Longmenshan section was assigned to *Phlogoiderhynchus* by Sartenaer (1985: 314), which is almost smooth, and smaller.

Occurrence.—This species is only found in the Panxi section of eastern Yunnan Province; middle part of the Yidade Formation (Early Frasnian).

Phlogoiderhynchus depressus (Wang, 1956)

Fig. 4C.

1956 *Paurorhyncha depressa* Wang (sp. nov.); Wang 1956: 172, pl. 5: D1–D5.

Material.—Two almost complete but exfoliated or somewhat deformed specimens and one broken ventral valve from sample PY2 (see Fig. 2).

Discussion.—Wang (1956) described two associated species from the Late Devonian Yidade (= Itate) Formation of the Poshi (now Panxi) section of eastern Yunnan (material is sparse and neither internal structures nor detailed horizon was given): *Paurorhyncha squamosa* and *P. depressa*, the latter differs by its depressed ventral valve. *Paurorhyncha* is a North American Famennian genus that differs by an elongated-triangular outline.

Major features of the studied specimens of *Phlogoiderhynchus depressus* include: about 17–20 plications of varied strength on each flank (rarely bifurcating or intercalating), 2–3 pairs of faint parietal plications at anterior margin, and about 9 to 12 in sinus or on fold; dorsal fold extending from mid-length; ornament of weak growth lamellae and weak, dense growth lines; internally, dorsal valve with a high median septum extending to about mid-length, crural base similar to that of *Ph. arefactus* Veevers, 1959a and *Ph. polonicus* (Roemer,

1866) (see Biernat and Szulczewski 1975 for internal structure); no dental plates. It differs from *Phlogoiderhynchus polonicus* as illustrated by Biernat and Szulczewski (1975) and Baliński (2006) by less transverse, but more oval outline, a flat-topped fold, and a less protruding tongue.

Occurrence.—Same as previous. This species is also found in the Panxi section of eastern Yunnan Province; middle part of the Yidade Formation (Early Frasnian).

Superfamily Pugnacoidea Rzhonsnitskaya, 1956
Family Pugnacidae Rzhonsnitskaya, 1956
Genus *Pugnax* Hall and Clarke, 1893
Pugnax cf. *triplicata* (Chen, 1978 in Xu et al. 1978)

Fig. 4D.

1978 cf. *Striatopugnax triplicata* Chen (gen. et sp. nov.); Chen in Xu et al. 1978: 323, pl. 138: 2, 5, 8.

1984 cf. *Striatopugnax triplicata* Chen; Chen 1984: 116–117, text-figs. 14–17, pl. 4: 6–15, pl. 15: 4.

Material.—Eight specimens, poorly preserved, from the Caiziyan section. Samples: GC24 (1 specimen), GC23 (1 specimen), GC20 (1 specimen), GC19–30 (1 specimen), GC21–24 (3 specimens), ?GC8–9 (1 specimen).

Discussion.—Chen (in Xu et al. 1978) established *Striatopugnax* with *S. triplicata* Chen, 1978 (in Xu et al. 1978) as the type species, characterized by its micro-ornament of radial striae. Savage et al. (2002: 1165) synonimized it with *Pugnax*.

Although the specimens studied herein are quite similar to Chen's (1984) specimens of *Pugnax triplicata* (for example, short dental plates and 4 costae on fold; the left one on the studied specimen must be broken away judging from the shell contour), they differ by a much bigger size (approximately 18.7 mm wide, 16.9 mm long, and 12.6 mm thick for the figured specimen) from Chen's (1984) figured specimens (around 12.5 mm wide and 8.5 mm thick); their greatest width is located slightly more anteriorly; their lateral flanks are smooth without costae. The studied specimens are externally also similar to *Pugnax* sp. cf. *Pugnax pugnus* described by Veevers (1959a: 110–113), except for their smaller size.

Occurrence.—The present species occurs in Beds 19–24 (and also ?Middle Givetian beds 8–9) of the Caiziyan section, approximately *Pa. transitans* Zone.

Genus *Coeloterorhynchus* Sartenaer, 1966
Coeloterorhynchus sp.

Fig. 4E.

Material.—Four specimens from the Caiziyan section. Samples: GC24 (1 specimen), GC23 (1 specimen), GC21–24 (1 specimen), ?GC8–9 (1 specimen).

Discussion.—The studied specimens have four costae on fold, three costae in sinus, and two to three costae on each flank, which diminish in strength laterally. As no internal structures are available, shells are tentatively assigned to *Coeloterorhynchus* by external morphology, which is very similar to the type species of the genus (Sartenaer 1966: pl. 2: 2). It is different from superficially similar *Porostica zhonghuaensis* Chen in Xu et al. (1978) and *Calvinaria beichuanensis* Chen in Xu et al. (1978) from the Early Frasnian of the Longmenshan area in having a smaller size, a less transverse shell, and higher tongue.

Occurrence.—Same as previous. The present species occurs in Beds 21–24 (and also ?Middle Givetian beds 8–9) of the Caiziyan section, approximately *Pa. transitans* Zone.

Order Atrypida Rzhonsnitskaya, 1960
Family Atrypidae Gill, 1871
Subfamily Variatrypinae Copper, 1978
Genus *Desquamatia* Alekseeva, 1960
Desquamatia cf. *kimberleyensis* (Coleman, 1951)

Figs. 5–7.

1951 cf. *Atrypa desquamata kimberleyensis* Coleman, n. subsp.; Coleman 1951: 683–684, pl. 101: 7–19.

1971 cf. *Desquamatia* (*Synatrypa*) *kimberleyensis* (Coleman); Roberts 1971: 168–171, text-figs. 40, 41, pl. 38: 1–22.

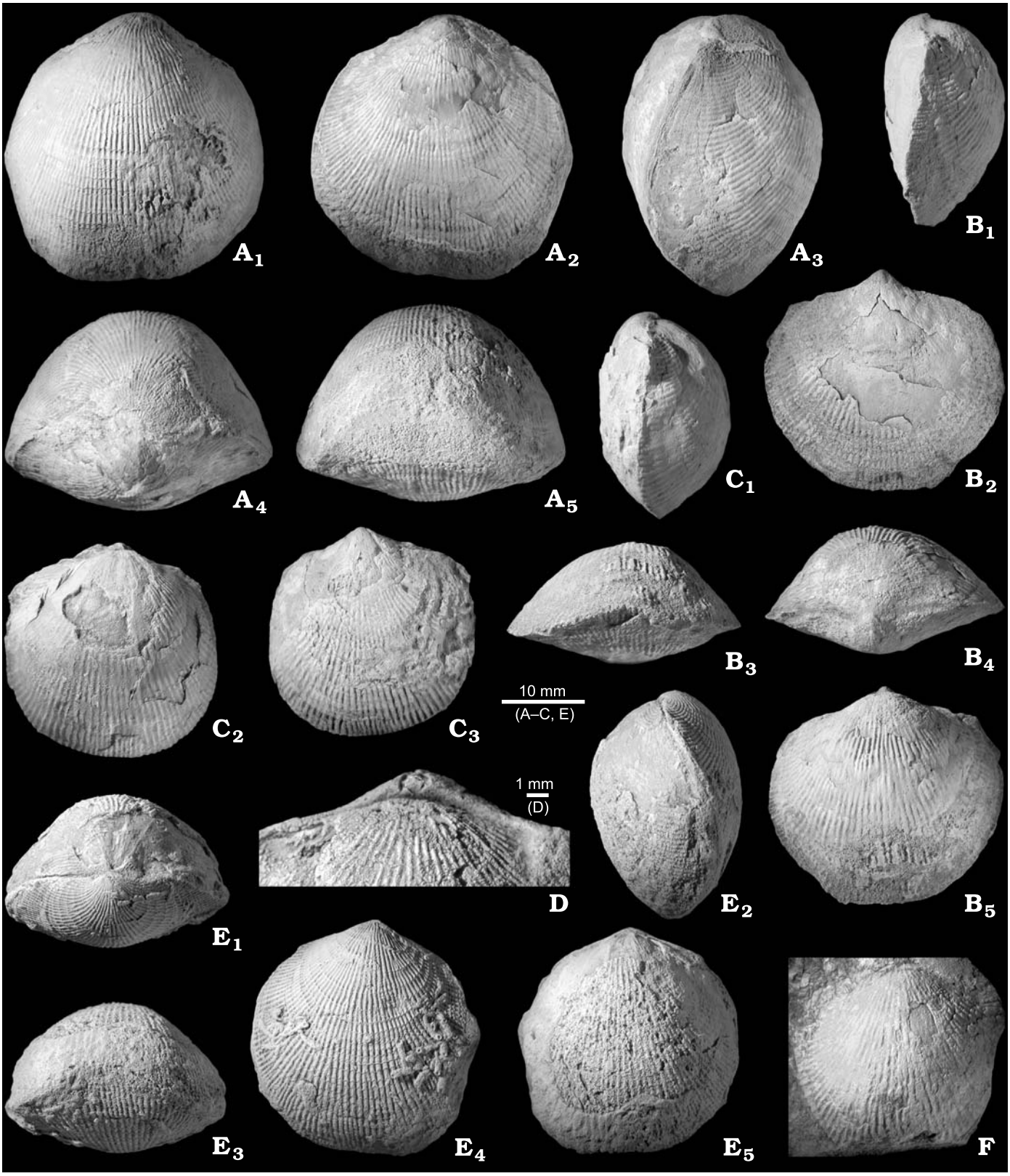
1978 cf. *Desquamatia* (*Synatrypa*) *kimberleyensis* (Coleman, 1951); Grey 1978: 20–33, text-figs. 10–16, pl. 2: 1 (specimens of figs. 2, 3 need restudy); in addition, Veevers (1959a: 121) and Grey (1978: 20) also regarded *Atrypa multimoda* Coleman as a synonym of *D. kimberleyensis*.

Material.—28 specimens from eastern Yunnan (most are well preserved) and northern Guangxi (poorly preserved). Samples: PY4 (10 specimens), PY5 (8 specimens); 10 specimens from the Caiziyan section of Guilin.

Description.—Shell medium-sized for genus, generally 25–30 mm wide in adults; transversely to slightly elongatedly oval; strongly to medium dorsi-biconvex in lateral profile. Surface covered with fine costae, about 7–8 costae per 5 mm from mid-length anteriorly of adult shells; costa number increases by bifurcation chiefly on ventral valve and intercalation on dorsal valve; micro-growth lines interrupted by variously spaced growth lamellae, about 9 growth lamellae per 10 mm in the middle part of shell, becoming denser to very dense in the anterior part. Ventral beak normally slightly incurved to adpressed in adult shells, with a minute area and small deltidial plates below the pedicle opening.

