Rugose corals and brachiopods across the Frasnian–Famennian boundary in central Hunan, South China

XUE-PING MA, YUAN-LIN SUN, WEI-CHENG HAO, and WEI-HUA LIAO

Ma, X.- P., Sun, Y.-L., Hao, W.-C., and Liao, W.-H. 2002. Rugose corals and brachiopods across the Frasnian–Famennian boundary in central Hunan, South China. *Acta Palaeontologica Polonica* 47 (2), 373–396.

We present taxonomic revision of rugose corals and brachiopods from several Frasnian–Fammenian (F–F) boundary sections in central Hunan Province, China. Diversity of shallow-water rugose corals gradually increased during the Frasnian, but ended with sudden extinction near the end of Frasnian. Ostracods were abundant during the Frasnian; their extinction coincided with anoxic deposition of the end-Frasnian black shale deposits. The early Famennian ostracod fauna is of low diversity. The brachiopod fauna of the late Frasnian (*Palmatolepis rhenana* and *Pa. linguiformis* zones) is dominated by atrypids, small-sized cyrtospiriferids, and the rhynchonellid *Hunanotoechia*. All atrypids disappeared before the F–F boundary with highest rates of extinction below the boundary (probably low in the *Pa. linguiformis* Zone). The Frasnian cyrtospiriferid fauna is also of low diversity and dominated by small taxa. All but one of the cyrtospiriferid taxa crossed the F–F boundary. The early Famennian post-extinction recovery brachiopod fauna was the result of rapid radiation of new forms shortly after the terminal Frasnian event. The early Famennian fauna is characterized by diverse cyrtospiriferids, abundant *Yunnanellina* and productoids. Above the early recovery fauna another fauna was recovered, with brachiopods *Hunanospirifer* and *Yunnanella* and is correlated with the late or latest *Pa. crepida* Zone. *Sinalosia rugosa* gen. et sp. nov. (Productida) is erected.

Key words: Rugosa, Ostracoda, Brachiopoda, Frasnian, Famennian, extinction, Hunan, China.

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Introduction

The Upper Devonian benthic brachiopod faunas of central Hunan were studied by Grabau (1931–1933), Tien (1938), and described in regional paleontological atlases (Yang et al. 1977; Liu et al. 1982). Studies of the coral fauna include work by Sun (1958) and palaeontological atlases of Jia et al. (1977) and Jiang (1982). These older studies provided little or no data on the stratigraphic distribution of the described taxa, most of which require taxonomic revision.

For example, most cyrtospiriferid specimens of Grabau's (1931–1933) extensive studies were bought from Chinese drugstores without geographic or stratigraphic locality data. The veracity of Grabaus's data on specimen labels is highly suspect and should be used with extreme caution. For example, most modern workers believe that Grabau's *Yunnanellina* specimens were originally collected from outcrops in Hunan Province, not Yunnan Province. Martelli's (1902) *Schizophoria paronai* specimen was said to have come from Shensi (now Shaanxi), but has not been confirmed by modern field-based investigations of current workers of the geological survey (Hou et al. 1996a: 161).

During the 1980s and early 1990s of the 20th century modern biostratigraphic investigations of the Devonian successions (including the Frasnian–Fammenian boundary) were conducted. These studies tended to focus on pelagic conodont, tentaculite, ammonite, and ostracod faunas (e.g., Bai et al. 1982, 1994; Ji and Ziegler 1993; Wang 1989). However, the pelagic sections are generally barren of benthic fossils, hence it is impossible to assess the impact of the F–F mass extinction on benthic faunas based on studies of those basinal sections.

Yu (2000) proposed four basic facies types for the Devonian marine deposits of South China. The Xiangzhou type is characterized mainly by carbonates and minor clastic deposits including shales and sandstones with abundant and diverse benthic fossils. The central Hunan region is the most important area of the Xiangzhou type for the Upper Devonian so that the Upper Devonian in China is also known as the Hunan Series. Even in central Hunan the sedimentary conditions were very diverse, including deposits of inner littoral, outer littoral, reef platform, and inter-reef basinal facies (Yu et al. 1990).

In recent years the Frasnian–Famennian extinction event has been the focus of a series of important stratigraphic and palaeontological investigations (Bai et al. 1994; Casier et al. 1997; Hou et al. 1996a, b; Ma 1993a, b, 1995, 1998; Ma and Day 1999, 2000; Sartenaer and Xu 1991; Zhang 1995). This paper outlines results of investigations whose goals have been to document the stratigraphic distribution of the important (most abundant and diverse) benthic groups across the

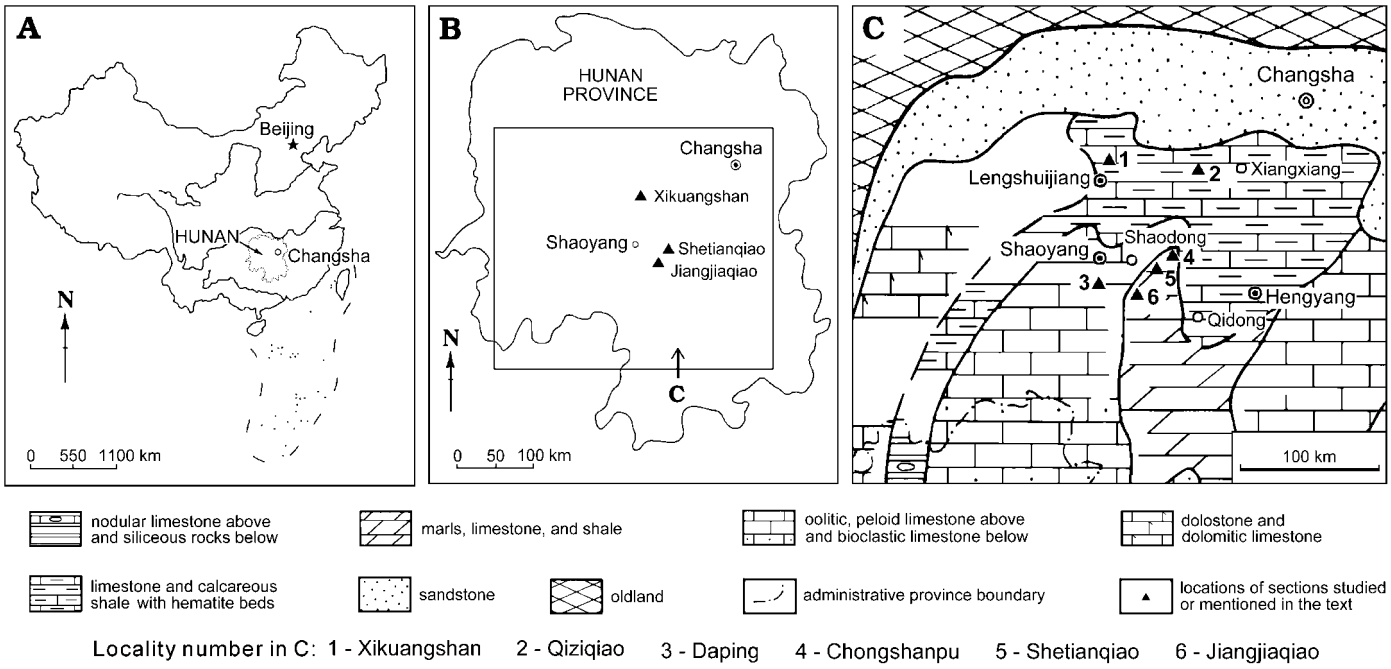

Fig. 1. Locality map showing important Frasnian–Fammenian (F–F) sections (solid triangles) in central Hunan Province. **A**. Location of Hunan Province in China. **B**. Location of studied sections in Hunan Province. **C**. Lithofacies map of central Hunan (based on Hou et al. 1988, slightly revised).

F–F boundary interval in central Hunan, as well as taxonomic revision of the brachiopod fauna.

Frasnian–Fammenian stratigraphical sections and fossil distribution

Xikuangshan section.—This section is located in an antimony ore field called Hsikuangshan (now spelled Xikuangshan) north of Lengshuijiang City (Fig. 1), which is the type locality for the Hsikuangshan Formation (= Hsikuangshan Limestone of Tien 1938) and the Changlungchie (now spelled Changlongjie) Formation (= Changlungchie Shale of Tien 1938). During the Late Devonian, this area was located in the outer littoral to shallow sub-tidal zones. Wang et al. (1986) and Bai et al. (1994) recently described the Upper Devonian strata in this area. In this region, the Frasnian–Famennian (F–F) boundary interval is well exposed and yields abundant benthic fossils including brachiopods, corals (late Frasnian), and ostracods. Distribution of rugose corals and brachiopods in the very late Frasnian is shown in Fig. 2A.

Distribution of the ostracods across the F–F boundary in the Xikuangshan section.—Most of the ostracod species recovered from the latest Frasnian and early Famennian belong to the superfamilies Bairdiacea and Healdiacea with smaller numbers of taxa of the Leperditellacea and Paraparchitacea. Generally, ostracod faunas in early Famennian (*Palmatolepis triangularis* through *Pa. crepida* zones) strata are of low diversity, but yield abundant large instars of species of the Healdiacea. Strata correlated with the Lower *Pa. triangularis* Zone yield a very sparse and low diversity fauna (see biostratigraphic discussion in Ma and Bai 2002). Of the 36 species in the F–F interval (Fig. 3), 23 are restricted to the Frasnian including Entomozoacea gen. et sp. indet., *Paraparchites* sp., *Cryptobairdia* sp., *Bairdia* sp. 3, *Roundyella*? sp., and *Cavellina placida.* Eight cross the F–F boundary including *Polytilites* sp., Primitiopsacea gen. et sp. indet., *Samarella* sp., *Perimarginia ovata*, *Acratia* sp., and *Bairdia naumovae.* Only five taxa have their first occurrences in the early Famennian.

Shetianqiao section.—Shetianqiao (spelled Shetienchiao in old literature) is the name of a small town about 25 km southeast of Shaodong Town. The area is located within the Late Devonian inter-reef basin characterized by the accumulation of marly facies. This section serves as the type section for the Shetienchiao Formation or Stage (about equivalent to the Frasnian). However, the Shetienchiao brachiopod fauna has not been adequately described.

The upper part of the Shetienchiao Formation is characterized by abundant brachiopods, among which small-sized "*Cyrtospirifer*" has been mentioned by previous investigators (Chen 1996: 80; Ma and Day 2000: 447; Zhao et al. 1978: 79). Our recent study shows that so-called small-sized "*Cyrtospirifer*" includes three different species (Ma and Sun 2001).

The F–F boundary interval is well exposed along a newly paved road. Towards the F–F boundary fossils become almost entirely barren. Fossil distribution in the late Frasnian interval is shown in Fig. 2B. The lithology below the interval shown in

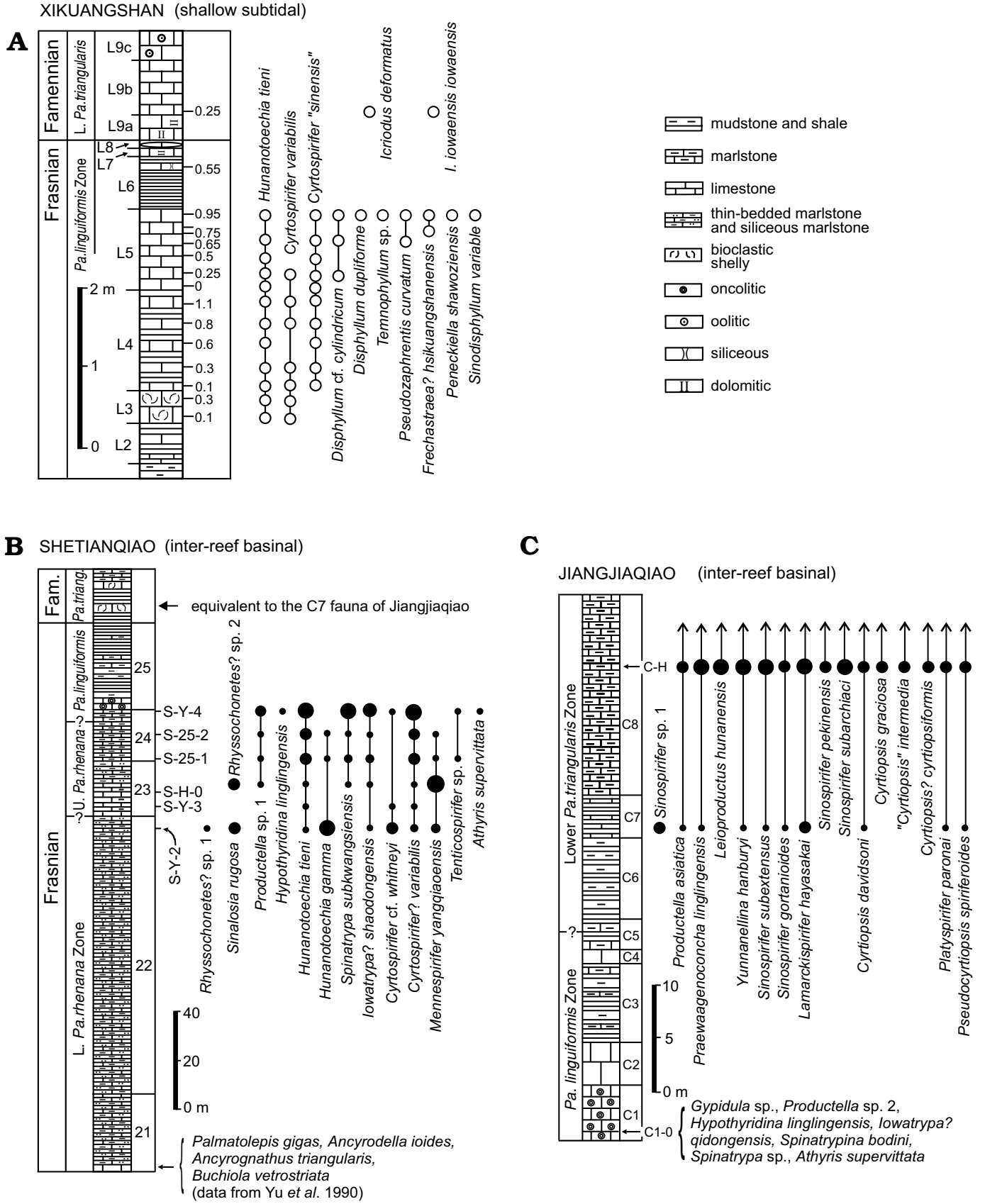

Fig. 2. Stratigraphy of the F–F boundary interval of the Xikuangshan (**A**), Shetianqiao (**B**), and Jiangjiaqiao (**C**) sections and distribution of benthic fossils. Diameter of solid dots relates to relative abundance of specimens. Lithology of the Shetianqiao section is from the Regional Geological Survey Team of Hunan in Hou et al. (1988), modified based on our own data.