Internally secondary shell thickening prominent (Fig. 6). Ventral valve with deeply incised muscle field; with dental nuclei; tooth of normal size, with well-developed accessory lobe. Dorsally, muscle field slightly incised, with a low, centrally grooved median ridge; crural base subrounded (Fig. 7C), crus

Fig. 5. Atrypid *Desquamatia* cf. *kimberleyensis* (Coleman, 1951) from the Early and Middle Frasnian of the Panxi and Caiziyan sections. **A**. PUM05006, sample PY4, Panxi section, probably Middle Frasnian, dorsal (A_1), ventral (A_2), lateral (A_3), posterior (A_4), and anterior (A_5) views of the biggest shell, 31.8 mm wide, slightly greater than 33.0 mm long, 23.8 mm thick, ventral beak broken. **B**. PUM05007, sample PY4, Panxi section, probably Middle →



Frasnian, lateral (B_1), ventral (B_2), anterior (B_3), posterior (B_4), and dorsal (B_5) views of a rounded exfoliated shell, 27.7 mm wide, 25.6 mm long, and about 14.5 mm thick. **C**. PUM05008, sample PY4, Panxi section, probably Middle Frasnian, lateral (C_1), dorsal (C_2), and ventral (C_3) views of the sectioned specimen (Fig. 6). **D**. PUM05009, sample PY5, Panxi section, probably Middle Frasnian, ventral beak broken, showing small conjunct deltidial plates (note that true foramen (approximately dashed line) takes up only a small part at the bottom of the seen later enlarged hole). **E**. PUM05010, sample PY5, Panxi section, probably Middle Frasnian, posterior (E_1), lateral (E_2), anterior (E_3), ventral (E_4), and dorsal (E_5) views, 26.7 mm wide, 27.7 mm long, 18.5 mm thick, adpressed ventral beak. **F**. PUM05011, sample GC22, Caiziyan section, Early Frasnian, dorsal view.

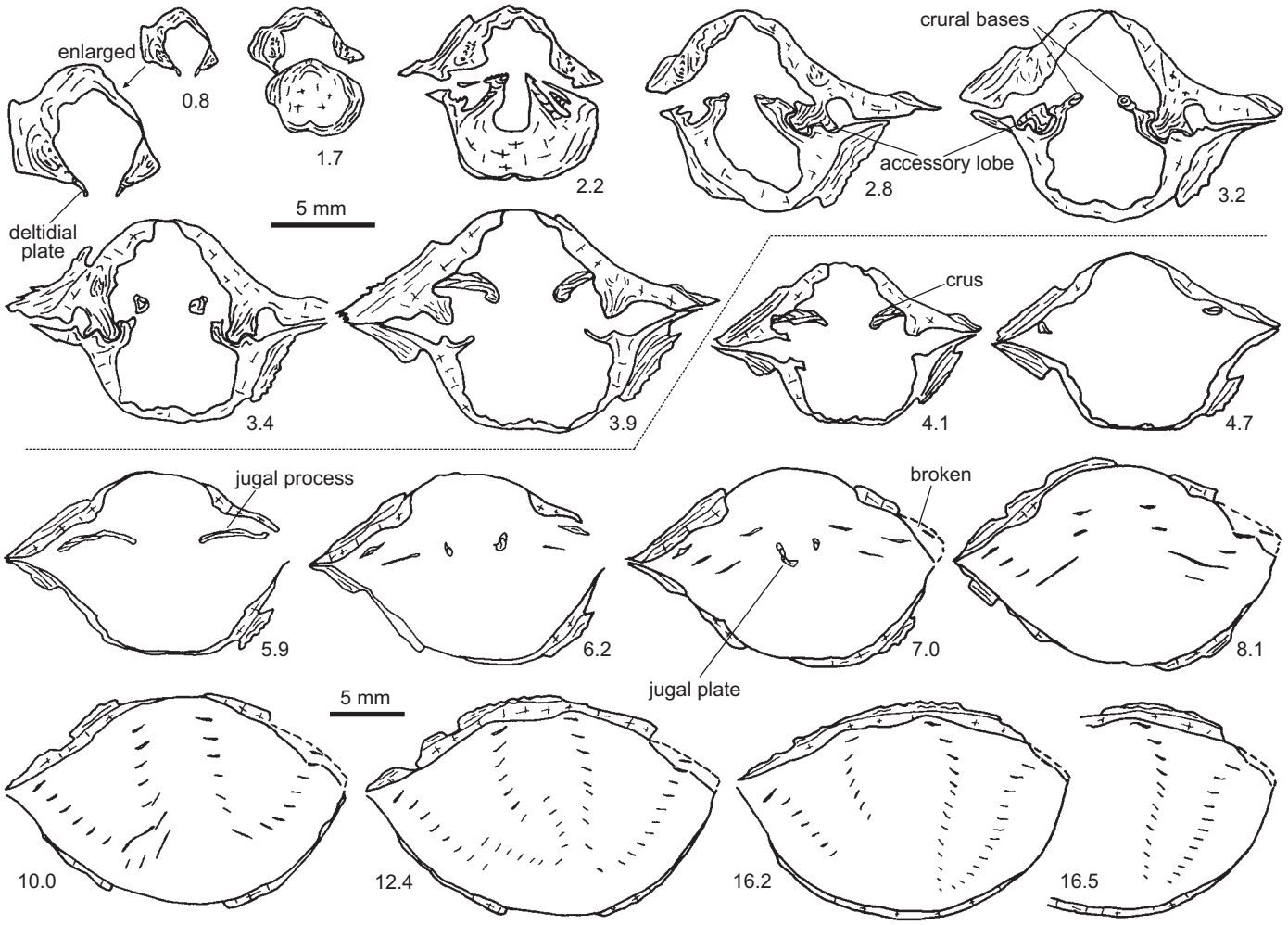


Fig. 6. Transverse serial sections of *Desquamatia* cf. *kimberleyensis* (Coleman, 1951), PUM05008, sample PY4, Panxi section, probably Middle Frasnian, specimen figured in Fig. 5C. Acetate peel number: 05A. Numbers refer to distance in mm from the ventral apex.

relatively large; disjunct jugal process tipped by small jugal plate; spiralia with about 14–15 whorls for sectioned specimen (about 26 mm wide and long), directed dorso-medianly.

Discussion.—When Coleman (1951) described the *Atrypa* fauna from the Devonian of western Australia, he did not designate a holotype for *Atrypa desquamata kimberleyensis*. Grey (1978) subsequently designated specimen UWA 26247a as the holotype for *Desquamatia* (*Synatrypa*) *kimberleyensis* and UWA 26273c as the holotype for *Atrypa reticularis teicherti* Coleman, 1951 (elevated to species level and assigned to *Kyrtatrypa* by Grey 1978). Unfortunately both holotypes are not well preserved in terms of micro-ornament. Both holotype and paratype specimens of the two species have about the same number of costae: 6–7 costae per 5 mm in the anterior part of shell, which is confirmed by our own counting on their figures (Coleman 1951: pl. 100: 1–10; pl. 101: 7–11, 18, 19). *Kyrtatrypa teicherti* has been based on only five specimens and there were no young forms in the collection (Coleman 1951: 681) at that time. According to Coleman (1951) and Grey (1978), *D. kimberleyensis* is distinct from *Kyrtatrypa teicherti* chiefly by the presence of an area and deltidial plates. However, it is not easy to differentiate bigger specimens of *D. kimberleyensis* from *Kyrtatrypa teicherti* as they are similar in the nature of the area. The two forms are also similar in internal structures of adult specimens except that the latter has a prominent robust dorsal median septum as demonstrated by Veevers (1959a) and Grey (1978); the number of spires is also similar (6–9 whorls; see of Veevers 1959a: text-fig. 70 and Roberts 1971: fig. 41).

The studied Yunnan specimens are similar to but larger than both Australian *K. teicherti* and *D. kimberleyensis*, and seemingly have more numerous and finer costae. Internally they are different from *K. teicherti* in their less prominent dorsal median septum and less deeply impressed dorsal muscle field; they differ from *D. kimberleyensis* type specimens by usually having a slightly incurved to adpressed beak, but this difference could well be a result of older shells. The most significant difference from the Australian material lies in the number of spiral whorls (about 14–15 whorls revealed by the near 26 mm wide specimen of the Chinese form *versus* about 8–9 whorls in 21–22 mm wide specimens of the two Australian forms). Further study is required to demonstrate whether

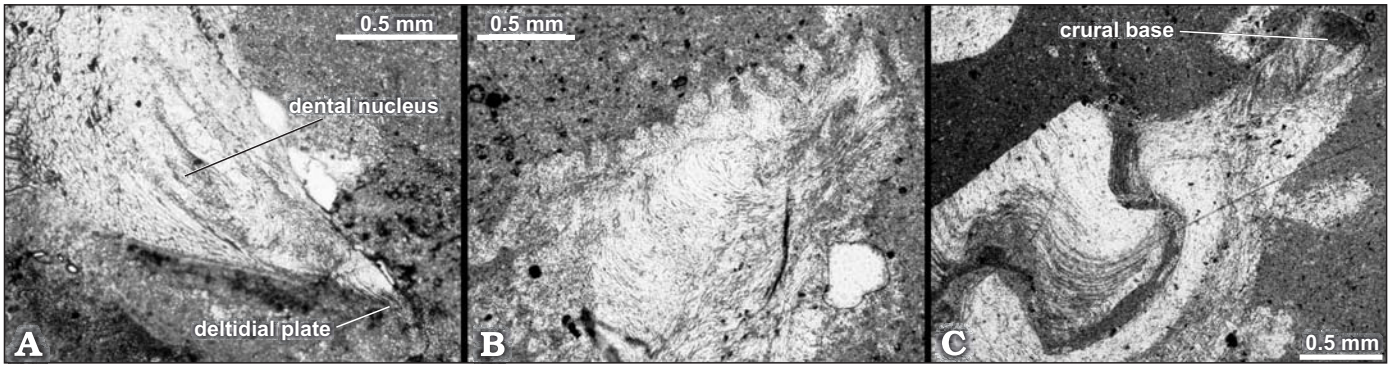


Fig. 7. Photographs of acetate peels of *Desquamatia* cf. *kimberleyensis* (Coleman, 1951) from the Middle Frasnian of the Panxi section, PUM05008, sample PY4 (same specimen as Fig. 5C). **A**. Left side at 0.8 mm. **B**. Left inner socket ridge at 2.2 mm showing combed knots (traces of muscle attachment?). **C**. Left tooth and socket at 3.2 mm.

there is a difference in the number of spires for similar sized specimens from South China and western Australia.

The Chinese specimens are also similar to *Desquamatia* (*Seratrypa*) *typica* (Chen, 1983), for example, in rib number, nature of ventral beak, etc. They can be distinguished by their smaller size, well developed concentric lamellae (*versus* absence of concentric ornament in *D. typica* according to its original description and illustrations), the presence of dental nuclei (*versus* none in *D. typica*) and fewer spiralia whorls (14–15 *versus* about 20 in *D. typica*). *D.* cf. *kimberleyensis* differs from varieties and mutations of "*Atrypa desquamata*" described by Grabau (1931) in having finer and denser costae at various degrees (e.g., mutation *alpha*, mutation *beta*, var. *magna*, mutation *hunanensis*, and mutation *kansuensis*). The Chinese specimens also differ from *Desquamatia richthofeni* (Kayser, 1883) in shell shape (dorsibiconvex and with a uniplicate anterior commissure); the ventral valve of the latter species is convex only in the umbonal region and concave in the remaining part of the shell and has no sinus or fold. Our material is also distinct from *Desquamatia peshiensis* (Grabau, 1931) in having a small incurved ventral beak, dorsibiconvex lateral profile, and shell outline of about equal width and length (*versus* highly protruding ventral beak, about equibiconvex lateral profile, and elongated shell outline in the latter species). *D. peshiensis* also has a robust dorsal median septum and prominent dental cavities (Chen 1983: 277, text-fig. 12). Of the Frasnian atrypids described by Copper (1967) from the Bergisches Land, Germany, only the finely ribbed variety of *Desquamatia* (*Seratrypa*) *pectinata* (his pl. 25: 1–3) and *Desquamatia schroeteri* have a similar number of ribs near the anterior margin, comparable to that of our studied species. It differs from the two German species in having much denser growth lamellae and from the former by having a much deeper ventral muscle field and more whorls in the spiralia (14–15 *versus* 8–10 for similar sized specimens); the internal structure of *D. schroeteri* is not known.

Specimens from the Early Frasnian of the Caiziyan section are similar, but have slightly coarser ribs (about 5–6 costae per 5 mm at anterior margins). As they are generally not as well preserved and no internal structures have been revealed, they are provisionally assigned to *Desquamatia* cf. *kimberleyensis* (e.g., Fig. 5F).

Occurrence.—The studied specimens were collected in the Panxi section of eastern Yunnan and the Caiziyan section of northeastern Guangxi, approximately the Frasnian *Palmatolepis transitans–Pa. punctata* zones.

Desquamatia qiziqiaoensis sp. nov.

Figs. 8, 9.

1978 ?*Desquamatia* (*Synatrypa*) *kimberleyensis* (Coleman, 1951); Grey 1978: 20–33, pl. 2: 2–3.

2005 *Desquamatia* (*Desquamatia*) cf. *minor* (Chen, 1983); Ma et al. 2005: 443–445, text-fig. 5, pl. 2: 6–15 (not others).

Holotype: PUM05014 (Fig. 8C), a complete adult shell.

Type horizon: Middle part of the Longkouchong Formation, bed 14 of Tan et al. (1987) or bed 3 of Yu et al. (1990: 96), Middle Frasnian.

Type locality: On the north side of a railway near the Qiziqiao railway station, Hunan Province, China.

Etymology: From the name of the locality, where it is most abundant.

Diagnosis.—Small sized *Desquamatia* with about 9–10 costae per 5 mm at the anterior margin, weakly dorsi-biconvex, tiny dental cavities or nuclei. From the most similar *Desquamatia minor* Chen, 1983 differs in having tiny dental cavities. From *D. schroeteri* differs in having slightly denser growth lammellae, denser costae, and narrower interspaces.

Material.—Sample PY5 from the Panxi section, probably Middle Frasnian (18 specimens). About 150 specimens from the Longkouchong Formation of the Qiziqiao section (about 85 various sized specimens were collected from a 5 cm thick layer in an area of 20 × 40 cm for sample QZQ3).

Description.—Shell small, generally 20–25 mm wide in adults; hinge slightly curved, about 1/2 and 2/3 width of shell in large and small specimens, respectively; suboval in shape, weakly dorsi-biconvex in lateral profile; anterior commissure rectimarginate in small specimens and somewhat strongly uniplicate in specimens over 20 mm wide. Surface covered with fine costae, about 9–10 costae per 5 mm at anterior margin; costae rounded, separated by furrows of narrower to equal width; increase of number of

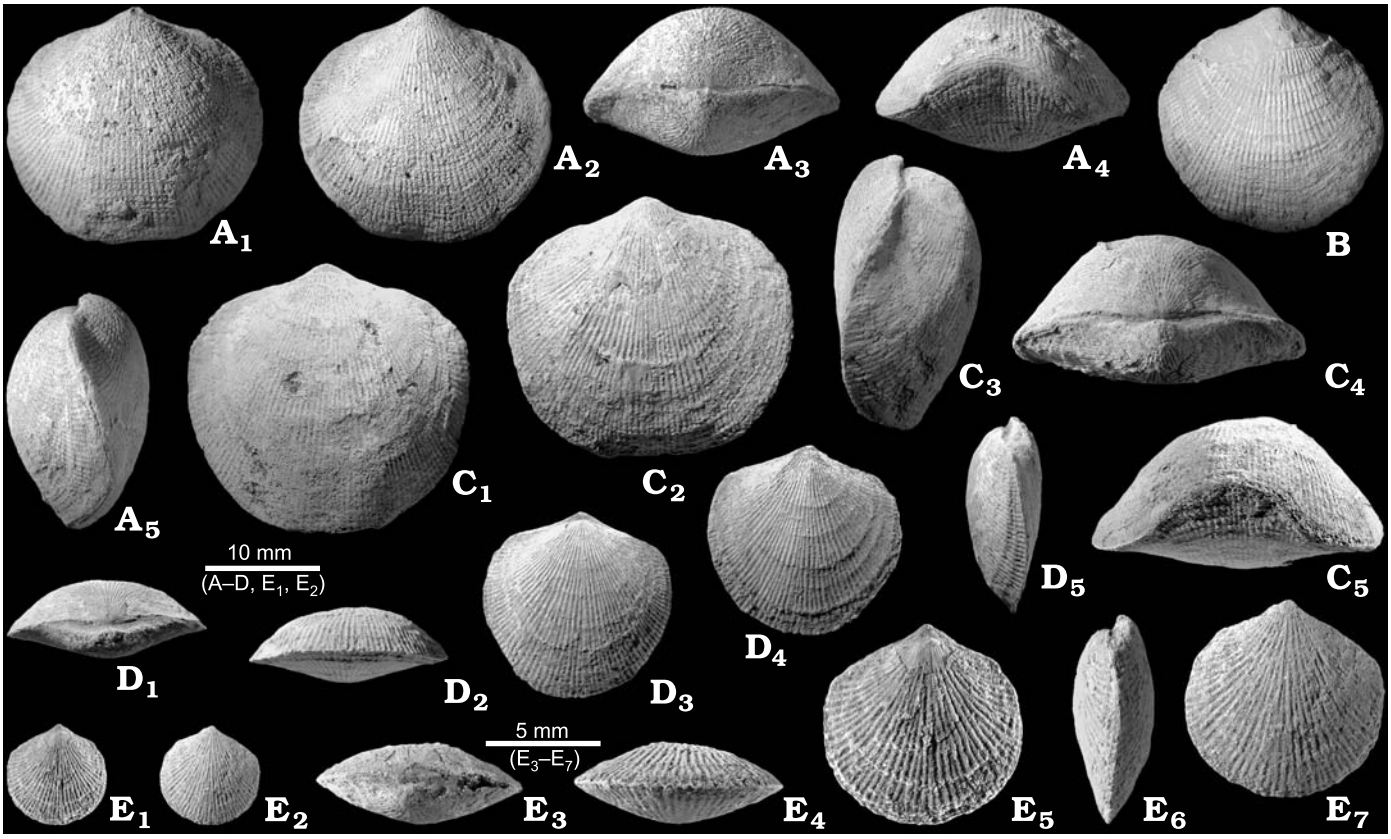


Fig. 8. Atrypid *Desquamatia qiziqiaoensis* sp. nov. from the Middle Frasnian of the Panxi and Qiziqiao sections. **A**. PUM05012, sample PY5, Panxi section, probably Middle Frasnian, dorsal (A_1), ventral (A_2), posterior (A_3), anterior (A_4), and lateral (A_5) views showing the general shape of a silicified specimen, 22.2 mm wide, 20.6 mm long, 12.9 mm thick. **B**. PUM05013, sample PY5, Panxi section, probably Middle Frasnian, ventral view showing nature of ribbing and concentric growth lamellae of a non-silicified specimen, 19.9 mm wide, 19.3 mm long, 11.8 mm thick. **C**. PUM05014 (holotype), sample QZQ1–3, Qiziqiao section, Middle Frasnian, dorsal (C_1), ventral (C_2), lateral (C_3), posterior (C_4), and anterior (C_5) views. **D**. PUM05015, sample QZQ3, Qiziqiao section, Middle Frasnian, posterior (D_1), anterior (D_2), dorsal (D_3), ventral (D_4), and lateral (D_5) views. **E**. PUM05016, sample QZQ3, Qiziqiao section, Middle Frasnian, dorsal (E_1, E_5), ventral (E_2, E_7), posterior (E_3), anterior (E_4), and lateral (E_6) views.

costae on ventral valve chiefly by bifurcation and on dorsal valve chiefly by intercalation. Variably spaced growth lamellae, generally about 5 per 5 mm to as many as 10 per 5 mm. Ventral beak normally slightly incurved, interarea small, with a pair of deltidial plates bounding a small submesothyrid foramen (about 0.75 mm in diameter for both specimens PUM05014 in Fig. 8C and PUM05015 in Fig. 8D) on its lower-lateral sides.

Internally secondary shell thickening distinct (Fig. 9). Ventral valve with incised muscle field; very tiny dental cavities, or dental nuclei; teeth strong, each with a well-developed accessory lobe. Dorsally, muscle field with a low, centrally grooved median ridge; inner socket ridges distinct, middle socket ridges low but robust, outer socket ridges indistinct; crural bases small, arising from tips of supporting socket plates (term used as Copper 2002: 1381, fig. 933); crura relatively strong, feathered, rapidly widened laterally in cross section.

Discussion.—These specimens are not regarded as juveniles or younger specimens of *Desquamatia* cf. *kimberleyensis* because the younger portion of the latter shell still seems to possess coarser costae than our new species. Grey's own figured specimens of *D. kimberleyensis* (Grey 1978: pl. 2: 2–3, specimens GSWA F9541 and F9542) possess finer and more numerous costae (10 costae per 5 mm at the anterior margin) than the holotype and are similar to the present species from South China in terms of external morphology (rib number and small straight interarea), rather than to the type specimens of *D. kimberleyensis*. *D. qiziqiaoensis* differs from *D. kimberleyensis* (Coleman, 1951) in its 9–10 costae *versus* 7–8 per 5 mm.