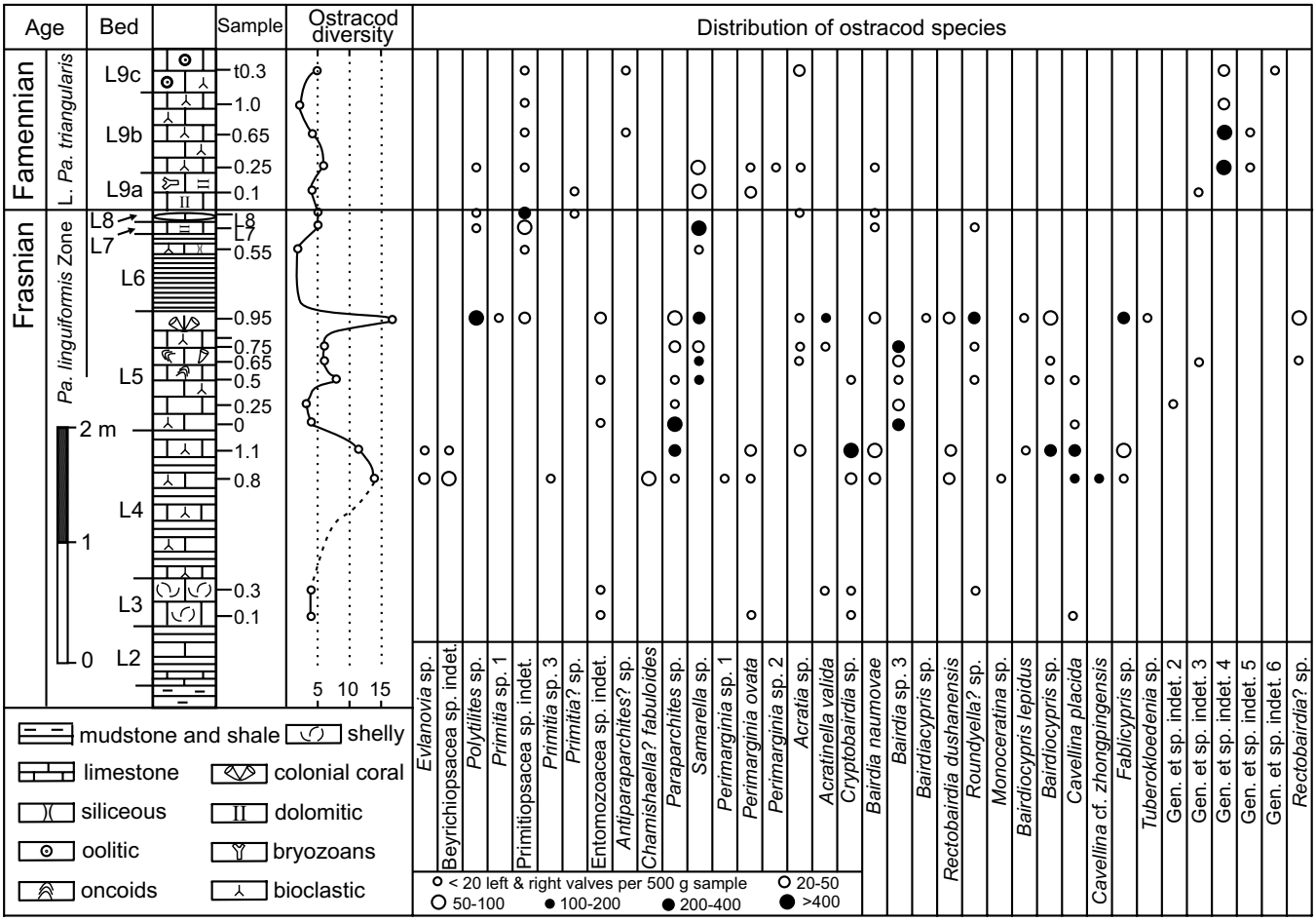

Fig. 3. Stratigraphy of the F–F boundary interval of the Xikuangshan section and the distribution of ostracodes.

Fig. 2B consists of about 540 m of thin-bedded silty marls or marlstones above and 135 m thick thin-bedded black silty shales intercalated with minor siliceous rocks in the lower part. The fauna is characterized and dominated by pelagic taxa including *Buchiola retrostriata* (bivalves), *Manticoceras* sp. (ammonites), *Richterina* sp. (ostracods), *Leiorhynchus* sp. and *Chonetes* sp. (brachiopods), and tentaculites at the base of the interval including *Striatostyliolina* sp., *Styliolina* sp., and *Homoctenus ultimus derkaouaensis* (data from Hou and Wang 1988; Yu et al. 1990; and our own observations).

Jiangjiaqiao section.—This section is located midway between the two small towns of Buyunqiao and Jiangjiaqiao. Administratively the section is located in the western part of the County of Qidong. The section is developed in the deeper marly facies, and is characterized by the abundance of brachiopods, especially the early Famennian cyrtospiriferid-*Yunnanellina*-productoid assemblage above the F–F boundary. The *Yunnanellina* lineage and the *Cyrtiopsis* group above the F–F boundary and atrypids below have been described by Ma (1995, 1998) and Ma and Day (1999). There are still many forms to be revised (Ma and Day in preparation). Fossil distribution is shown in Fig. 2C.

Patterns of extinction, survival, and recovery of major benthic groups in South China

Extinction.—The Lower Kellwasser event does not seem to have a significant impact on the benthic fauna in central Hunan. In fact no physical evidence of this event has been found so far.

A significant biomass and diversity loss of the brachiopods occurred in the lower part of the *Pa. linguiformis* Zone of central Hunan (Fig. 4). Brachiopods that apparently disappeared at this horizon include the atrypoids *Iowatrypa*? *qidongensis*, *Iowatrypa*? *shaodongensis*, *Spinatrypa subkwangsiensis*, *Spinatrypina bodini*, and the pentameroid *Gypidula* sp. About 1 m below the F–F boundary only rare "*Radiatrypa maanshanensis*" and *Desquamatia shetienchiaoensis* can be found in the Chongshanpu section (Ma 1998). Further data are needed to confirm whether this disappearance in the lower *Pa. linguiformis* Zone is local, regional, or global.

The most significant extinction event occurred near the end of the Frasnian, which coincided with the Upper Kell-

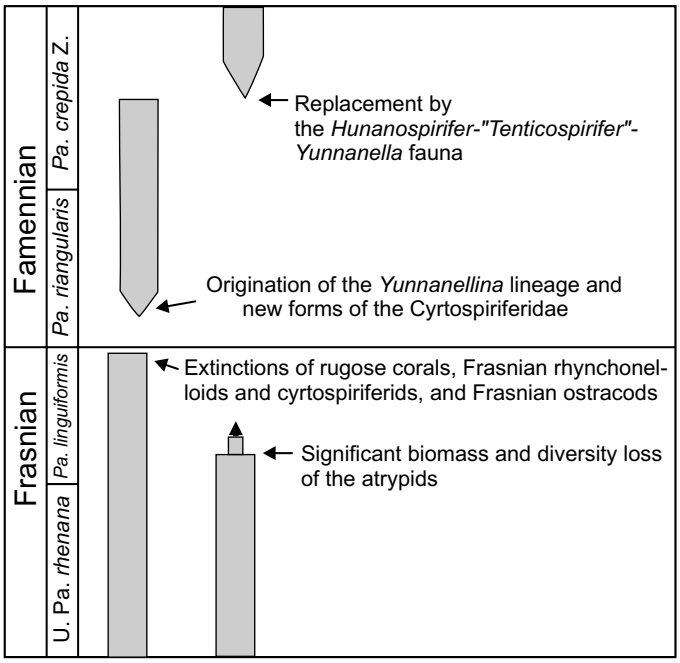

Fig. 4. Model showing faunal extinction, origination, and replacement in the Upper Devonian of South China.

wasser event in Europe. In South China this extinction event is well exemplified by the Xikuangshan and Chongshanpu sections (Bai et al. 1994; Ma 1998).

In the Xikuangshan section, this extinction event happened at the top of bed L5 (Fig. 3) and involved loss of colonial corals, the brachiopods *Hunanotoechia tieni*, *Cyrtospirifer*? *variabilis*, and *C.* "*sinensis*" (= *Tenticospirifer gortani* figured in Ma 1994), and many species of ostracods (Ma and Bai 1996). In the Chongshanpu section abundant colonial and solitary corals also became extinct at this horizon (Ma 1998).

Generally speaking, the diversity and number of the late Frasnian ostracods are very high, whereas in the early Famennian (including upper part of the Changlongjie Formation through the Tuzitang Member of the Xikuangshan Formation), ostracods may be very abundant in many horizons, but diversity is very low. Their major extinction horizon is the same as that of the corals at top of bed L5.

In the Xikuangshan section the L6–L9a interval represents a hypoxic condition and low ostracod diversity. However, the supposed equivalent interval in the Lijiaping section yields relatively diverse ostracods and "the assemblage is not characteristic of oxygen-depleted water conditions" (Casier et al. 1997). They further suggested that the F–F boundary should be placed at the base of the black shale and carbonate interval. Thus the Lijiaping section needs restudy to determine the position of the F–F boundary.

The development of Frasnian rugose corals of central Hunan may be divided into three phases (Yu et al. 1990). The first phase is characterized by the *Sinodisphyllum* fauna of low diversity (but high abundance); this fauna is within the lower Frasnian Lungkouchung Formation. The second phase is characterized by the diverse *Hexagonaria–Disphyllum* fauna, together with algae, stromatoporoids, and tabulate corals forming the biostrome in the middle part of the Frasnian. The third phase is characterized by the *Phillipsastrea–Disphyllum– Mictophyllum* fauna with the highest diversity in the Frasnian. This gradual increase of number of rugose genera in tropical North American successions during the Frasnian has been demonstrated by Sorauf and Pedder (1986), and more recently by McLean (in McLean and Klapper 1998) in the near equatorial carbonate platforms of the Frasnian in western Canada. In the Xikuangshan section rugose corals are very diverse and abundant in the upper part of bed L5, as well as in bed T3 of the Chongshanpu section (Ma 1998) including species of *Disphyllum*, *Sinodisphyllum*, *Pseudozaphrentis*, *Temnophyllum*, *Phillipsastrea*, *Mictophyllum*, *Peneckiella*, *Macgeea*, and *Hunanophrentis*. These shallow water rugose corals suddenly became extinct shortly after reaching their height of diversity and abundance in the late Frasnian.

Survivor faunas.—No Frasnian rugose corals range into the early Famennian in South China. The only shallow water rugose coral confirmed to be present in the deposits of the upper part of the early Famennian strata in Hunan is *Smithiphyllum* which occurs in the lower part of the Magunao Member or its equivalent (probably Uppermost *Pa. crepida* to Lower *Pa. rhomboidea* zones; see Wang and Zuo 1983). This genus has long been known as a survivor of the F–F mass extinction (Sorauf and Pedder 1986).

Major elements of the Frasnian brachiopod fauna were mostly extinct before or at the end of the Frasnian. All atrypids became extinct below the F–F boundary. Occurrences of some atrypids in early Famennian strata of the Baqi section (Wang and Bai 1988) and the Maanshan section (Jia et al. 1988) have been demonstrated to have been reworked from pre-extinction Frasnian deposits (Bai et al. 1994; Ma 1998). The cyrtospiriferids *Cyrtospirifer* cf. *whitneyi* (Hall, 1858), *C.* "*sinensis*" (Grabau, 1931), *C.*? *variabilis* Ma and Sun, 2001 became extinct by the close of the Frasnian and are not known in the Famennian strata of South China.