Sectioning has not revealed spiralia (the figured specimen herein has been ground to near mid-length), otherwise it is similar to *D.* cf. *kimberleyensis* internally. Externally it can be distinguished from the latter by its smaller size, finer and more numerous costae (generally 9–10 costae per 5 mm in the present species *versus* 7–8 costae per 5 mm in *D.* cf. *kimberleyensis*). The new species differs from *D. minor* Chen, 1983 (compare with Chen 1983: 288, fig. 22) and *D.* cf. *minor* from Guizhou Province of South China (compare with Ma et al. 2005: 443, fig. 4) in its tiny dental cavities (*versus* large dental cavities in the latter two). It also differs from *D.*

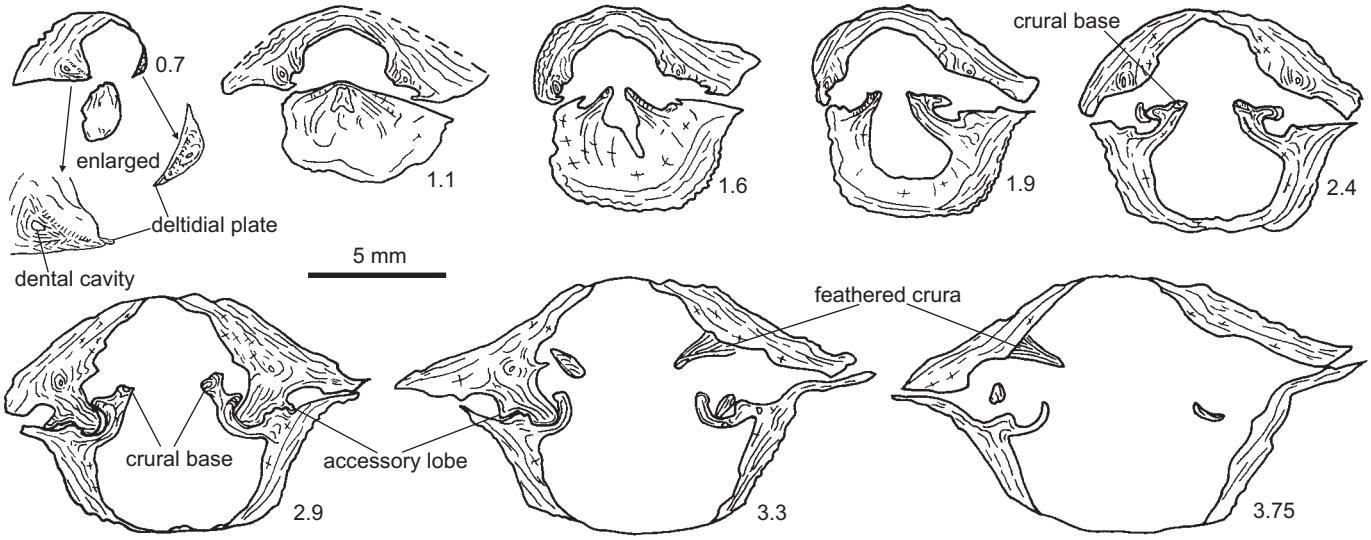


Fig. 9. Transverse serial sections of *Desquamatia qiziqiaoensis* sp. nov. Specimen PUM05017 (24.3 mm wide, 24.6 mm long, and 11.8 mm thick), acetate peel number: 05B, sample QZQ3, Qiziqiao section, Middle Frasnian. Numbers refer to distance in mm from the ventral apex.

schroeteri Copper, 1967 in having somewhat denser growth lamellae, denser costae, and narrower interspaces.

Occurrence.—Abundant in Bed 14 of the Qiziqiao section (Fig. 2), correlated with the Early *Palmatolepis hassi* conodont Zone; it is also present in the middle part of the Yidade Formation of the Panxi section (Fig. 2).

Subfamily Spinatrypinae Copper, 1978

Genus *Spinatrypa* Stainbrook, 1951

Spinatrypa subkwangsiensis (Tien, 1938)

Fig. 10C–G.

1938 *Atrypa aspera* var. *subkwangsiensis* sp. nov.; Tien 1938: 100–101, pl. 8: 1–4, 17.

1983 *Spinatrypa subkwangsiensis* (Tien); Chen 1983: 321, pl. 30: 5a–f.

2002 *Spinatrypa subkwangsiensis* (Tien, 1938); Ma et al. 2002: 388, fig. 11A–E.

2005 *Spinatrypa subkwangsiensis* (Tien, 1938); Ma et al. 2005: 441, pl. 1: 9–18.

Material.—One dorsal valve from the middle part of the Longkouchong Formation of the Qiziqiao section. About 50 specimens from the basal part of the Qilijiang Formation, most of which are complete shells.

Discussion.—The dorsal valve figured in Fig. 10C is about 12.7 mm wide and 12.4 mm long, with about 25 ribs on the whole shell surface and 4.5 ribs per 5 mm at the anterior margin, which is transitional between *Spinatrypina douvillei* (Mansuy, 1912) and *Isospinatrypa bodini* (Mansuy, 1912) that have respectively about 5 ribs per 5 mm and 4 ribs per 5 mm at the anterior margin (from counting on Mansuy's 1912 illustrations). However, its seemingly spiny ornamentation and much convex dorsal valve of the studied specimen suggest that it should be assigned to *Spinatrypa*. It is morphologically consistent with *S. subkwangsiensis* Group B of Ma et al. (2002: 388, with finer and more ribs than Group A).

Relatively abundant specimens in the basal part of the Qilijiang Formation in the Qiziqiao section (Fig. 10D–G for example) are small-sized specimens similar to those reported by Ma et al. (2005, pl.1: 9–18). They are generally less than 10 mm in width, biconvex (in specimens smaller than 8 mm in width) to medium dorsi-biconvex (in larger specimens), with about 18 ribs (for specimens of Fig. 10F, G) and 20–25 ribs (for specimens of Fig. 10D, E). Larger specimens show spiny bases (Fig.10E_3) or traces of spines (Fig. 10D_1). A submesothyrid subrounded foramen (0.5 to 0.75 mm in diameter, depending on shell size) is bounded by a pair of deltidial plates on its lower-lateral sides. These specimens of sample QZQ4 are smaller than *Spinatrypa discoforma* Chen, 1983; they have a dorsi-biconvex profile (*versus* biconvex to ventribiconvex in *S. discoforma*), more ribs (20–25 *versus* 15–20 in *S. discoforma*) and a well developed foramen defined by a pair of deltidial plates (foramen and deltidial plates in *S. discoforma* are "obsolescent and not present" according to its original description by Chen 1983: 321–322). By comparison with similar-sized specimens of *Spinatrypa subkwangsiensis* Group A from the Shetianqiao section (Ma et al. 2002), these specimens seem to possess higher but narrower ribs, much denser growth lamellae, and finer spines or spine bases. It can not be ruled out that they actually are mature specimens and represent a distinct species of *Spinatrypa* or *Isospinatrypa*, pending more material available for study and comparisons.

Occurrence.—This species is widely distributed in South China, both geographically and stratigraphically, e.g., in the Givetian–Frasnian interval of central Hunan and northern Sichuan (e.g., Tien 1938; Chen 1983; Ma et al. 2002). The studied specimens are from Beds 14 and 20 of the Qiziqiao section (Fig. 2), correlated with the *Palmatolepis hassi* to lower part of the Early *Pa. rhenana* conodont zones.

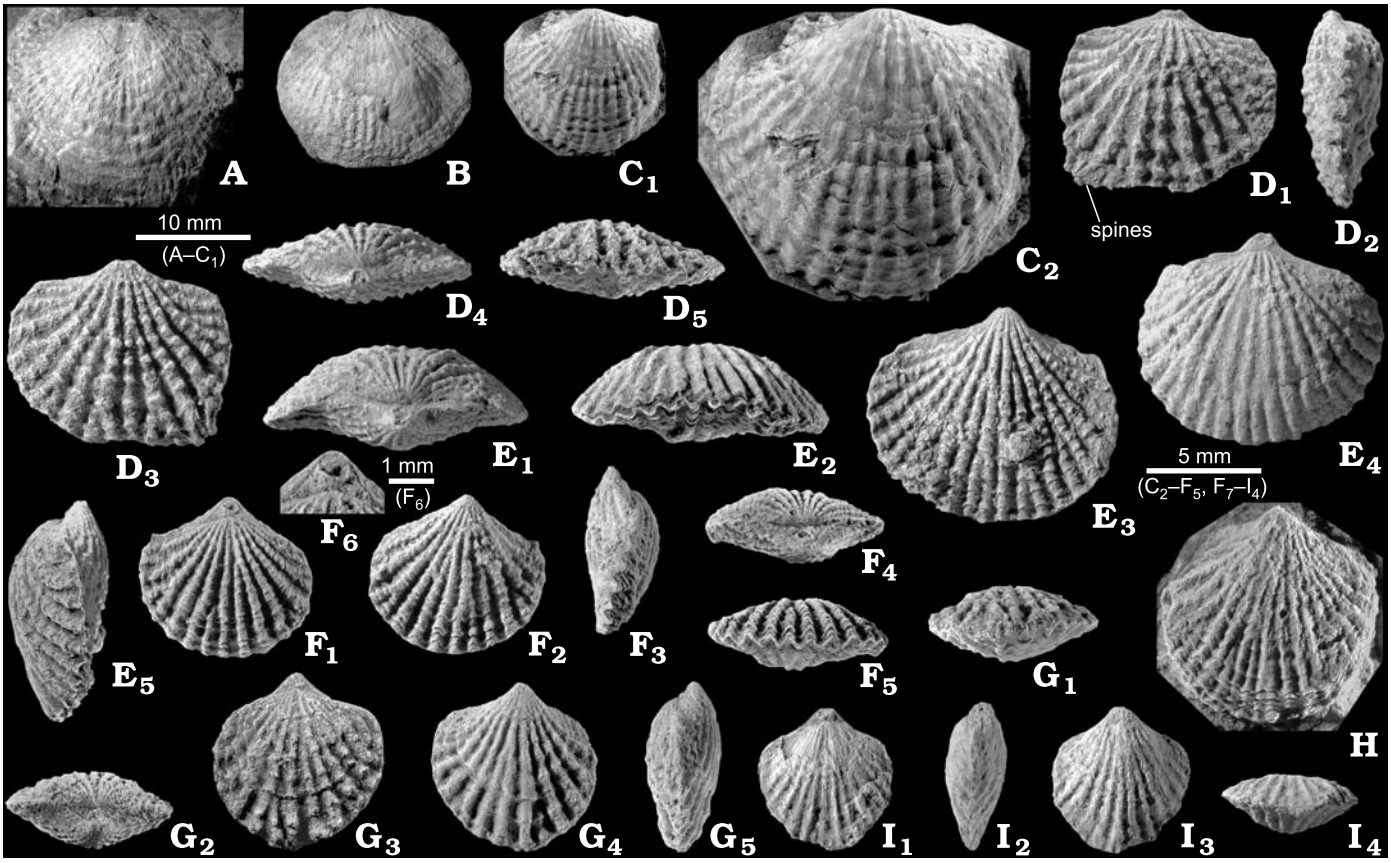


Fig. 10. The spinatrypinae brachiopods from the Early and Middle Frasnian of the Caiziyan and Qiziqiao sections. **A**, **B**. *Spinatrypina douvillei* (Mansuy, 1912). **A**. PUM05018, sample GC21–24, Caiziyan section, Early Frasnian, dorsal view of an exfoliated specimen on slab. **B**. PUM05019, sample GC21–24, Caiziyan section, Early Frasnian, dorsal view of another exfoliated specimen on slab. **C**–**G**. *Spinatrypa subkwangsiensis* (Tien, 1938) Group B. **C**. PUM05020, sample QZQ1–3, Qiziqiao section, Middle Frasnian, dorsal view of an exfoliated specimen on slab. **D**. PUM05021, sample QZQ4, Qiziqiao section, probably Late Frasnian, dorsal (D_1), lateral (D_2), ventral (D_3), posterior (D_4), and anterior (D_5) views of an adult(?), note spiny bases and broken spines. **E**. PUM05022, sample QZQ4, Qiziqiao section, probably Late Frasnian, posterior (E_1), anterior (E_2), ventral (E_3), dorsal (E_4), and lateral (E_5) views of another adult (?) with a well preserved foramen bounded by a pair of conjunct deltidial plates at the bottom. **F**. PUM05023, sample QZQ4, Qiziqiao section, probably Late Frasnian, dorsal (F_1), ventral (F_2), lateral (F_3), posterior (F_4), anterior (F_5), and enlarged area (F_6) views of a juvenile with a well preserved foramen bounded by a pair of conjunct deltidial plates at the bottom. **G**. PUM05024, sample QZQ4, Qiziqiao section, probably Late Frasnian, anterior (G_1), posterior (G_2), dorsal (G_3), ventral (G_4), and lateral (G_5) views of another juvenile. **H**–**I**. *Spinatrypina lungkouchungensis* (Tien, 1938). **H**. PUM05025, sample QZQ4, Qiziqiao section, probably Late Frasnian, ventral view, specimen is on slab. **I**. PUM05026, sample QZQ3, Qiziqiao section, Middle Frasnian, dorsal (I_1), lateral (I_2), ventral (I_3), and anterior (I_4) views of a juvenile.

Genus *Spinatrypina* Rzhonsnitskaya, 1964

Spinatrypina douvillei (Mansuy, 1912)

Fig. 10A, B.

1912 *Atrypa Douvillei* nov. sp.; Mansuy 1912: 74, pl. 13: 9a–h.
1931 *Atrypa douvillii* Mansuy; Grabau 1931: 194–197, pl. 15: 15, pl. 22: 5–10.
1938 *Atrypa douvillii* Mansuy; Tien 1938: 95–97, pl. 13: 5–10, 13.
1983 *Spinatrypina douvillii* (Mansuy); Chen 1983: 316, pl. 31: 3–5.

Material.—About 50 poorly preserved shells, valves, and fragments from the Early Frasnian of the Caiziyan section (samples GC8–9, GC20, and GC21–24). Three complete shells from the ?Middle Frasnian of the Panxi section (sample PY5).

Discussion.—The specimen of Fig. 10A is a heavily exfoliated, weakly convex dorsal valve, with about 40–45 ribs (approximately 19.0 mm wide, 16.5 mm long, exact rib number is uncertain), with about 6 ribs per 5 mm near the anterior. Another figured specimen (Fig. 10B) is also a dorsal valve, which is subrounded in outline, slightly convex, with about (5–) 6 ribs per 5 mm at anterior margin (around 30–35 ribs on whole surface; size is about 17.0 mm wide, 13.9 mm long).

The outline, dorsal valve convexity, and nature of ribbing are basically in agreement with *Spinatrypina douvillei* (Mansuy, 1912) and material described by subsequent workers from South China (e.g., Chen 1983) [see Grabau (1931: 194) for an English translation of Mansuy's original French description]. Grabau (1931: 194) changed the name *douvillei* (to honor M.H. Douvillé by Mansuy 1912) to *douvillii* without giving any reasons, which has since been followed by subsequent workers, such as Tien (1938), Wang et al. (1964), and Chen (1983).

Occurrence.—Same as the previous species in geographic and stratigraphic distribution. The studied specimens are from the

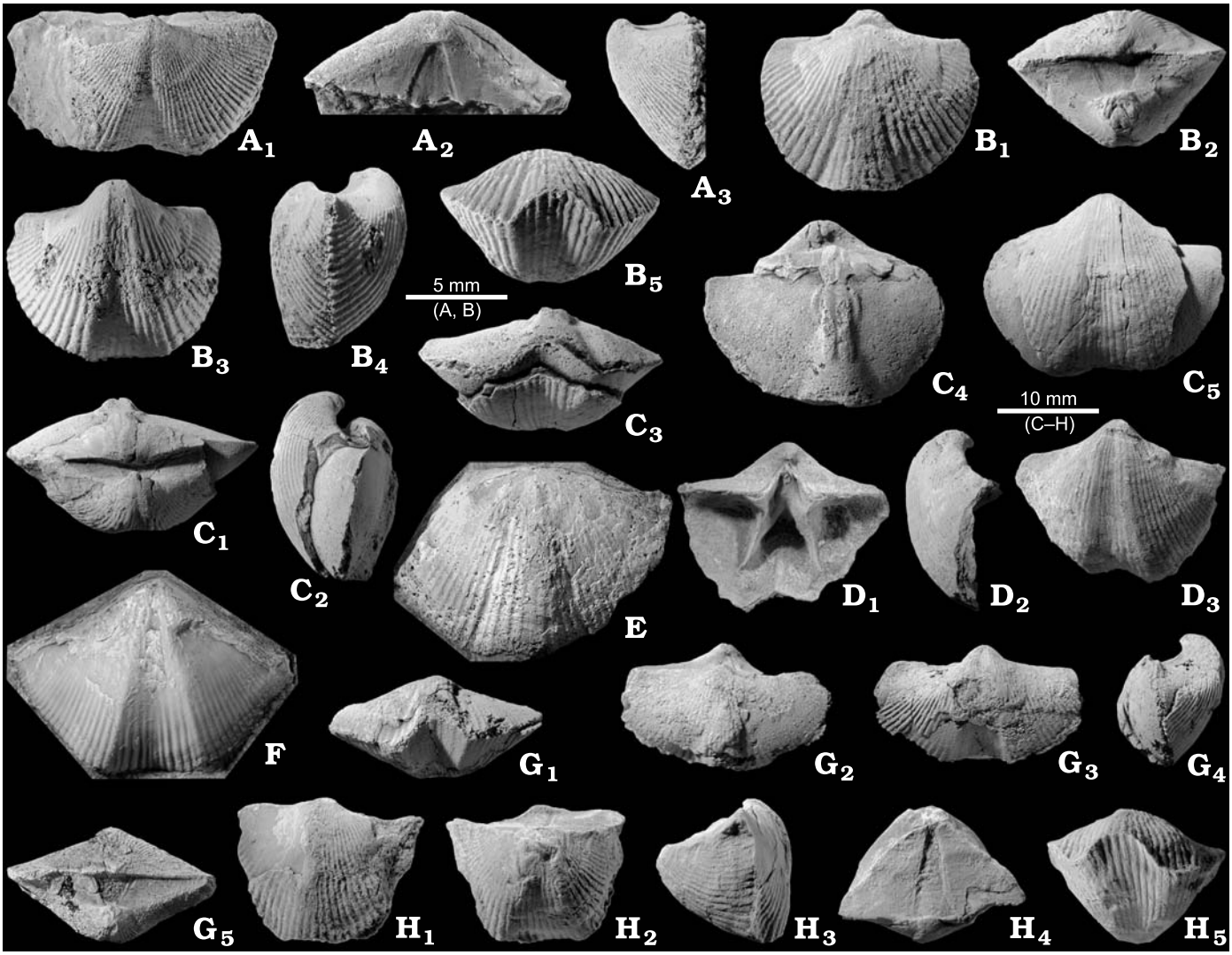


Fig. 11. Plicate spiriferid brachiopods from the Frasnian of the Qiziqiao and Qifengzhen sections. **A**. *Theodossia*? sp. PUM05027, sample QZQ4, Qiziqiao section, probably early Late Frasnian (cardinal extremities somewhat broken), ventral (A_1), area (A_2), and lateral (A_3) views of a ventral valve. **B–D**. *Cyrtospirifer*? sp. **B**. PUM05028, sample QZQ3, Qiziqiao section, Middle Frasnian, dorsal (B_1), posterior (B_2), ventral (B_3), lateral (B_4), and anterior (B_5) views of a juvenile. **C**. PUM05029, sample QZQ1, Qiziqiao section, Middle Frasnian, posterior (C_1), lateral (C_2), anterior (C_3), dorsal (C_4), and ventral (C_5) views, note the thick shell material. **D**. PUM05030, sample QZQ1–3, Qiziqiao section, Middle Frasnian, ventral interior (D_1), lateral (D_2), and ventral exterior (D_3) views, note thickened ventral posterior. **E**, **F**. *Cyrtospirifer* cf. *sichuanensis* Chen in Xu et al. (1978). **E**. PUM05031, dorsal view of a heavily exfoliated specimen of sample GQ6 of the Qifengzhen section in the vicinity of Guilin, about 17 m above the base of the "Gubi Formation" (Zhong et al. 1992). **F**. PUM05032, sample QZQ1, Qiziqiao section, Middle Frasnian, ventral view of an entirely exfoliated specimen. **G**. *Cyrtospirifer* cf. *extensa* Ching et Liu in Wang et al. 1982; PUM05033, sample QZQ1, Qiziqiao section, Middle Frasnian (cardinal extremities somewhat broken), anterior (G_1), dorsal (G_2), ventral (G_3), lateral (G_4), and posterior (G_5) views. **H**. *Pyramidaspirifer* cf. *helenae* (Fenton, 1918); PUM05034, sample QZQ4, Qiziqiao section, probably early Late Frasnian, dorsal (H_1), ventral (H_2), lateral (H_3), area (H_4), and anterior (H_5) views of a slightly distorted shell.

Caiziyan and Panxi sections (Fig. 2), correlated with the *Palmatolepis transitans–Pa. punctata* conodont zones.

Spinatrypina lungkouchungensis (Tien, 1938)

Fig. 10H, I.

1938 *Atrypa douvillii* var. *lungkouchungensis* Tien (var. nov.); Tien 1938: 97–98, pl. 13: 14–16.

Material.—Four specimens. Samples: QZQ1–3 (2 specimens), QZQ3 (1 juvenile), QZQ4 (1 specimen). QZQ1–3 and QZQ3, Qiziqiao section, Middle Frasnian; QZQ4, Qiziqiao section, probably Late Frasnian.

Discussion.—Tien (1938) described one species and a variety of the same species of *Spinatrypina* from the same sample of the Lungkouchung (now spelled Longkouchong) section: *Atrypa douvillii* var. *lungkouchungensis* Tien, 1938 and *A. douvillii* Mansuy, 1912. The former is characterized by an elongated outline, with the ventral valve being more convex than the dorsal valve; the latter is characterized by a somewhat biconvex profile and subrounded outline. Because of few specimens (both Tien's original and our new collections), it is difficult to determine at this stage if these differences represent intraspecific variation or are two species.

The studied specimens are not sufficiently well preserved to show the overall morphology except the juvenile (Fig. 10I) that has a slightly elongated outline. They are all assigned to *Spinatrypina lungkouchungensis* (Tien, 1938).