Our study of Tien's and Grabau's specimens shows that early Frasnian *Sinospirifer sinensis* and *S. subextensus* from the Lungkouchung bed (described by Tien 1938) should be considered to be a single species, although the Lungkouchong occurrence has not been supported by our new field investigations. This Frasnian form is almost identical with early Famennian *S. subextensus* of the Jiangjiaqiao section. Because of poor preservation, the micro-ornament and characteristics of the pseudodeltidium of *Sinospirifer sinensis* (not described by Tien and not preserved in his material) are unknown. If Frasnian *S. sinensis* sensu Tien, 1938 and Famennian *S. subextensus* prove to be synonyms, then it would prove to be the sole survivor of the Frasnian *Cyrtospirifer* species of South China.

Some specimens of *C.*? *variabilis* are also similar to early Famennian *S. subextensus* in the thickened delthyrial cavity.

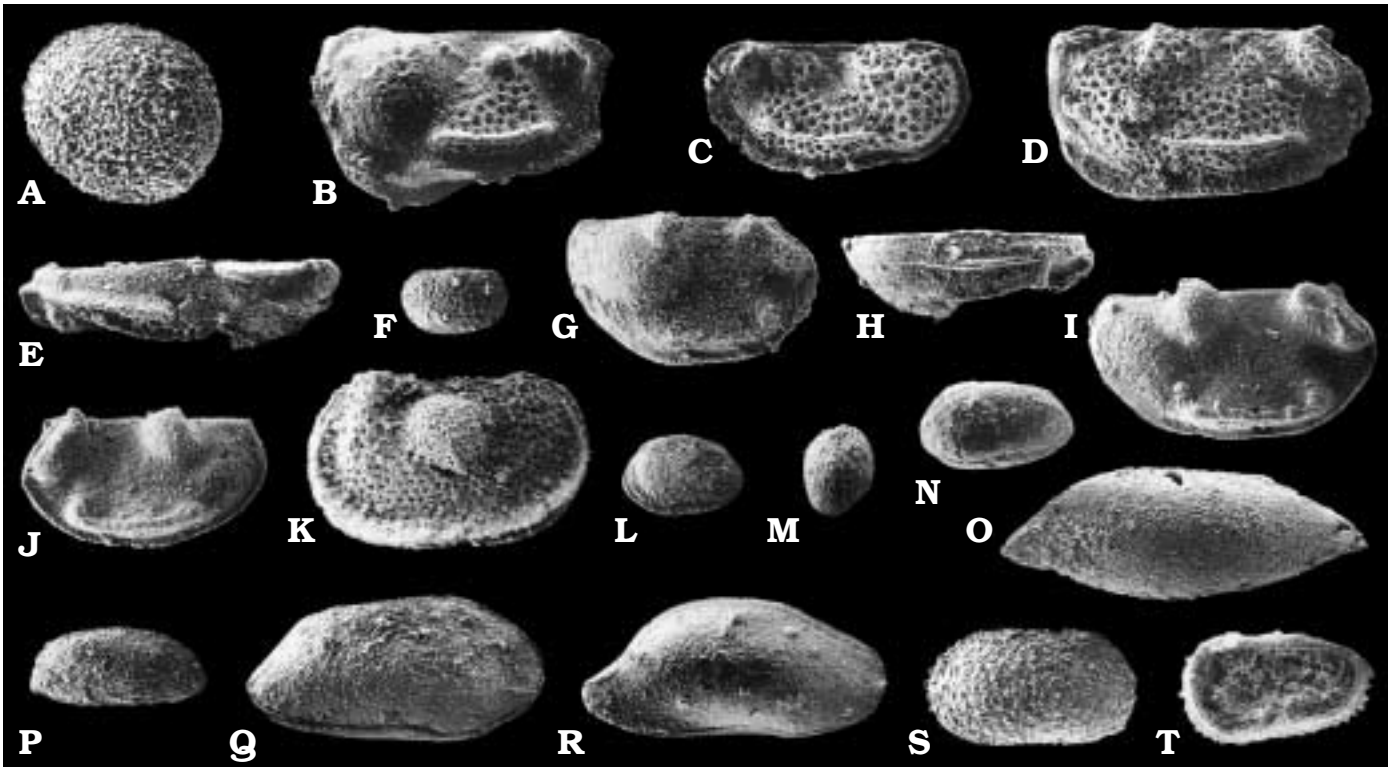

Fig. 5. Ostracods from the Frasnian–Famennian boundary interval of the Xikuangshan section. All × 40 except otherwise indicated. **A**. Entomozoacea gen. et sp. indet., sample L5/0.95, specimen cat. no. PUM 00074, × 75. **B**–**E**. *Evlanovia* sp., sample L4/0.8. **B**. Right valve of a female, PUM 00075. **C**. Left valve of a female, PUM 00076. **D**. Right valve of a male, PUM 00077. **E**. Ventral view of right valve of a female, PUM 00078. **F**. *Paraparchites* sp., left valve, sample L4/0.8, PUM 00079. **G**–**J**. Beyrichiopsacea gen. et sp. indet., sample L4/0.8. **G**. Left valve of a female, PUM 00080. **H**. Ventral view of right valve of a female, PUM 00081. **I**. Left valve of a male, PUM 00082. **J**. Right valve of a male, PUM 00083. **K**. *Polytilites* sp. Left valve, sample L5/0.95, PUM 00084. **L**. *Cryptobairdia* sp. Carapace in right lateral view, slightly oblique, so that dorsal overlapping is concealed; sample L5/0.5, PUM 00085. **M**, **N**. *Samarella* sp., sample L5/0.5. **M**. Posterior view of specimen PUM 00086 showing valve overlapping at dorsal and ventral margins. **N**. Carapace in right lateral view, PUM 00087. **O**. *Acratia* sp., Carapace in left lateral view, PUM 00088, sample L5/0.95. **P**. *Acratinella valida* Shi, 1964, right valve, PUM 00089, sample L5/0.95. **Q**. *Rectobairdia dushanensis* (Shi, 1964), carapace in right lateral (slightly oblique) view, PUM 00090, sample L4/0.8. **R**. *Bairdia naumovae* Egorov, 1953, carapace in right lateral view, PUM 00091, sample L4/0.8. **S**, **T**. *Roundyella*? sp., sample L5/0.95. **S**. Left valve, PUM 00092. **T**. Internal view showing short spines on valve margin, PUM 00093.

However, *C.*? *variabilis* is very small and has much fewer sinal plications.

A large number of Upper Devonian rhynchonellid species were assigned to *Camarotoechia* by Wang et al. (1964), and later to *Ptychomaletoechia* by Yang et al. (1977). The record and taxonomy of the Upper Devonian rhynchonellids requires substantial restudy and revision before a clear picture of their distribution can be presented. Nevertheless, it seems that those forms are not abundant in the F–F interval in central Hunan. *Hypothyridina linglingensis* Wang, 1956a and *Hunanotoechia tieni* Ma, 1993, which are commonly seen in the *Pa. linguiformis* Zone in the inter-reef basinal facies, have not been found in the early Famennian strata.

Ostracods were greatly affected by the end-Frasnian anoxic event (Figs. 5 and 6). Most ostracods that flourished in the central Hunan area during the late Frasnian became extinct. Some ostracods cross the F–F boundary, for example, *Polytilites* sp., Primitiopsacea gen. et sp. indet, *Samarella* sp., *Perimarginia ovata* Hou, 1955, *Acratia* sp., and *Bairdia naumovae* Egrov, 1953. It should be noted that these taxa are largely confined to the L9b–L9c interval, which is composed of skeletal and oolitic grainstones. Therefore it cannot be ruled out that those forms could be reworked late Frasnian forms.

Recovery and post-extinction radiations.—The Famennian benthic megafauna of central Hunan is dominated by a rhynchonellid-cyrtospiriferid-productoid brachiopod assemblage. New forms of these groups seem to originate relatively quickly after the F–F event (Fig. 4). The *Yunnanellina* rhynchonellid lineage originated in the interval of the lower *Pa. triangularis* Zone. Its ancestor is not known. The *Yunnanella* fauna usually occurs in the Upper or Uppermost *Pa. crepida* Zone. An internal mold of *Yunnanella* sp. was found in bed L12 (about 10 m above bed L9c on Fig. 3) of the Xikuangshan section (Middle *Pa. triangularis* Zone) which implies that the *Yunnanella* lineage probably also originated very early in the early Famennian (Ma 1994: pl. 38: 8).

New cyrtospiriferids also originated and radiated shortly after the F–F extinction. These include at least six genera of the Cyrtospiriferidae, namely *Sinospirifer*, *Lamarckispirifer*, *Cyrtiopsis*, *Platyspirifer*, *Pseudocyrtiopsis*, plus "*S*". *gorta-*

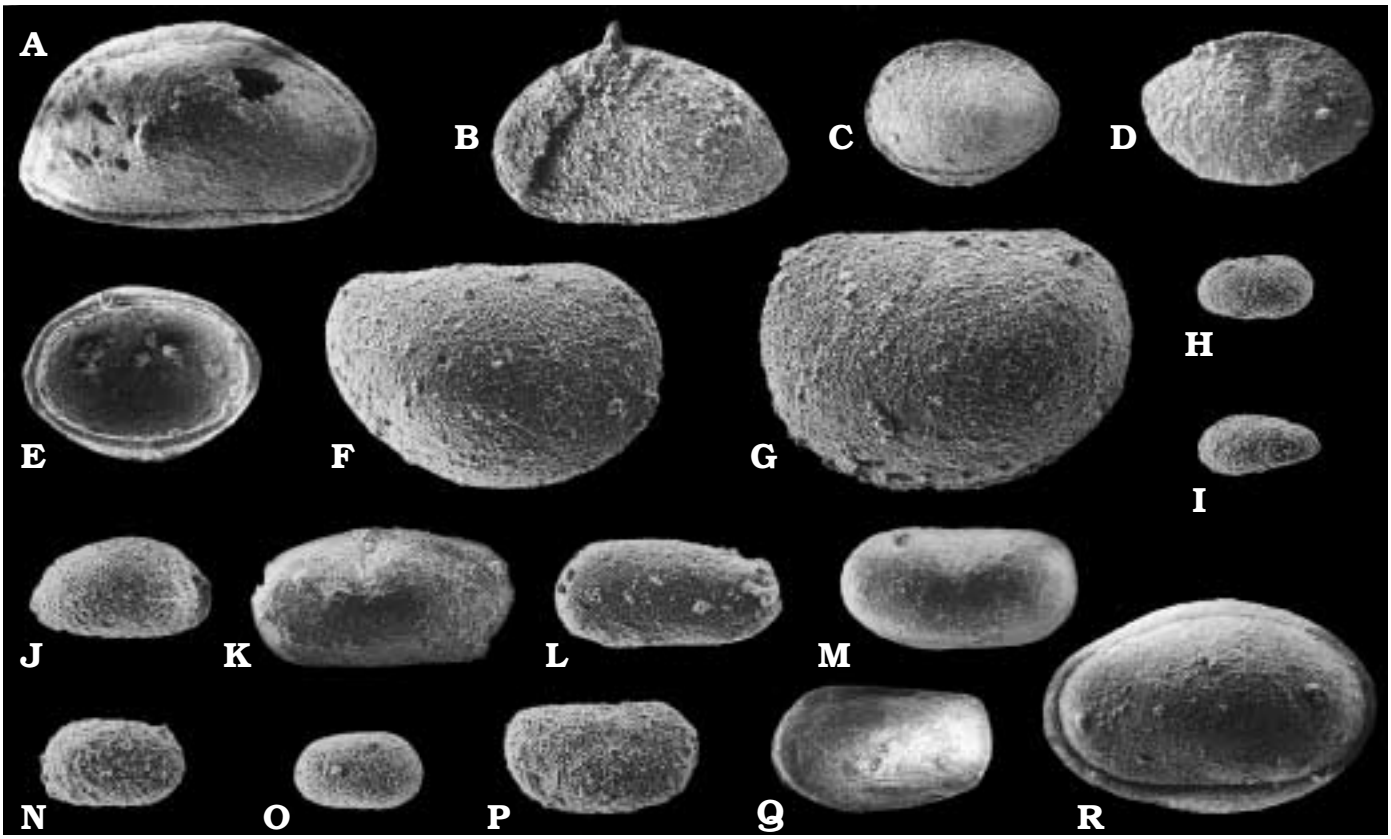

Fig. 6. Ostracods from the Frasnian–Famennian boundary interval of the Xikuangshan section. **A**, **B**. *Bairdiocypris* sp., sample L5/top (= L5/0.95), top of bed L5. **A**. Carapace in right lateral view, PUM 00096. **B**. Left valve, PUM 00097. **C**. *Cavellina placida* Shi, 1964, sample L4/0.8, carapace in left lateral view, PUM 00098. **D**. *Perimarginia ovata* Hou, 1955, sample L4/0.8, left valve, PUM 00099. **E**. *Cavellina* cf. *zhongpingensis* Wang, 1982; interior of right valve, PUM 00100, posterior inflated, sample L4/0.8. **F**, **G**. *Chamishaella*? *fabuloides* Wei, 1983, sample L4/0.8, lateral views of right valve, PUM 00101 and left valve, PUM 00102. **H**. Gen. et sp. indet. 3, right valve, PUM 00105, sample L9/t0.3. **I**. Gen. et sp. indte. 2, left valve, PUM 00107, sample L9/t0.3. **J**. Gen. et sp. indet. 1, right valve, PUM 00106, sample L9/t0.3. **K**. *Perimarginia* sp. 1, left valve, PUM 00103, sample L4/0.8. **L**. *Fablicypris* sp. Left valve, PUM 00104, sample L4/1.1. **M**, **P**, **Q**. Primitiopsacea gen. et sp. indet. **M**. Right valve, PUM 00108, sample L9/0.25. **P**. Right valve, PUM 00109, sample L7. **Q**. Carapace in left lateral view, PUM 00094, sample L12/0.7-0.8. **N**, **O**. Gen. et sp. indet. 4. **N**. PUM 00110, sample L9/t0.3. **O**. PUM 00111, sample L9/0.25. **R**. *Cavellina* cf. *zhongpingensis* Wang, 1982. Carapace in left lateral view, PUM 00095, sample L4/0.8. **A**–**G**, **Q**, **R**, × 40; **H**–**P**, × 42.

nioides, "*Cyrtiopsis*" *intermedia*, and *Cyrtiopsis*? *cyrtiopsiformis* (generic assignment needs further study). This cyrtospiriferid assemblage persisted to the Upper or Uppermost *Pa. crepida* Zone and then was replaced by the *Yunnanella-Hunanospirifer-"Tenticospirifer"* assemblage.

Systematic palaeontology

All illustrated specimens are housed in the collection of the Department of Geology, Peking University in Beijing (abbreviated PUM).

Rugose corals

(X.P. Ma and W.H. Liao)

Suborder Columnariina Soshkina, 1941
Family Disphyllidae Hill, 1939
Genus *Disphyllum* De Fromental, 1861

Disphyllum cf. *cylindricum* Sun in Wang et al., 1955

Fig. 7A, B.

cf. *Disphyllum cylindricum* Sun; H.Z. Wang et al. 1955: 32, pl. 12: 5, 6, 9.
cf. *Tabulophyllum cylindricum* Sun (sp. nov.); Sun 1958: 10, pl. 1: 3, pl. 2: 1.

Material.—Four specimens.

Remarks.—Phacelloid in form; individual cylindrical, 8 to 9 mm in diameter; major and minor septa around 20 respectively; the majors are about 1/3 length of diameter; septa are rarely thickened at the dissepimentarium, thinning inwardly. In longitudinal section, there are one to several rows of dissepiments; the outer row is larger and the inner rows are smaller, which differs from Sun' type specimens.

Occurrence.—Xiangxiang County, Frasnian; Xikuangshan, latest Frasnian.

Disphyllum dupliforme Kong, 1978

Figs. 7H, 8L.

Disphyllum dupliforme Kong, n. sp.; Kong and Huang 1978: 72, pl. 23: 9a, b.

Material.—Over 20 specimens.

Remarks.—Our specimens have the following characters: Phacelloid to massive-phacelloid; individual cylindrical, generally 7 mm in diameter, commonly connected laterally; there are 17–20 major septa which almost reach the center; the minor septa are 1/3 to 1/2 length of the major; septa in some individuals are weakly to strongly thickened; in longitudinal section there are generally only one row of dissepiments with their top being convex; a discontinuous inner wall is present between the dissepimentarium and the tabularium; tabularium wide, tabulae generally incomplete, rarely complete.

The above features are about the same as those of the original material from Guizhou Province (Kong and Huang 1978).

Occurrence.—Dushan in southern Guizhou Province; in central Hunan Province this form is abundant and widely distributed, e.g., in the Chongshanpu, Daping, and Xikuangshan sections. All these occurrences are of Frasnian age.

Genus *Temnophyllum* Walther, 1928

Temnophyllum sp.

Fig. 8C, D.

Material.—Two specimens.

Remarks.—This form is solitary, cylindrical, with a diameter of 7–10 mm, and 19–20 major and minor septa respectively. Major septa long, nearly reaching the center; minor septa reach 1/3 to 1/2 length of the major. Outer part of the septum is strongly dilated so as to form a marginal stereozone. In longitudinal section there are one to two rows of hemispherical dissepiments; tabularium wide, tabulae very incomplete.

Occurrence.—Xikuangshan section of central Hunan Province, latest Frasnian.

Genus *Phillipsastrea* d'Orbigny, 1849

Phillipsastrea nevadensis Stumm, 1940

Fig. 7D, E.

Phillipsastrea nevadensis n. sp.; Stumm 1940: 66, pl. 7: 13, pl. 8: 15a, b.

Material.—Ten different-sized specimens.

Remarks.—Massive, wall between individuals lost, with septa of neighboring individuals being in contact. There are 10–12 major septa which generally extend to the center. Both major and minor septa are dilated at the inner margin of the dissepimentarium; dilation of the majors slightly more inwardly extended. In the tabularium, the majors are very delicate; the tabularium is 2 to 2.5 mm wide; distance between neighboring tabularia is about 3 mm. There are commonly one row of horse-shoe dissepiments forming the tabularium wall and some fan-like dissepiments outwardly. The tabulae are divided into peripheral series and axial series, with the latter being 10 or more per 5 mm.

The Hunan specimens basically resemble *P. nevadensis* in the strong dilation of septa at the inner margin of the dissepimentarium, delicate septa in the tabularium reaching the center, and smaller number of septa. However, the tabularium is narrower in the Hunan specimens (2 to 2.5 mm vs. 3 mm in North American specimens) and neighboring tabularia in our specimens are much closer to each other (about 3 mm from margin to margin) than those of the North American specimens (about 5 mm) as illustrated by Stumm (1940) and McLean (1994).

Occurrence.—Central Hunan in the Chongshanpu section; latest Frasnian.

Phillipsastrea sp.

Fig. 7F, G.

Material.—One specimen.

Remarks.—The specimen is cerioid–astreoid in form with 10 to 12 major and minor septa respectively, both commonly dilated, but discontinuously so as to give a feeble carina appearance. The major septa are weak in the tabularium. The boundary between individual corallites is relatively distinct, characterized either by traces of thin epitheca or by contact of septa of neighboring corallites. The tabularium is 2–2.5 mm wide, commonly with incomplete tabulae. Horse-shoe dissepiments are not developed.

This form is different from Hunan specimens of *Phillipsastrea nevadensis* in that the latter species possesses horse-shoe dissepiments and strongly dilated septa at outer margin of the tabularium and has no boundary epitheca between neighboring corallites. It is similar to *P. hunanensis* Jiang, 1982, but the latter species has more septa (13 to 17 major and minor septa respectively) and intermittent horse-shoe dissepiments.

Occurrence.—Central Hunan at the Chongshanpu section; latest Frasnian.

Genus *Frechastraea* Scrutton, 1968

Frechastraea? *hsikuangshanensis* Ma, 1994

Fig. 7C, I.

Frechastrea? *hsikuangshanensis* n. sp.; Ma 1994: 199, pl. 45: 1–3.

Material.—Four specimens.

Remarks. —This is an astreoid-aphroid form characterized by the absence of horse-shoe dissepiments, large corallites united by dissepiments, and major septa only slightly entering the tabularium. Coralla are circular or oval in outline. The boundary between neighboring corallites is generally not readily defined. Individual calicular pits, where observable, are often fairly deep, with a diameter of 5–6 mm and their centers being spaced 12–15 mm apart. Major septa are 12–14 in number and commonly dilated, showing a granular structure as feeble carinae. Tabularia are generally 5 mm in diameter, with about 3 tabellae per millimeter. The present species may be distinguished from *Frechastraea dushanensis* Kong, 1978, and *F. guizhouensis* Kong, 1978 of the Frasnian Wangchengpo Formation of Guizhou Province, China by its large size, about two times the size of the two Guizhou species.

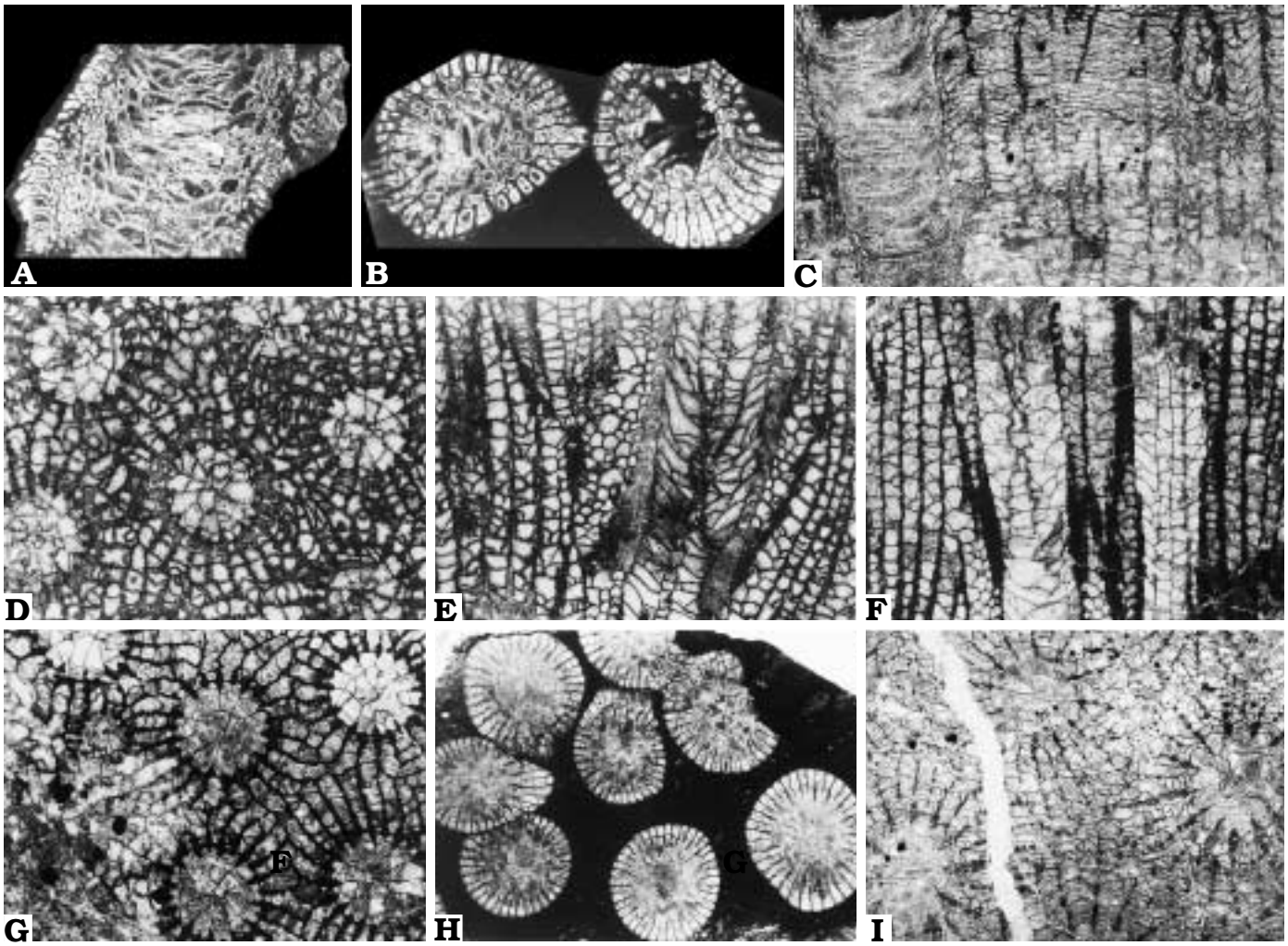

Fig. 7. Latest Frasnian (upper part of the *Pa. linguiformis* Zone) rugose corals from central Hunan. **A**, **B**. *Disphyllum* cf. *cylindricum* Sun, 1955, longitudinal and transverse sections, PUM 93593, sample L5/0.3-0.4; **A** × 3.8, **B** × 3.2. **C**, **I**. *Frechastraea*? *hsikuangshanensis* Ma, 1994., sample L5/0.85, longitudinal (× 3.6) and transverse (× 2.65) sections of the holotype specimen, PUM 93602. **D**, **E**. *Phillipsastrea nevadensis* Stumm, 1940, transverse and longitudinal sections of specimen PUM 93606, bed T3 of the Chongshanpu Section (see Ma 1998 for stratigraphy); × 5.5. **F**, **G**. *Phillipsastrea* sp., longitudinal and transverse sections, PUM 93606, bed T3; × 5.5. **H**. *Disphyllum dupliforme* Kong, 1978, transverse section, PUM 93592, from the top of the Frasnian of Taotang, about 2 km north of the Xikuangshan section (see Fig. 8L for longitudinal section); × 2.3.

Occurrence.—Central Hunan Province at the Xikuangshan area; latest Frasnian.

Genus *Peneckiella* Soshkina, 1939
Peneckiella shawoziensis He, 1978

Fig. 8A, B.