Occurrence.—So far the present species has been only reported from the Qiziqiao section, correlated with the *Palmatolepis hassi* to lower part of the Early *Pa. rhenana* conodont zones.

Order Spiriferida Waagen, 1883
Superfamily Theodossioidea Ivanova, 1959
Family Theodossiidae Ivanova, 1959
Genus *Theodossia* Nalivkin, 1925
Theodossia? sp.

Fig. 11A.

Material.—Sample QZQ4 (five specimens including dorsal and ventral valves). Qiziqiao section, probably Late Frasnian.

Discussion.—The species has about 22–25 costae on each flank and is tentatively assigned to *Theodossia* by its sinus (without bounding plications), and lack of delthyrial plate. The type species of *Theodossia* (*T. anossofi*) as figured by Verneuil (1845: 153–155, pl. 4: 3) possesses much coarser costae and a much shorter hinge. Sample DS65 (Dushan section, Middle Frasnian) is similar to the type species (the plicate spiriferids of the Dushan section will be described in a separate paper). Shell ornamentation of the studied species is similar to that of *T. hungerfordi* (Hall, 1858) from the Late Frasnian of Iowa (USA), especially sinal ornamentation (i.e., with the exception of the central costa that bifurcates anteriorly and is finer, other sinal costae simple and almost as strong as flank plications); beyond this, differences between the two forms are obvious in many respects: ventral area (catacline to slightly curved apsacline *versus* curved apsacline), sinus (with totally 13 sinal costae at anterior commissure, triangular in cross section *versus* shallow, flat-bottomed), and shell shape (transverse *versus* sub-rounded).

Occurrence.—Qiziqiao section (Fig. 1), correlated with the lower part of the Early *Palmatolepis rhenana* conodont Zone.

Superfamily Cyrtospiriferoidea Termier and Termier, 1949
Family Cyrtospiriferidae Termier and Termier, 1949
Genus *Cyrtospirifer* Nalivkin, 1924 in Frederiks 1924
Cyrtospirifer cf. *extensa* Ching and Liu, 1982 in Wang et al. 1982

Fig. 11G.

1982 cf. *Cyrtospirifer extensa* Ching et Liu (sp. nov.); Wang et al. 1982: 237–238, pl. 74 : 8a–e.

Material.—One more or less complete shell (figured) and two poorly preserved dorsal valves from the Lungkouchung Formation in the Qiziqiao section (sample QZQ1).

Discussion.—The studied specimens have the following main features: delthyrial plate covering posterior 1/3 of delthyrium, sinal plications generally fewer than 10 in number, with 1 lateral sinal plication on each side and a pair of simple primary plications, flank plications about 23 on each side, rounded and separated by deep furrows of about same width, shell material thin with secondary fibrous layer developed and secondary thickening is not developed (so that plication pattern can be imprinted on internal mould surface).

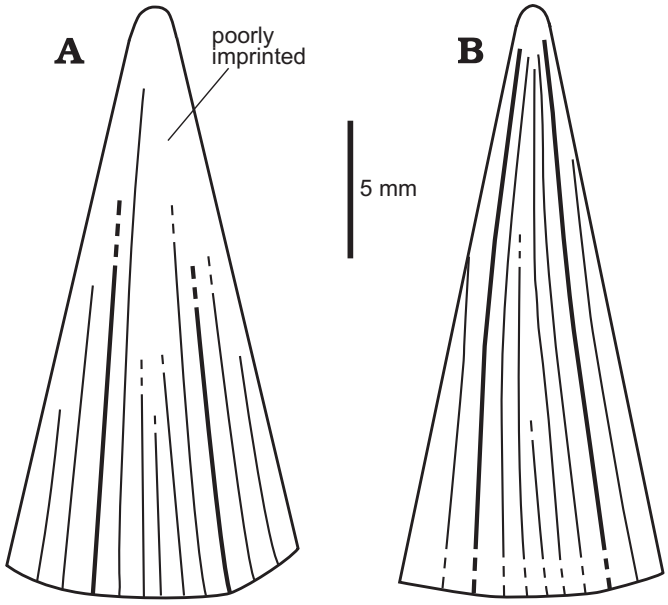


Fig. 12. **A**. Sinal plication pattern of *Cyrtospirifer* cf. *sichuanensis* Chen, 1978, specimen illustrated on Fig. 11F. **B**. Sinal plication pattern of *Cyrtospirifer*? sp., specimen illustrated on Fig. 11C.

The shell outline is similar to that of *Cyrtospirifer extensa* Ching and Liu in Wang et al. (1982) from the Frasnian of eastern South China (Lianhua County, Jiangxi Province), but differs in having a large ventral interarea (*versus* a short and low interarea in *C. extensa* although its shell size is even larger). It is distinct from *Cyrtospirifer*? *variabilis* Ma and Sun, 2001 from the Shetianqiao and Xikuangshan sections in having a much more transverse shell outline and a well developed delthyrial plate (*versus* a very short delthyrial plate in *Cyrtospirifer*? *variabilis*).

Occurrence.—The present species occurs in Bed 14 of the Qiziqiao section (Fig. 2), correlated with the *Palmatolepis hassi* conodont Zone.

Cyrtospirifer cf. *sichuanensis* Chen, 1978 in Xu et al. 1978

Figs. 11E, F, 12A, 13.

1978 cf. *Cyrtospirifer sichuanensis* Chen (sp. nov.); Xu et al. 1978: 374, pl. 149: 2, 3.

2003 *Cyrtospirifer* "*sinensis*" (Grabau, 1931); Ma and Day 2003: 276, figs. 6.15, 6.16, 6.20–6.22, 6.24, 6.25 (not 6.19 and 6.23).

Material.—Fourteen specimens from sample QZQ1 (including nine ventral valves, three dorsal valves, and two com-

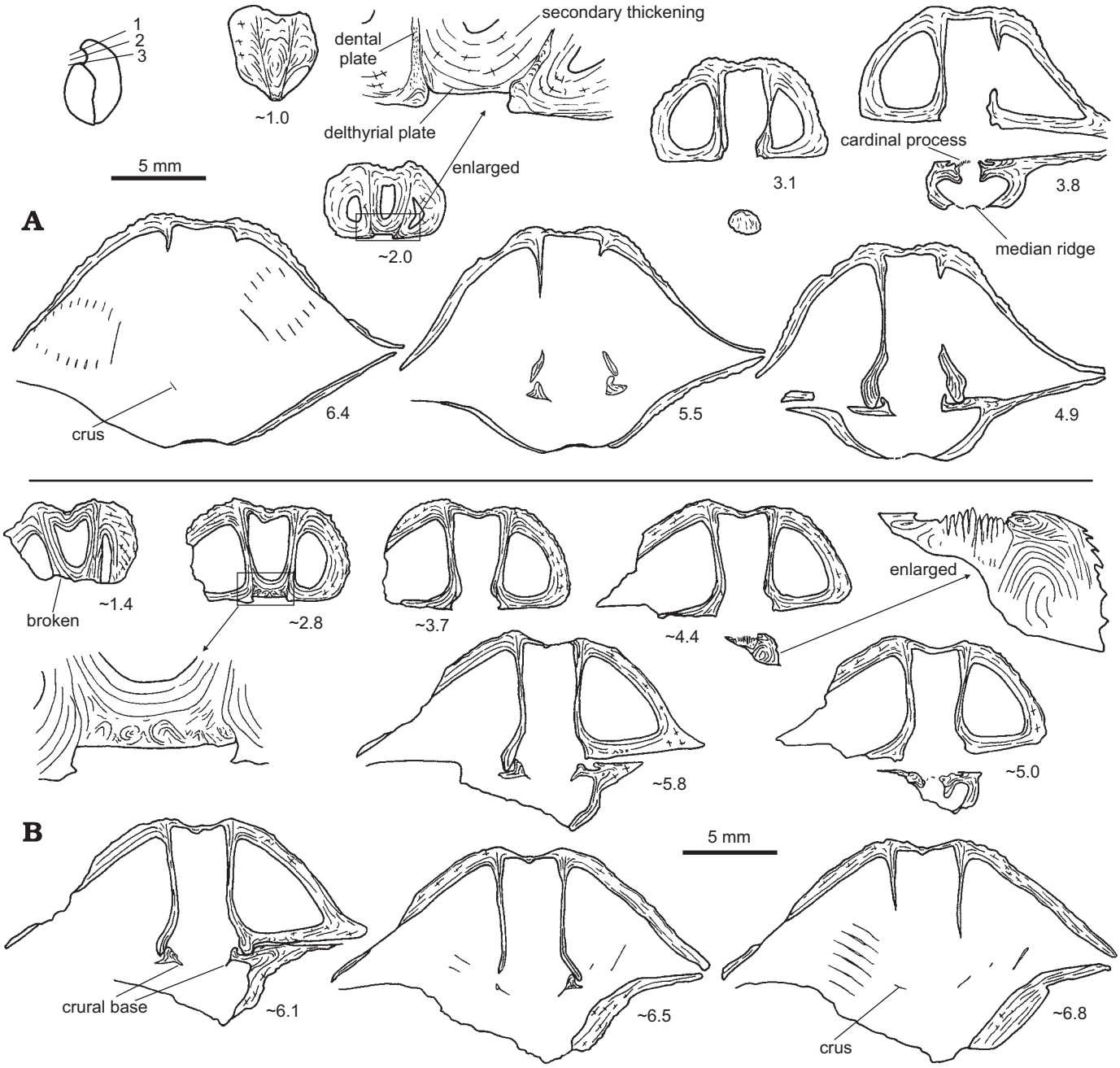


Fig. 13. Transverse serial sections of *Cyrtospirifer* cf. *sichuanensis* Chen, 1978; Qiziqiao section, Middle Frasnian. Numbers refer to distance in mm from the ventral apex. **A**. Specimen PUM05035, numbers 1–3 on the lateral profile indicate the first three sections at ~1.0, ~2.0, 3.1 mm; acetate peel number: 05C, sample QZQ1. **B**. Specimen PUM05036, acetate peel number: 05E, sample QZQ1.

plete shells), two fragmentary ventral valves from sample QZQ4, and one heavily exfoliated dorsal valve from sample GQ6 of the Qifengzhen section (see figure explanation). In addition, there are about 20 relatively well preserved specimens and many broken ones from the latest Frasnian of the Xikuangshan section in central Hunan and Tien's (1938) original specimens presumably from the Longkouchong locality for comparison.