Peneckiella shawoziensis n. sp.; He 1978: 128, pl. 61: 2, 3.

Material.—Two specimens.

Remarks.—This is a phacelloid form; individual 5 mm in diameter, with one row of *Peneckiella*-type dissepiments and 18–20 major and minor septa respectively; the major septa are generally 1/3 length of the radius, some being slightly longer; the minor septa are slightly shorter than the major. The tabularium is wide, with 7 complete tabulae per 5 mm which are horizontal or slightly convex upwards. This species is characterized by short and thin septa, the *Peneckiella*-type dissepiments, and small size.

Occurrence.—Sichuan Province, Frasnian; central Hunan Province in the Xikuangshan section, latest Frasnian.

Suborder Cyathophyllina Nicholson in Nicholson and Lydekker, 1889
Family Cyathophyllidae Dana, 1846
Genus *Sinodisphyllum* Sun, 1958

Type species: *Disphyllum* (*Sinodisphyllum*) *variabile* Sun, 1958; Lungkouchung Member, Shetienchiao Formation (Frasnian); Xiangxiang, Hunan, China.

Emended diagnosis.—Solitary charactophyllid coral. Septal arrangement radial, septa smooth without carinae; major septa long, showing weak to moderate peripheral dilation, tapering

gradually towards corallum axis; minor septa distinct, generally as long as width of dissepimentarium. Fossula absent. Trabeculae of *Charactophyllum*-type. Dissepimentarium with two to five rows of inclined small vesicles; tabularium with a variable arrangement of complete tabulae and/or tabellae, which normally are split periaxially.

Remarks.—Sun (1958) erected the new subgenus *Disphyllum (Sinodisphyllum)*. Since then, its systematic status has been questioned and remains uncertain (Liao 1996). In fact, the significant difference is that *Sinodisphyllum* is solitary rather than fasciculate.

Fontaine (1961) considered *Sinodisphyllum* invalid because of its inadequate description. For that reason, Strusz (1965) agreed with Fontaine's idea that *Sinodisphyllum* was a senior synonym of *Mansuyphyllum*. Pedder (1965) proposed that *Sinodisphyllum* Sun should be considered to be a synonym of *Mictophyllum* Lang and Smith. Moreover, he also considered that the type species of *Sinodisphyllum* (*Sinodisphyllum variable* Sun) was a better representative of *Mictophyllum* than the type species of *Mictophyllum* selected by the original authors of the genus. He believed that there is a trend towards suppression of the minor septa and development of a herringbone dissepimentarium. *Mictophyllum nobile* is almost devoid of minor septa and represents a form very near the end of this trend. He noted that the trabeculae of *Sinodisphyllum* are disphyllid with relatively small but numerous dissepiments that are commonly inosculate. The tabulae may be short or long in longitudinal section and peripherally may be downturned, upturned or simply abut against adjacent tabula or dissepiments (Pedder 1965: 202–203).

However, other researchers (Liao 1977; Liao and Birenheide 1989; McLean 1993; Wang 1995) have considered *Sinodisphyllum* to be valid. Liao and Birenheide (1989) regarded *Sinodisphyllum* as a charactophyllid, characterized by long, thin tapering projections. They proposed that *Mansuyphyllum* Fontaine, 1961 and *Aristophyllum* Bulvanker et al., 1975 are junior synonyms of *Sinodisphyllum*. They also argued that some Russian species assigned to *Campophyllum* (*C. litvinovitshae* Soshkina, 1949) should also belong to *Sinodisphyllum*. Wang (1995) claimed that the trabeculae of *Sinodisphyllum* are disphyllid, and the higher matching coefficient between *Sinodisphyllum* and *Pseudozaphrentis* is the result of adaptive convergence.

Occurrence.—South China and Russian platforms; late Givetian to Frasnian.

Sinodisphyllum variable Sun, 1958

Fig. 8E–G, I.

Sinodisphyllum variable n. sp.; Sun 1958: 12, pl. 4: 1, 2, pl. 5: 1, pl. 6: 1.

Material.—Eight specimens.

Remarks.—Our specimens are conico-cylindrical in form. The number of septa increases with diameter, from 27 majors at a diameter of 13.5 mm to 34 at a diameter of 23–29 mm. The outer zone of the septum is weakly to moderately dilated, forming or without forming an inner wall at the inner margin of the dissepimentarium. The majors are long, becoming thin in the inner zone; the minor septa are very short, only 1/5 length of the majors. The dissepimentarium is wide; the dissepiments are mainly concentric, commonly with a few rows of dense herringbone dissepiments near the inner margin of the dissepimentarium, in which case the tabularium is generally divided into three distinct parts. In longitudinal section, variously sized dissepiments are arranged in 5 to 7 rows. Tabulae are incomplete, 1/2 diameter wide; the axial series of tabellae are sometimes cystose, in which case the dissepiments are generally concentric in cross section.

Specimens of *S. simplex* Sun, 1958 are characterized by scolecoid form, smaller diameter, more septa, complete tabulae (Fig. 8H), and mainly herringbone-shaped dissepiments. These specimens co-occur with *S. variable*.

Occurrence.—Central Hunan Province in Xiangxiang County and at the Xikuangshan and Chongshanpu sections; Frasnian.

Sinodisphyllum litvinovitshae (Soshkina, 1949)

Fig. 8J, K.

Campophyllum litvinovitshae sp. n.; Soshkina 1949: 86–88, pls. 38–39, pl. 40: 1–3.

Sinodisphyllum litvinovitshae (Soshkina, 1949); Liao 1977: 43, pl. 1: 6–8, pl. 3: 3.

Material.—Three specimens.

Remarks.—There are 22 major septa at a diameter of 11–12 mm and 31 at a diameter of 18–19 mm; the major septa are thin and long, but not reaching the center; the outer or middle zone is only slightly dilated; the minor septa are very short. There are few and scattered concentric large dissepiments at the outer part and several rows of relatively dense small herringbone dissepiments at the inner part. The tabularium is wide; the axial series is wide and flat, with unevenly distributed tabellae, about 20 per centimeter. This species is distinguished from *S. variable* in its shorter minor septa, and fewer and scattered outer dissepiments.

Occurrence.—Russia and South China (Guizhou Province, central Hunan Province); late Givetian to latest Frasnian.

Brachiopoda

(X.P. Ma and Y.L. Sun)

Order Productida Sarytcheva and Sokolskaya, 1959
Suborder Chonetidina Muir-Wood, 1955
Superfamily Chonetoidea Bronn, 1862
Family Chonetidae Bronn, 1862

Remarks.—Chonetids from the Upper Devonian (except for the upper Famennian) of South China have not been described in previous studies. Here we illustrate two species from the upper Frasnian. These two species are different from *Chonetes* cf. *ornatus* Schumard described by Hou (1965) from the upper Famennian Shaodong Formation of central Hunan and species of *Retichonetes* Muir-Wood, 1962 in having more numerous concentric fila and finer costae.

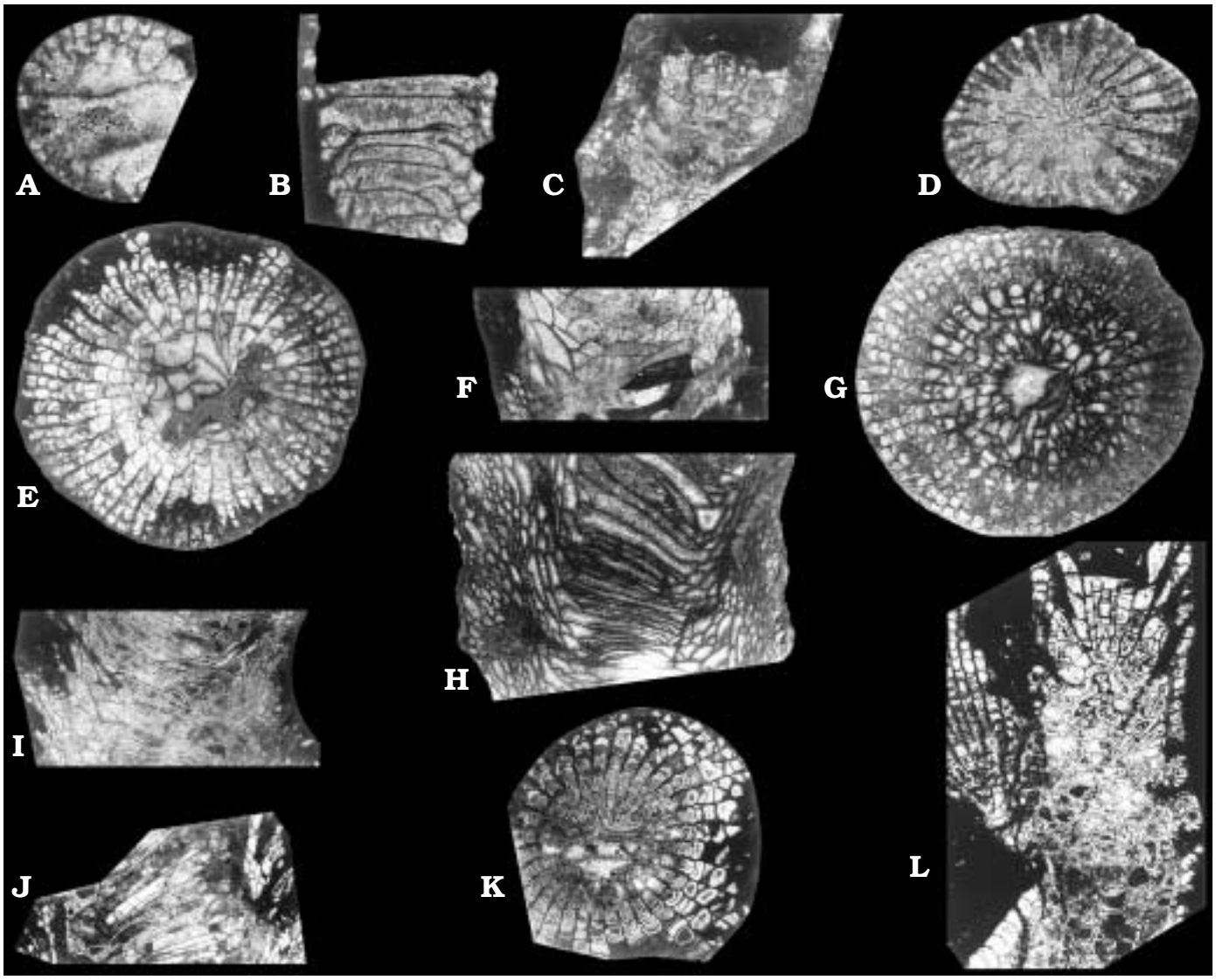

Fig. 8. Latest Frasnian (upper part of the *Pa. linguiformis* Zone) rugose corals from central Hunan. **A**, **B**. *Peneckiella shawoziensis* He, 1978. Transverse and longitudinal sections, specimen PUM 93595, sample L5/top0.2 (upper 20 cm of bed L5; × 6). **C**, **D**. *Temnophyllum* sp. Longitudinal and transverse sections, PUM 93594, sample L5/top0.2; × 4. **E**–**G**, **I**. *Sinodisphyllum variable* Sun, 1958. **E**, **F**. Transverse and longitudinal sections, PUM 93600, bed T3 of the Chongshanpu section; × 2.3. **G**. Transverse section, PUM 00072, bed T3, × 2.3. **I**. Longitudinal section, PUM 93596, sample L5/top0.2, × 2.3. **H**. *Sinodisphyllum simplex* Sun, 1958. Longitudinal section, PUM 93601, bed T3, × 2.3. **J**, **K**. *Sinodisphyllum litvinovitshae* (Soshkina, 1949) from the top of the Frasnian of Taotang, about 2 km north of the Xikuangshan section. **J**. Longitudinal section, PUM 00073, × 2.3. **K**. Transverse section, PUM 93599, × 2.3. **L**. *Disphyllum dupliforme* Kong, 1978, longitudinal section, PUM 93592, same specimen as Fig. 7H, × 4.

They are tentatively assigned to *Rhyssochonetes* Johnson, 1970 of the Dagnachonetinae Racheboeuf, 1981. The classification scheme of the Chonetidina by Racheboeuf (2000) is used in this paper.

Subfamily Dagnachonetinae Racheboeuf, 1981

Genus *Rhyssochonetes* Johnson, 1970

Rhyssochonetes? sp. 1

Fig. 9A, B.

Material.—Two specimens, one of which is well preserved.

Remarks.—The current specimens are similar to species of *Rhyssochonetes* in their external morphology, such as the transverse outline, moderately to strongly concavoconvex profile, symmetrically arranged orthomorph oblique spines, distinct radial ornamentation of rounded costae (with intercalated costae from mid-length) crossed by fine, closely-spaced concentric fila, and in lacking accessory septa in the interior of the dorsal valve. They differ from species of *Rhyssochonetes* in lacking dorsal median septum.

Occurrence.—Central Hunan Province; in the Shetianqiao section (sample S-Y-2), late Frasnian.

Rhyssochonetes? sp. 2

Fig. 9C–E, S.

Material.—Over 50 complete shells.