Discussion.—Specimens from the Longkouchong Formation are mostly poorly preserved. Tien (1938) described two species of *Cyrtospirifer* from the same formation at this locality, here considered as one (Ma and Day 2003). So far no specimens similar to those figured by Tien (1938) have been recovered, but Tien's specimens are worn shells that do not have micro-ornament preserved, and a general shape similar to *Sinospirifer subextensus* (Martelli, 1902) from the Early Famennian of central Hunan Province (Ma et al. 2003; Ma and Day in press). One of Tien's specimens has a small shell area with preserved micro-ornament of the *whitneyi–subextensus* type (i.e., with pustules both on shell plications and

in interspaces, which is typical of *Cyrtospirifer whitneyi* and *Sinospirifer subextensus*), and a thickened ventral posterior (Tien 1938: pl. 16: 1, specimen 6231). Two specimens (Tien 1938: pl. 16: 2–3, specimens 6285 and 6235) are seen to have traces of a delthyrial cover that is identical with that of *S. subextensus*. As large-sized Frasnian *Cyrtospirifer* (e.g., *C.* "*sinensis*" in Ma and Day 2003) from South China have not been found so far to have pustule-like micro-ornament and *subextensus*-like delthyrial covering, it cannot be ruled out that Tien's specimens came from the Early Famennian, and were labeled erroneously. Tien (1938) never mentioned the most common brachiopod (i.e., *Desquamatia qiziqiaoensis* in the present paper) from the same horizon and locality.

Two cyrtospiriferids were described from the Longmenshan section of Sichuan Province in southwestern China (Xu et al. 1978): *Cyrtospirifer sinensis* (Grabau, 1931) and *C. sichuanensis* Chen, 1978, but their internal structures and micro-ornament were not described. Externally the present specimens are similar to *C. sichuanensis* in shell size and number of sinal plications, but differ in having extended cardinal extremities. Restudy of the Late Frasnian *Cyrtospirifer* "*sinensis*" specimens of the Xikuangshan section shows that they do not possess a thickened ventral posterior as described by Ma and Day (2003: 276), whose description was then based on specimen PUM 98057 illustrated by fig. 6.19 from the Chongshanpu section. The present specimens are different from the Xikuangshan specimens in having fewer sinal plications (generally fewer than 10 *versus* generally 10–15), but shells are smaller in size. *C.* cf. *sichuanensis* is distinct from *Cyrtospirifer*? *variabilis* Ma and Sun, 2001 from the Shetianqiao and Xikuangshan sections in its larger size and in having a distinct delthyrial plate (*versus* a very short delthyrial plate in *Cyrtospirifer*? *variabilis*).

The shell is similar to *Cyrtospirifer kermanensis* Brice, 1999 described from Iran, but it differs in the absence of fine spines and radial striae and its adult specimens (Fig. 11E, F) differ in having more alate cardinal extremities.

Occurrence.—This species occurs in the Middle and Late Frasnian of South China. The studied specimens are from Beds 14 and 20 of the Qiziqiao section of central Hunan (Fig. 2), correlated with the *Palmatolepis hassi* Zone to the lower part of the Early *Pa. rhenana* Zone and 17 m above the base of the "Gubi" Formation (see Zhong et al. 1992).

Cyrtospirifer? sp.

Figs. 11B–D, 12B, 14.

Material.—Fifteen ventral valves, mostly poorly preserved, including 14 from sample QZQ1 and one from sample QZQ1–3; two complete shells, including one from sample QZQ1 and one juvenile from sample QZQ3. One ventral valve from Middle Frasnian Dushan section (sample DS64) is questionably assigned here.

Discussion.—Main features of this species are: shell material thick and dorsal adductor muscle field narrow, with anterior pair elongated and deeply incised, separated by a low myophragm. This species differs from other species of *Cyrtospirifer* in its greatly thickened ventral posterior, instead of a delthyrial plate. It is similar to North American *Regelia* (Middle to Late Frasnian), but differs in having a more curved ventral interarea (*versus* a much less curved to a catacline ventral interarea in *Regelia*).

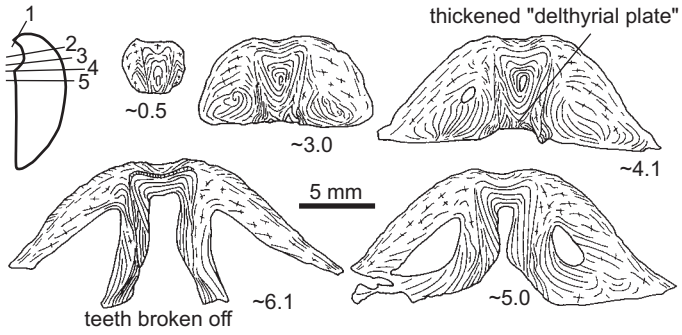


Fig. 14. Transverse serial sections of *Cyrtospirifer*? sp., sample QZQ1, Qiziqiao section, Middle Frasnian. Specimen PUM05037, acetate peel number 05D. Numbers refer to approximate distance in mm from the ventral apex; numbers 1–6 on the lateral profile indicate the successive position of sections.

Occurrence.—So far this species is mainly present in Bed 14 of the Qiziqiao section of central Hunan, correlated with the *Palmatolepis hassi* conodont Zone.

Superfamily Uncertain
Family Conispiriferidae Ma and Day, 2000
Genus *Pyramidaspirifer* Ma and Day, 2000

Pyramidaspirifer cf. *helenae* (Fenton, 1918)

Fig. 11H.

1918 cf. *Spirifer cyrtinaformis helenae* nov. var.; Fenton 1918: 216, pl. 6: 11–17.

1982 cf. *Tenticospirifer* cf. *T. cyrtinaformis* (Hall and Whitfield, 1872); Cooper and Dutro 1982: 112, pl. 33: 9–15.

Material.—One poorly preserved, distorted specimen (sample QZQ4) from the basal part of the Qilijiang Formation in the Qiziqiao section.

Description.—Flank plications simple, with about 17 on each flank, diminishing in strength laterally; sinal plications also simple, except for the central one, which bifurcates and is slightly weaker, totally 8 in number anteriorly; sinus shallow but distinct, originating near posterior end, without primary plications; fold only appearing at mid-length, with weaker plications centrally, transitions between fold and flanks gradual, without a distinct delimiting furrow on each side.

Discussion.—The nature of the fold and sinus (no primary plications in the sinus and no delimiting furrow on each side of fold) excludes it from the Cyrtospiriferidae (e.g., *Tenticospirifer*). The shell is similar to North American Late Frasnian *Pyramidaspirifer helenae* (Fenton, 1918) except that the Qiziqiao specimen has a more swollen ventral valve.

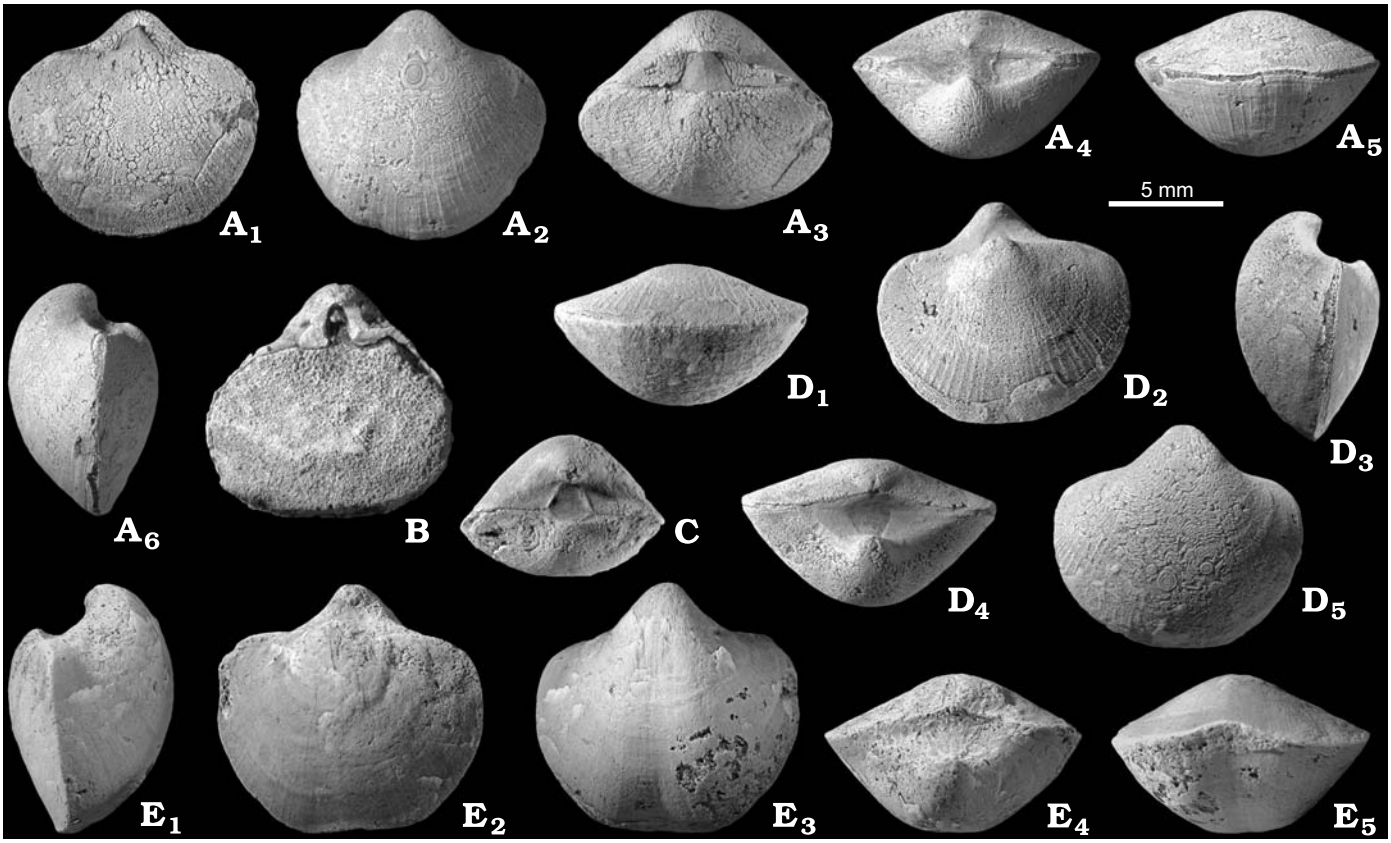


Fig. 15. "Smooth-shelled" spiriferid *Emanuella* aff. *takwanensis* (Kayser, 1883) from the Early and Middle Frasnian of the Caiziyan and Dushan sections. All are of sample PY5, Panxi section, probably Middle Frasnian, except PUM03013, sample DS59, Dushan section, Early Frasnian; the primary layer is not preserved in all specimens figured here. **A**. PUM05038, dorsal (A_1), ventral (A_2), area (A_3), posterior (A_4), anterior (A_5), and lateral (A_6) views. **B**. PUM05039, showing the structure similar to the delthyrial plate in the posterior part of the delthyrium. **C**. PUM05040, area view showing traces of pseudodeltidium on sides of the delthyrium. **D**. PUM05041, anterior (D_1), dorsal (D_2), lateral (D_3), posterior (D_4), and ventral (D_5) views. **E**. PUM03013, lateral (E_1), dorsal (E_2), ventral (E_3), posterior (E_4), and anterior (E_5) views.

Pyramidaspirifer has only been recognized in the Late Frasnian of North America, and this extends its geographic distribution to South China.

Occurrence.—The present species occurs in Bed 20 of the Qiziqiao section of central Hunan, correlated with the lower part of the Early *Palmatolepis rhenana* Zone.