Remarks. —The present shells have the following main characters: shell small, weakly to moderately concavoconvex, transversely oval; ventral interarea apsacline, with well developed pseudodeltidium; dorsal interarea catacline, with chilidium. The diagnostic features of this form are its hinge spines, which are orthomorph parallel (a character which are different from species of *Rhyssochonetes*) and symmetrically arranged (Fig. 9E, S), and its ornamentation which consists of very weak radial parvicostellae and concentric undulating fila. Some specimens only show concentric undulating fila and others show both radial and concentric ornaments. This form is different from *Rhyssochonetes*? sp. 1 in its much weaker surface ornament and less convex ventral valve. Its general features suggest an assignment to the Dagnachonetinae of the Chonetidae. However, its internal structures are unknown, hence its taxonomic affiliation cannot be established with certainty at present.

Occurrence.—Central Hunan Province; in the Shetianqiao section (sample S-H-0), late Frasnian.

Suborder Productidina Waagen, 1883
Superfamily Productoidea Gray, 1840
Family Productellidae Schuchert, 1929
Subfamily Productellinae Schuchert, 1929
Genus *Productella* Hall, 1867
Productella sp. 1

Fig. 9L, M.

Material.—25 specimens, most of which are poorly preserved.

Remarks.—This form is characterized by small size, surface with rugae and growth lines. Spines are only present on the ventral valve. Both ventral and dorsal interareas are slit-like. These specimens have a more transverse outline and more numerous spines on the ventral valve than *Productella shetienchiaoensis* Tien, 1938. Tien's species is much smaller than *P.* sp. 1, with a width around 6.5 mm (not "natural size" as in Tien's plate explanation).

Occurrence.—In the Shetianqiao section occurring at several horizons; late Frasnian.

Productella asiatica Tien, 1938

Fig. 9J, K.

Productella lachrymosa var. *asiatica* Tien (var. nov.); Tien 1938: 17–19, pl. 1: 4–6.

Productella lachrymosa var. *asiatica* Tien; Liu et al. 1982: 180, pl. 129: 12.

Material.—Fifty complete specimens.

Remarks.—Our specimens are similar in nearly all respects to Tien's specimens, especially specimen 6254 (his pl. 1: 5). However, the surfaces of our new specimens are marked by less distinct tubercles and continuous plicae compared with the holotype.

Occurrence.—Not abundant at any given horizon but is found in nearly every sample in the early Famennian strata (*Pa. triangularis* Zone) of central and southern Hunan (e.g., in Xiangxiang, Shaodong, Qidong, Lingling Counties, etc).

Productella sp. 2

Fig. 9I.

Remarks.—Only one specimen from the very late Frasnian *Pa. linguiformis* Zone (sample C1-0) of the Jiangjiaqiao section. The unique feature of the single specimen is small number of spines on the dorsal valve. Generally dorsal spines are not observed on shells of the Productellidae until the Tournaisian according to Brunton and Lazarev (1997).

Family Productidae Gray, 1840
Subfamily Leioproductinae Muir-Wood and Cooper, 1960
Tribe Leioproductini Muir-Wood and Cooper, 1960
Genus *Leioproductus* Stainbrook, 1947
Leioproductus hunanensis Liu, 1982

Fig. 9F–H.

Leioproductus hunanensis Liu (sp. nov.); Liu et al. 1982: 181–182, pl. 130: 4.

Material.—About 200 specimens, most of which only partially preserved.

Remarks.—This species is very similar to species of *Ardiviscus* Lazarev, 1986 in shell size and strength of spines. Because the internal structure of the present species is not known (especially the presence or absence of cardinal process pit, which can be used to differentiate *Leioproductus* from *Ardiviscus*) the Hunan species is retained in *Leioproductus* at present. *Leioproductus hunanensis* may be conspecific with *Productella subaculeata* mut. *alpha* Grabau (1931–33: pl. 4: 9) from the Upper Devonian (early Famennian) Yaoso Group of South China.

Occurrence.—Qidong County of central Hunan; early Famennian (*Pa. triangularis* through *Pa. crepida* zones).

Superfamily Echinoconchoidea Stehli, 1954
Family Sentosiidae McKellar, 1970
Subfamily Caucasiproductinae Lazarev, 1987
Genus *Praewaagenoconcha* Sokolskaya, 1948
Praewaagenoconcha linglingensis (Wang, 1956b)

Fig. 9N–R.

Productellana linglingensis sp. nov.; Wang 1956b: 396–398, pl. 8: 1–7.

Material.—About 130 well preserved specimens.

Remarks.—Wang (1956b) originally assigned this species to *Productellana* Stainbrook, 1950, but did not give any description concerning its internal structures. *Productellana* is very small, with a few scattered spines on the dorsal valve, whereas the present species has numerous spines. An isolated dorsal valve in our material clearly shows the presence of hinge sockets (Fig. 9R) which are narrow and nearly parallel

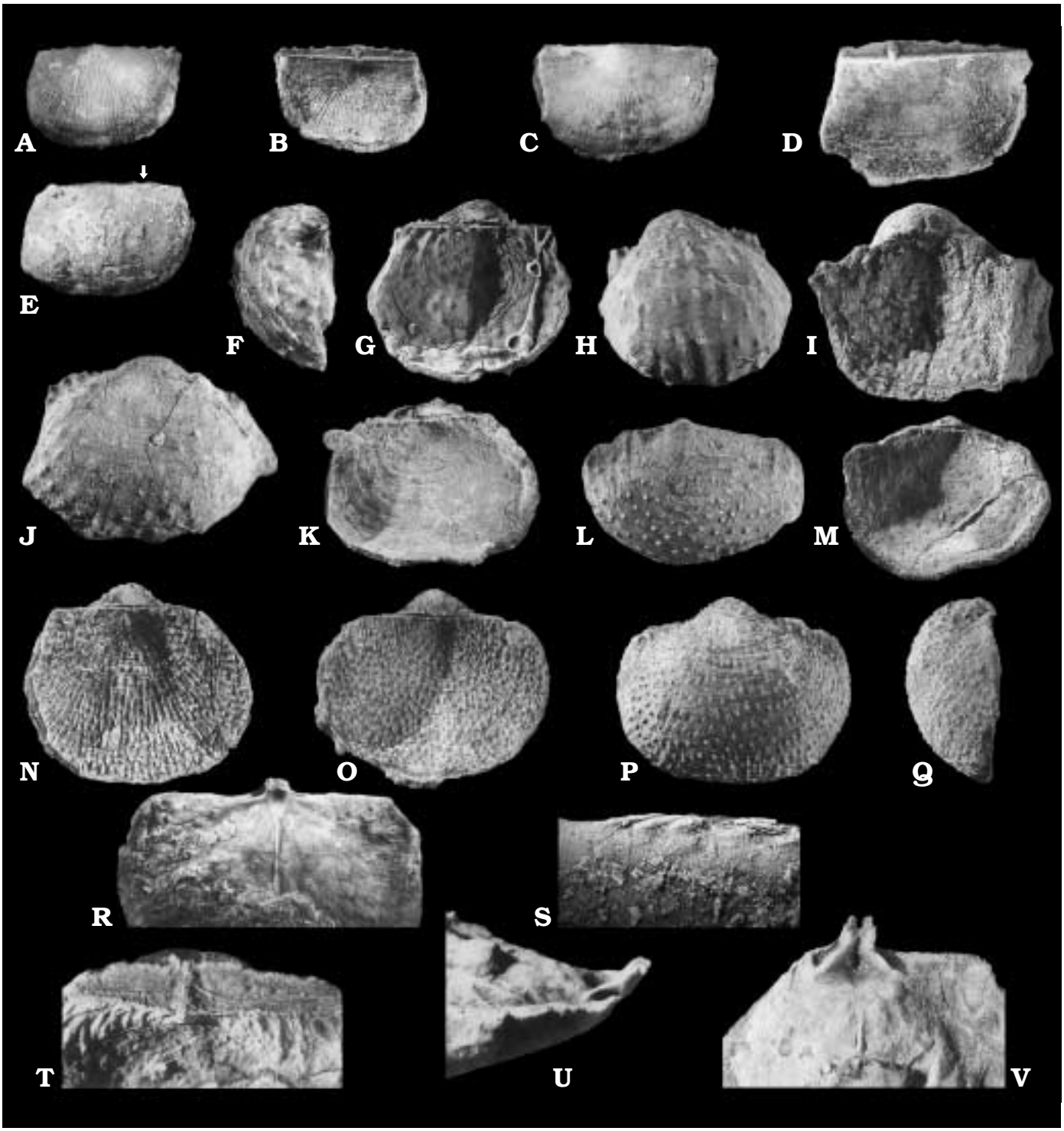

Fig. 9. **A**, **B**. *Rhyssochonetes*? sp. 1, sample S-Y-2, ventral and dorsal views, PUM 00055; × 3. **C**–**E**, **S**. *Rhyssochonetes*? sp. 2, sample S-H-0. **C**. Ventral view, PUM 00062, × 3. **D**. Dorsal view showing the interarea, PUM 00048, × 5. **E**. Ventral view, note the orthomorph parallel arranged hinge spines (arrowed), PUM 00061b, × 3. **S**. Enlargement of arrowed area of E, × 11.5. **F**–**H**. *Leioproductus hunanensis* Liu, 1982, sample C-H, lateral, dorsal and ventral views, PUM 00031, × 2. **I**. *Productella* sp. 2, sample C1-0, dorsal view showing some spines present on the valve, PUM 00035, × 3. **J**, **K**. *Productella lachrymosa* var. *asiatica* Tien, 1938; sample C7. **J**. Ventral view, PUM 00002, × 1.5. **K**. Dorsal view, PUM 00032, × 2. **L**, **M**. *Productella* sp. 1, sample S-Y-4. **L**. Ventral view, PUM 00018, × 2. **M**. Dorsal view, PUM 00015, × 2. **N**–**R**. *Praewaagenoconcha linglingensis* (Wang, 1956), sample C-H. **N**. Dorsal view, PUM 00030, × 2. **O**. Dorsal view, PUM 00034, × 2. **P**, **Q**. Ventral and lateral views, PUM 00024; × 2. **R**. Dorsal interior showing the slit-like sockets, PUM 00059, × 3.3. **T**–**V**. *Sinalosia rugosa* gen. et sp. nov., sample S-Y-2. **T**. Showing the distinct interarea with ventral pseudodeltidium and dorsal chilidium, which is medially divided by cardinal process as to form a narrow V-shaped slit gap, PUM 01001, × 6. **U**, **V**. Lateral and internal views of cardinal process, PUM 01002; × 6.

to the posterior margin. Hence it should be assigned to *Praewaagenoconcha* of the Caucasiproductinae that is characterized by the presence of well-developed teeth and sockets (Brunton et al. 2000). *Praewaagenoconcha linglingensis* is similar to Middle Devonian *Productella productoides* var. *sinensis* Grabau, 1931 in overall shell form, but in the latter, the spines are coarser and their bases are nearly parallel to the shell surface.

Occurrences.—Central and southern Hunan Province; in the Jiangjiaqiao section, early Famennian (*Pa. triangularis* to *Pa. crepida* zones).

Suborder Strophalosiidina Schuchert, 1913
Superfamily Strophalosioidea Schuchert, 1913
Family Araksalosiidae Lazarev, 1989
Subfamily Rhytialosiinae Lazarev, 1989
Genus *Sinalosia* gen. nov.

Type species: *Sinalosia rugosa* sp. nov.; Late Devonian (late Frasnian), central Hunan Province, China.

Derivation of the name: Sin, from the ancient name for China; alosia, a brachiopod generic suffix commonly used in the Strophalossidina.

Diagnosis.—Small to medium sized araksalosiid with a distinct interarea, delthyrium and notothyrium closed by pseudodeltidium and chilidium, weak spines only on ventral valve and nearly parallel to shell surface, rugae prominent on both valves.

Remarks.—The presence of prominent undulose rugae indicates that the new genus should belong to the Rhytialosiinae. It is similar to *Rhytialosia* Lazarev, 1989 in shell shape and distinct interareas (Brunton et al. 2000). However, the latter possesses very thick spines, a distinct cicatrix, and a dorsal median septum of full disk length. The new genus is also similar to *Veeversalosia* Lazarev, 1989 in shell shape and lacking strong hinge spines. However, the latter has spines on both valves and much narrower interareas. From *Donalosia* Lazarev, 1989 and *Devonalosia* Muir-Wood and Cooper, 1960 of the Donalosiinae the new genus may be distinguished by well-developed rugae on both valves and the presence of chilidium respectively.

Occurrence.—Central Hunan Province; Frasnian.

Species assigned.—Type species only.

Sinalosia rugosa sp. nov.

Figs. 9T–V, 10A–F.

Holotype: PUM 00017, well-preserved complete specimen; illustrated in Fig. 10A–C.

Type locality: Southern slope of a small unnamed hill southeast of Daoshitang, Heyi village, Yangqiao Township, Shaodong County, central Hunan Province.

Type horizon: Upper Shetianqiao Formation at a horizon corresponding to uppermost part of bed 22 of the Shetianqiao Formation (Hou and Wang 1988: 132), late Frasnian (probably Lower *Palmatolepis rhenana* conodont Zone or younger).