Superfamily Ambocoelioidea George, 1931
Family Ambocoeliidae George, 1931
Genus *Emanuella* Grabau, 1923
Emanuella aff. *takwanensis* (Kayser, 1883)

Figs. 15, 16.

1883 aff. *Nucleospira takwanensis* n. sp.; Kayser 1883: 84–85, pl. 10: 2, 2a–h.

1959 aff. *Emanuella takwanensis* Kayser 1883; Veevers 1959b: 903–906, text-figs. 3, 4A, 5.

1970 aff. *Emanuella takwanensis* Kayser 1883; Dürkoop 1970, text-fig. 56-2, pl. 17: 1a–e (photographs of lectotype).

Material.—Sample PY5, Panxi section, probably Middle Frasnian (65 specimens, most articulated, silicified) and a few slabs with abundant silicified specimens about 50 m upwards; sample DS59, Dushan section, Early Frasnian (10 specimens).

Description.—Shell medium to small sized (around 10 mm in width, generally not greater than 12 mm for adults); suboval in outline, ventribiconvex in lateral profile, anterior commissure rectimarginate to uniplicate; hinge line straight but shorter than greatest width; cardinal extremities rounded. Ventral area apsacline, slightly curved dorsally, delthyrium generally open (with traces of thin pseudodeltidial plates seen from both sides in rare specimens). Dorsal interarea low, anacline, notothyrium open. Surface smooth; concentric "growth lines" and radial "costellae" present on exfoliated shell surface. Micro-ornament of short discontinuous radial spines (or spine bases) arranged roughly in concentric bands and lying on shell surface within the primary layer on part of a small poorly preserved ventral valve (sample DS59), with a density about 10 spines per 1 mm within the same band.

Internally, ventral valve without dental plates (occasionally a dental plate may be seen, see Fig. 16D), instead with strong dental ridges (terms used as in Veevers 1959b), teeth relatively strong; thickened infilling present in posterior part of ventral valve, becoming thinner anteriorly to form a struc-

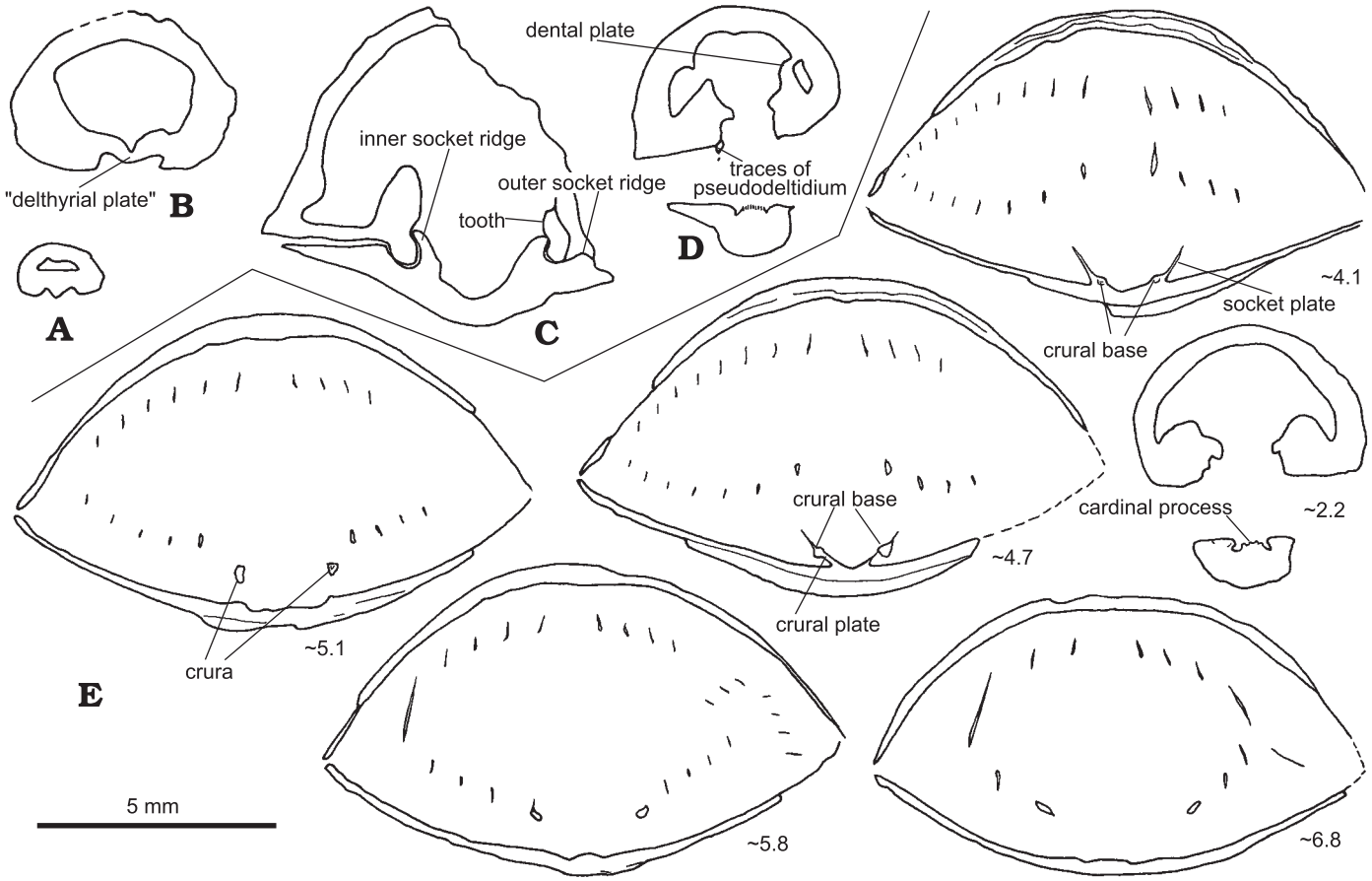


Fig. 16. Transverse sections of *Emanuella* aff. *takwanensis* (Kayser, 1883); all specimens are from sample PY5, Panxi section, probably Middle Frasnian. **A**–**D**. Sections at various distances from the ventral apex of specimens PUM05042~PUM05045; acetate peel numbers: 05J, 05G, 05I, and 05H respectively. **E**. Transverse serial sections of specimen PUM05046, acetate peel number: 05F; numbers refer to approximate distance in mm from the ventral apex.

ture similar to the delthyrial plate (Figs. 15B, 16A) (= pedicle collar of Veevers 1959b; the function of this structure is not certain at present as the position of the foramen can not be determined so that its relation with the pedicle is not known, therefore the name of the structure is left open for further study).

Dorsally, cardinal process low, with some vertical lamellae; sockets relatively deep; inner socket ridges high and strong, outer socket ridges fused to shell wall; socket plates (= outer hinge plates) fused to shell wall posteriorly, but becoming free and oblique anteriorly; crural plates (= inner hinge plates) extending ventro-laterally from shell wall, very slender; crural bases small and low, giving rise to relatively strong crura anteriorly. Spiralia with 7–8 whorls, directed laterally.

Discussion.—Externally shells are similar to species of *Ladjia* Veevers, 1959a in the presence of radial "costellae". However, Givetian *Emanuella* from the Panxi section also possess radial "costellae", and are still assigned in the genus *Emanuella*, which seems to disappear mostly in the late Middle Devonian, e.g., in the Guangxi and Hunan provinces (Hou 2000). Late Devonian *Emanuella* have been reported from South China, but without illustrations and solid biostratigraphic data, in the Panxi section of eastern Yunnan. Chen (1984) studied similar brachiopods from the Tuqiaozi Formation (Early Frasnian) of the Longmenshan section and redescribed *Zhonghuacoelia*, which is characterized by the presence of a pair of dental plates and small size. Veevers (1959a: 124) stated that the development of dental plates is transitional as he found that three of 100 dorsal and ventral valves from the same locality possessed variously developed dental plates. The presence of this structure in one of the Yunnan specimens (Fig. 16D) confirms that point of view.

The shell is similar to *Emanuella takwanensis* from the Middle Devonian (Givetian) of eastern Yunnan, so that in the description of the Panxi section (Yunnan compiling group 1978: 50), it is listed as *E. takwanensis*. It differs in having a smaller shell size, strong dental ridges, and outer socket ridges completely fused to the shell wall *versus* a free socket raised above shell wall by socket plate in Givetian *E. takwanensis* (compare Fig. 16C with Veevers 1959b: text-fig. 4A and Dürkoop 1970: text-fig. 56-1). This was supported by Xu et al. (1978: 359, text-fig. 46), and our own unpublished data. The nature of the socket relative to the shell wall in the

studied species is identical with that of *Emanuella torrida* Veevers, 1959a (i.e., sessile sockets of Veevers) and *E. laskarewi* Kelus, 1939, as figured by Dürkoop (1970: text-fig. 56-2), but the studied species differs from *E. torrida* in its spiralia with more whorls (7–8 in the studied species *versus* 6 at most according to Veevers' description). Spines or spine bases (micro-ornament) of the present species as seen from only one specimen are longer and arranged roughly in concentric bands. In addition, concentric "growth lines" and radial "costellae" can be seen on the exfoliated shell surface, not mentioned by Veevers (1959a) for his specimens. It is distinct form *Ladjia saltica* Veevers, 1959a in having a shorter hinge, and a smaller, narrower delthyrium.

Occurrence.—The species occurs in the Early and Middle Frasnian of South China (approximately the Frasnian part of Early *Mesotaxis falsiovalis* Zone through to the lower part of the *Palmatolepis hassi* Zone).

Concluding remarks

We have described 15 brachiopod species from the Early and Middle Frasnian strata in several sections in South China.

- Preliminary brachiopod data from South China shows that no significant faunal turnover was associated with the Middle Frasnian "*punctata* event" (= carbon isotopic anomaly) that has been recently recognized (e.g., Yans et al. in press), with a similar phenomenon in South China. The brachiopod faunal turnover near the *Palmatolepis punctata*–Early *Pa. hassi* zonal boundary documented in this paper slightly postdates the time of the "*punctata* event", in other words, it was coeval with the end of this major biogeochemical perturbation in the *Pa. punctata* Zone.
- This brachiopod faunal turnover in the *Palmatolepis punctata–Pa. hassi* zonal interval in South China is characterized by the disappearance of most rhynchonellids and emergence of plicate spiriferids.
- The plicate spiriferids of the Theodossioidea, Cyrtospiriferoidea (e.g., *Cyrtospirifer* and *Tenticospirifer*), and the Conispiriferidae first began to occur in the Middle Frasnian in South China (about *Pa. hassi–Pa. jamieae* zones, approximately MN zones 7–10).
- The Tuqiaozi Interval (about *Ancyrodella rotundiloba pristina* Zone through to *Palmatolepis punctata* Zone) is characterized by the *Yocrarhynchus–Phlogoiderhynchus* fauna, including abundant smooth-shelled spiriferids (*Emanuella* and *Zhonghuacoelia*), but lacks both *Stringocephalus* and the above mentioned plicate spiriferid brachiopods.

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