Derivation of the name: It is from well-developed rugae on both valves.

Diagnosis.—*Sinalosia* characterized by a concavo-convex profile, hinge line about equal to greatest width, ventral valve with cicatrix of attachment very weak to absent, rugae well developed on both valves, and delicate recumbent spines on ventral valve only.

Material.—Over 50 complete and incomplete shells.

Description.—Adult shell generally 2–2.5 cm in width, elliptical in outline, wider than long, concavo-convex in lateral profile, corpus shallow, hinge line about equal to or slightly shorter than greatest width.

Ventral valve moderately convex. Cicatrix of attachment very weak to absent. Interarea well developed; delthyrium small, triangular, closed by pseudodeltidium. Shell surface marked by rugae and alternating weak spines generally lying parallel to surface; hinge spines rare or absent, erect and slightly coarser if present.

Dorsal valve slightly concave, marked by rugae on whole surface; no spines. Interarea low; notothyrium relatively large (nearly equal to delthyrium in size), closed by chilidium, which is penetrated by a bifid cardinal process in some specimens (Fig. 9T).

Dorsal interior with a narrow and low median septum extending to about mid-length of shell; postero-ventrally directed bifid cardinal process high, with a small furrow on top of the cardinal process on each side; sockets short but deep; inner socket ridges well developed, posteriorly connected with the cardinal process. Ventral interiors unknown.

Remarks.—It seems that no similar forms have been recorded yet. This would be the first record of Devonian strophalosioids in China.

Occurrence.—Central Hunan in the Shetianqiao section; late Frasnian.

Order Rhynchonellida Kuhn, 1949
Superfamily Rhynchotrematoidea Schuchert, 1913
Family Trigonirhynchiidae Schmidt, 1965
Genus *Hunanotoechia* Ma, 1993b
Hunanotoechia tieni Ma, 1993b

Fig. 10R, S.

Hunanotoechia tieni gen. et sp. nov.; Ma 1993b: 723–724, text-figs. 2–6, pl. 1: 1–7, pl. 2: 1–6.

Material.—Around 300 specimens (200 from the Shetianqiao section and 100 from the Xikuangshan section).

Remarks.—This species is abundant in the late Frasnian of the Xikuangshan area and the Shetianqiao section. However, in the latter place, it is generally somewhat smaller than in Xikuangshan. For detailed description, see Ma (1993b).

Occurrence.—Central Hunan; Late Frasnian (?Lower, Upper *Pa. rhenana* Zone through *Pa. linguiformis* Zone).

Hunanotoechia gamma (Tien, 1938)

Fig. 10J–Q.

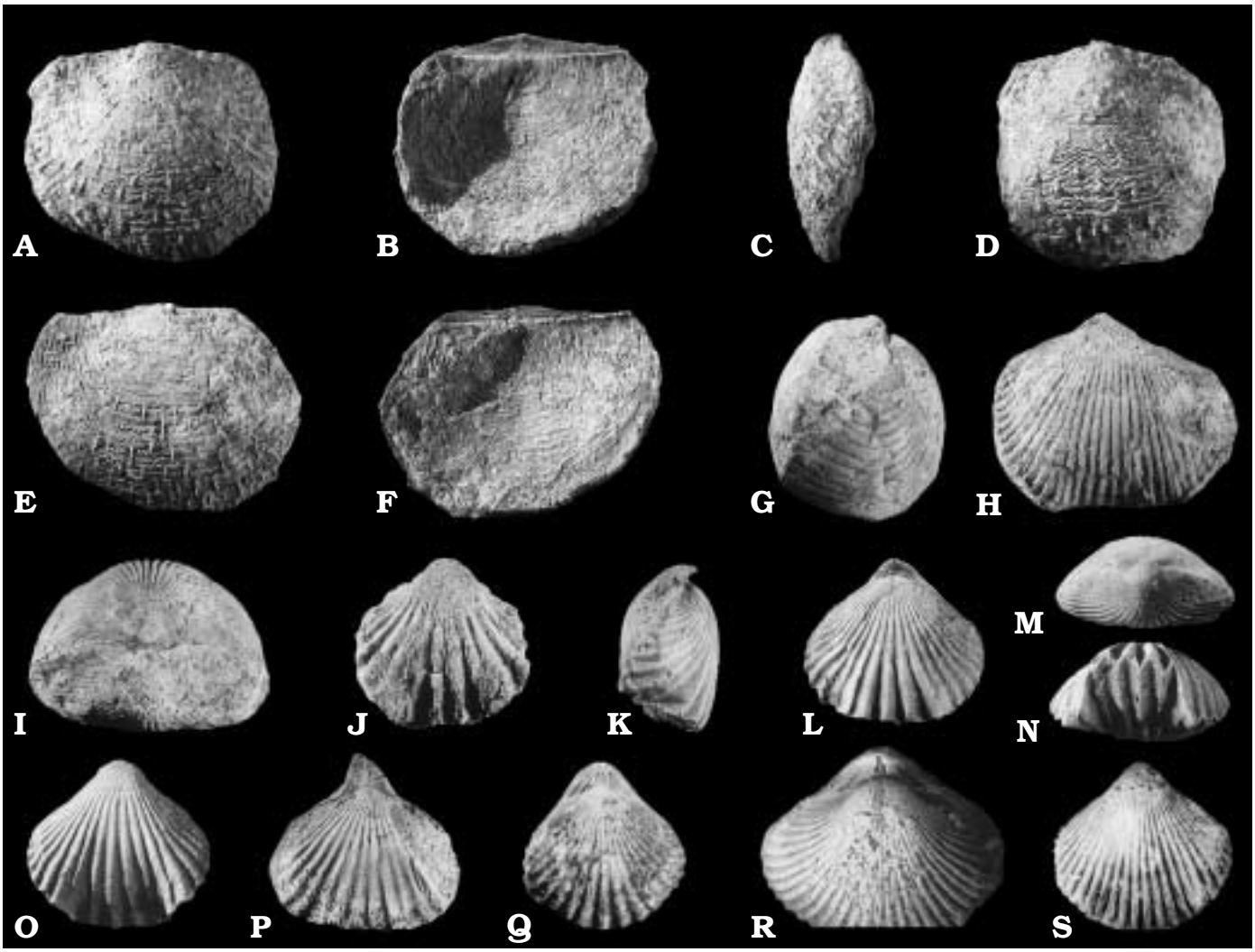

Fig. 10. **A–F**. *Sinalosia rugosa* gen. et sp. nov., sample S-Y-2. **A–C**. Ventral, dorsal and lateral views of holotype PUM 00017; × 2. **D**. Ventral view of paratype PUM 00019 showing its chevron ornamentation, × 2. **E**, **F**. Ventral and dorsal views of paratype PUM 00021; × 2. **G–I**. *Hypothyridina linglingensis* Wang, 1956a; sample S-Y-4, lateral, ventral and posterior views of PUM 00027; × 1.25. **J–Q**. *Hunanotoechia gamma* (Tien, 1938), sample S-Y-2. **J**. Ventral view of PUM 00042 showing the presence of only two sinal plications, × 3. **K–O**. Lateral, dorsal, posterior, anterior and ventral views of PUM 00051; × 3. **P**. Dorsal view of PUM 00041 showing a specimen with growth bizarre ventral beak, × 3. **Q**. Dorsal view of PUM 00054 showing the deltidial plates, × 5. **R**, **S**. *Hunanotoechia tieni* Ma, 1993; sample S-25-2, PUM 00053, enlarged dorsal view (**R**) showing the deltidial plates and the foramen, × 4 and ventral view (**S**), × 3.

Camarotoechia shetienchiaoensis var. (var. nov.); Tien 1938: 39–40, pl. 4: 13–15.

Camarotoechia gamma Tien; Wang et al. 1964: 359, pl. 60: 5–8.

Material.—Seventy-two well preserved specimens.

Remarks.—Our specimens agree in general morphology with Tien's species originally described from the Shetianqiao Formation of Xiangxiang County, for example, two to five sinal plications, zero to one parietal plication on each side, four to six sinal plications, and total number of shell plications (20–25: our observation shows that Tien's type specimens have 20–25 shell plications, not 14–18 as originally reported by Tien 1938: 39). Rare specimens have only two sinal plications (Fig. 10J).

Tien (1938) described *Camarotoechia shetienchiaoensis* and its three varieties: , , and . Wang et al. (1964) recognized only two species: *C. shetienchiaoensis* (including var.) and *C. gamma* (including var.). Our observation shows that all those taxa probably should be assigned to the same species. However, we would rather follow the opinion of Wang et al. (1964) in this paper pending more topotype specimens available to study their morphologic variations. This species is assigned to *Hunanotoechia* on the basis of its small size and similar general shape and ventral posterior. *H. tieni*, the type species of *Hunanotoechia*, is different from this species by having more shell plications (40–50 vs. 20–25).

Occurrence.—Shetianqiao section; late Frasnian (Lower to Upper *Pa. rhenana* zones).

Superfamily Uncinuloidea Rzhonsniskaya, 1956

Family Hypothyridinidae Rzhonsniskaya, 1956

Genus *Hypothyridina* Buckman, 1906
Hypothyridina linglingensis Wang, 1956a

Fig. 10G–I.

Hypothyridina linglingensis n. sp.; Wang 1956a: 173–174, pl. 3: C1–5.

Material.—Ten shells.

Remarks.—Our specimens are in agreement with *H. linglingensis* Wang, 1956a in general shape and size. Shell width is slightly greater than length, with greatest width around mid-length of shell and greatest thickness at the anterior margin. The dorsal valve is much more convex than the ventral valve. Dorsal fold is very low posteriorly and becomes well developed at the anterior margin. Ventral sinus is very shallow, becoming geniculated in right angle to meet the dorsal fold near the anterior margin. Ventral beak is small, incurved against that of the dorsal valve. External surface is covered by simple, low, and rounded plications, with 8–10 in sinus, 9–11 on fold, and 16 or more on each flank. The interspaces are narrow and linear. Occasionally one or two plications next to the fold or sinus may bifurcate.

Wang (1956a) described two species of *Hypothyridina* from the Upper Devonian of central Hunan based on only three specimens: *H. hunanensis* and *H. linglingensis*. He did not mention any features distinguishing the two forms. *Hypothyridina linglingensis* is different from the former by its smaller shell and flatter sinal plications. Whether these are intraspecific variations or not requires additional specimens for further study.

Occurrences.—This species is very rare in the late Frasnian (*Pa. linguiformis* Zone), nevertheless it can be found in all latest Frasnian deeper water shelf deposits in the Chongshanpu, Shetianqiao, and Jiangjiaqiao sections.

Order Atrypida Rzhonsnitskaya, 1960
Suborder Atrypidina Moore, 1952
Superfamily Atrypoidea Moore, 1952
Family Atrypidae Gill, 1871

Remarks.—Ma (1998) described and figured a few atrypid forms from the latest Frasnian of the Chongshanpu and Jiangjiaqiao sections of central Hunan Province. Later, abundant specimens of *Spinatrypa* and "*Costatrypa*" and rare *Iowatrypa*? *qidongensis* (Fig. 11P, Q) were collected from the Shetianqiao section.

Genus *Spinatrypa* Stainbrook, 1951
Spinatrypa subkwangsiensis (Tien, 1938)

Fig. 11A–E.

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

Spinatrypa subkwangsiensis (Tien); Liu et al. 1982: 198, pl. 144: 7.

Spinatrypa cf. *ninghsiangensis* Zhao; Ma 1998: 350, figs. 3, 4A–F.

Spinatrypa sp. A; Ma 1998: 350, fig. 4G–K.

Material.—Around 200 well preserved shells.

Remarks.—Preliminary study of abundant specimens from the Shetianqiao section shows that *S.* cf. *ninghsiangensis* and *S.* sp. A from the Chongshanpu section (Ma 1998) probably represent intraspecific variation. When Tien (1938) described the species, he did not designate a holotype. Study of Tien's type specimens indicates that they may be divided into two morphological groups. Group A is represented by specimens 6280 and 6183 (Tien 1938: pl. 13: 3, 4) with coarser ribs, wider interspaces, and fewer ribs (no more than 20); group B is represented by specimens 6181 and 6182 (Tien 1938: pl. 13: 1, 2) with finer and more ribs (around 25). Group A is identical with the *Spinatrypa* specimens from the Shetianqiao section.

Occurrence.—Widely distributed in central Hunan; Middle to Late Devonian (Frasnian).

Genus *Iowatrypa* Copper, 1973
Iowatrypa? *shaodongensis* sp. nov.

Figs. 11F–O, 12.

Costatrypa sp.; Ma 1998: 353–354, fig. 8B–F, ?figs. 7, 8G–K.

Holotype: PUM 00004, complete shell, illustrated in Fig. 11J–N.

Type locality: Daoshitang, Heyi village, Yangqiao Township, Shaodong County, central Hunan Province.

Type horizon: Upper Shetianqiao Formation at a horizon corresponding to basal part of bed 25 of the Shetianqiao Formation (Hou and Wang 1988: 132), latest Frasnian (probably *Palmatolepis linguiformis* Zone).

Derivation of the name: a county name in central Hunan from where the specimens were collected.

Material.—Over 150 well preserved complete specimens of various growth stages.

Diagnosis.—Large sized *Iowatrypa*? with long straight hinge line, tubular-imbricate ribs, conjunct deltidial plates, the presence of dental nucleus in stead of dental cavity, pedicle layer or collar, dorsal median septum, and 12 whirls of spiralium.

Description.—Adult shells generally ranging from 15 to 25 mm in width (largest shell over 25 mm), most shells wider than long, about equibiconvex; greatest width at hinge or slightly anteriorly or at midlength; surface marked by 50 to 70 tubular-imbricate ribs (more imbricate and less tubular ribs) of both bifurcation and implantation (chiefly by bifurcation on both valves); growth lamellae variously spaced, from 0.5 to 2 mm, generally 1 mm; anterior commissure uniplicate.

Ventral beak generally suberect to slightly incurved, but straight in young specimens; deltidial plates conjunct, minute foramen commonly infilled by pedicle structures.

Internally ventral valve with pedicle collar well-developed, partly fused to shell wall and dental nucleus, shell thickened posteriorly. Dorsal valve with knobbed cardinal process sitting on inner socket ridges and the median pit; ball-like crural bases developing anteriorly to feathered crura, disjunct jugum, 12 whorls of spiralium; with low and strong median septum.

Remarks.—This species has been reported as *Costatrypa* sp. from the *Pa. linguiformis* Zone of the Chongshanpu section of central Hunan (Ma 1998), but differs from true *Costatrypa* Copper, 1973 in having conjunct deltidial plates (Ma 1998: 354). Numerous new specimens from the Shetianqiao section show that this species is characterized by numerous well-developed fine more imbricate and less tubular ribs which

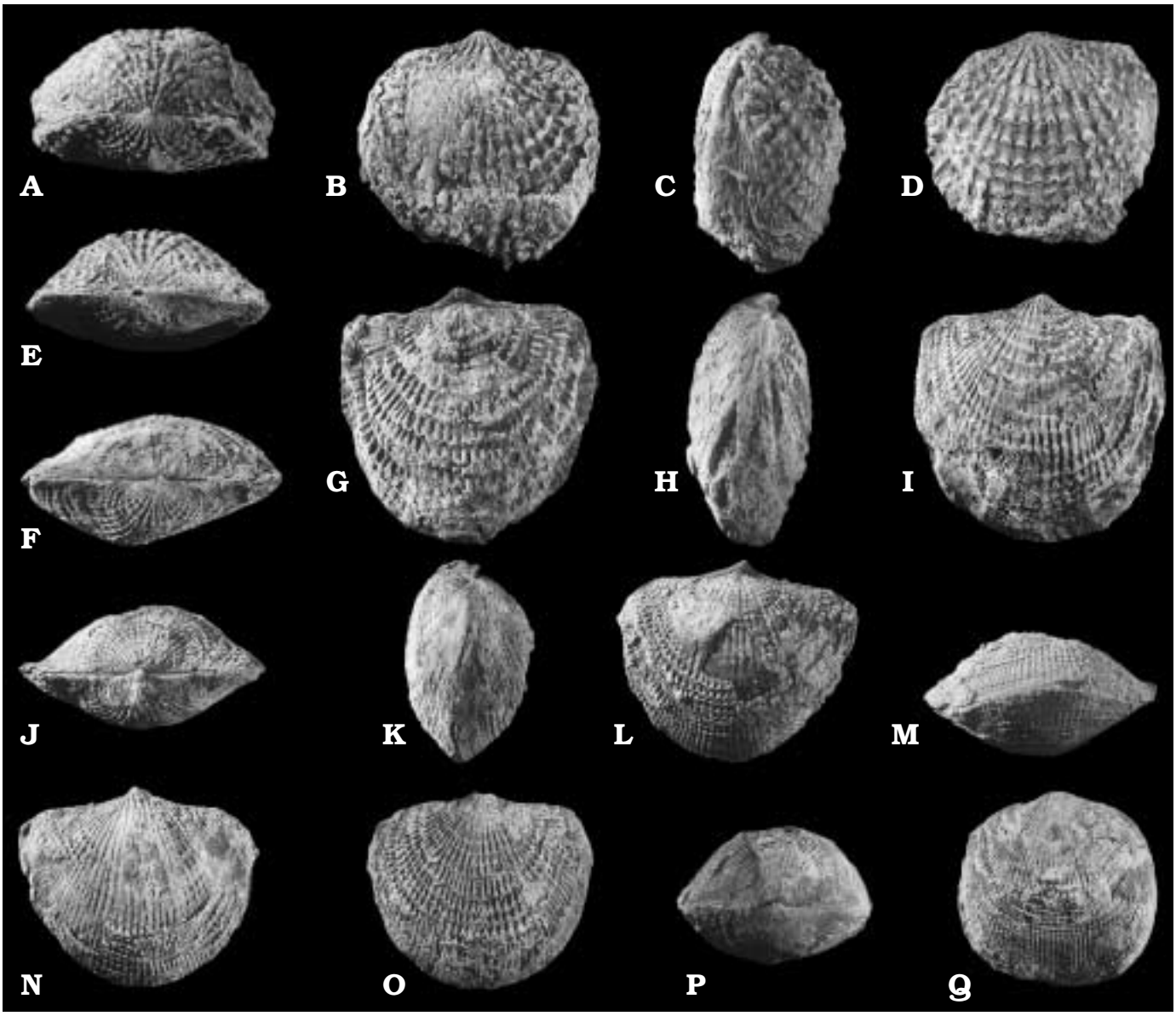

Fig. 11. **A**–**E**. *Spinatrypa subkwangsiensis* (Tien, 1938), sample S-Y-4. **A**–**C**. Posterior, ventral and lateral views of PUM 00016; × 2. **D**, **E**. Dorsal and posterior views of PUM 00020; × 2. **F**–**O**. *Iowatrypa*? *shaodongensis* sp. nov., S-Y-4. **F**–**I**. Posterior, dorsal, lateral, and ventral views of paratype PUM 00003; × 2. **J**–**N**. Posterior, lateral, dorsal, anterior and ventral views of holotype PUM 00004; × 2. **O**. Ventral view of paratype PUM 00001, × 1.5. **P**, **Q**. *Iowatrypa*? *qidongensis* Ma, 1998, sample S-Y-4, posterior and ventral views of PUM 00008; × 1.5.

suggests a generic assignment to *Spinatrypina* Rzhonsnitskaya, 1964 or *Iowatrypa*. However, the present species is different from species of *Spinatrypina* in lacking dental cavities. Therefore the species is tentatively assigned to *Iowatrypa*, but it is different from species of *Iowatrypa* Copper, 1973 in its larger size and having more numerous whorls of spiralium.

The new species is similar to Middle Devonian *Atrypa douvillii* Mansuy, 1912 from eastern Yunnan Province, which was later assigned into *Spinatrypina* by Chen (1983). The new species is different from *S. douvillii* by its larger size, wider and straighter hinge, more numerous plications (about 50 to 60 vs. about 44–48 for a similar-sized shell), and internally absence of dental cavities and more whorls (up to 12 vs. seven in *S. douvillii*) of spiralium. It is distinct from *Iowatrypa*? *qidongensis* Ma, 1998 by its larger size, coarser ribs, prominent ventral beak, and more whorls of spiralium. The present species is different from *Iowatrypa timanica* and *I. nalivkini* figured by Rzhonsnitskaya et al. (1998: fig. 21F–J) and *Anatrypa timanica* var. *markovskii* figured by Lyashenko (1959: pl. 26: 5–6) in its closely spaced and more imbricate lamellae. The new species is similar to ?*Waiotrypa pluvia* figured by Godefroid and Helsen (1998: fig. 8A–M) in general shell form and some internal structures (presence of a pedicle collar, cardinal process etc.). However, the latter has dental cavities and thick deltidial plates, and lacks a dorsal median septum. It is distinct from *I. rotundicollis* of Gode-

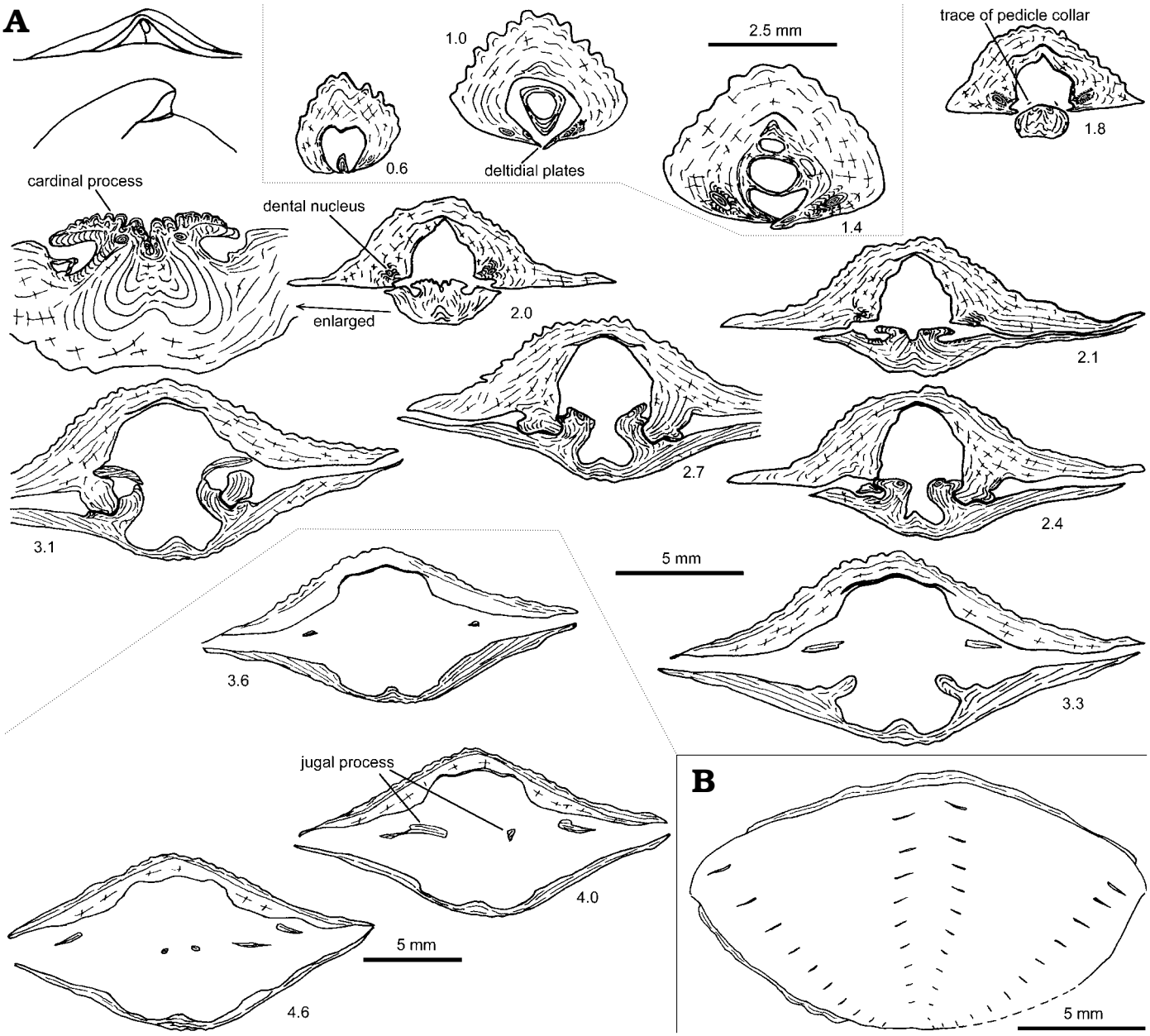

Fig. 12. Transverse serial sections of *Iowatrypa*? *shaodongensis* sp. nov. from the Shetianqiao section (sample S-Y-4). Numbers refer to distance in mm from the ventral apex. **A**. Specimen PUM 00069 (specimen of acetate peel – 00A). **B**. Transverse section showing the spiralium at its maximum number at a distance of 9.8 mm from the ventral apex. Specimen PUM 00070 (00B).

froid (1994) by its large shell size, more densely spaced lamellae, more prominent beak, presence of a pedicle collar, and more whorls of spiralium.

Occurrence.—Central Hunan Province, in the Shetianqiao and Chongshanpu sections; late Frasnian.

Order Athyridida Boucot, Johnson, and Staton, 1964
Suborder Athyrididina Boucot, Johnson, and Staton, 1964
Superfamily Athyridoidea Davidson, 1881
Family Athyrididae Davidson, 1881
Subfamily Athyridinae Davidson, 1881
Genus *Athyris* McCoy, 1844
Athyris supervittata Tien, 1938

Fig. 13Q–U.

Athyris supervittata Tien (sp. nov.); Tien 1938: 83–84, pl. 11: 7.

Material.—Eleven complete specimens.

Remarks.—Tien (1938) first described this species from the middle Frasnian of the Qiziqiao section. Comparison of our specimens with Tien's shows that the latter is not a fully mature specimen. Fold and sinus may be very distinct at the anterior margin in mature specimens, with the shell on either

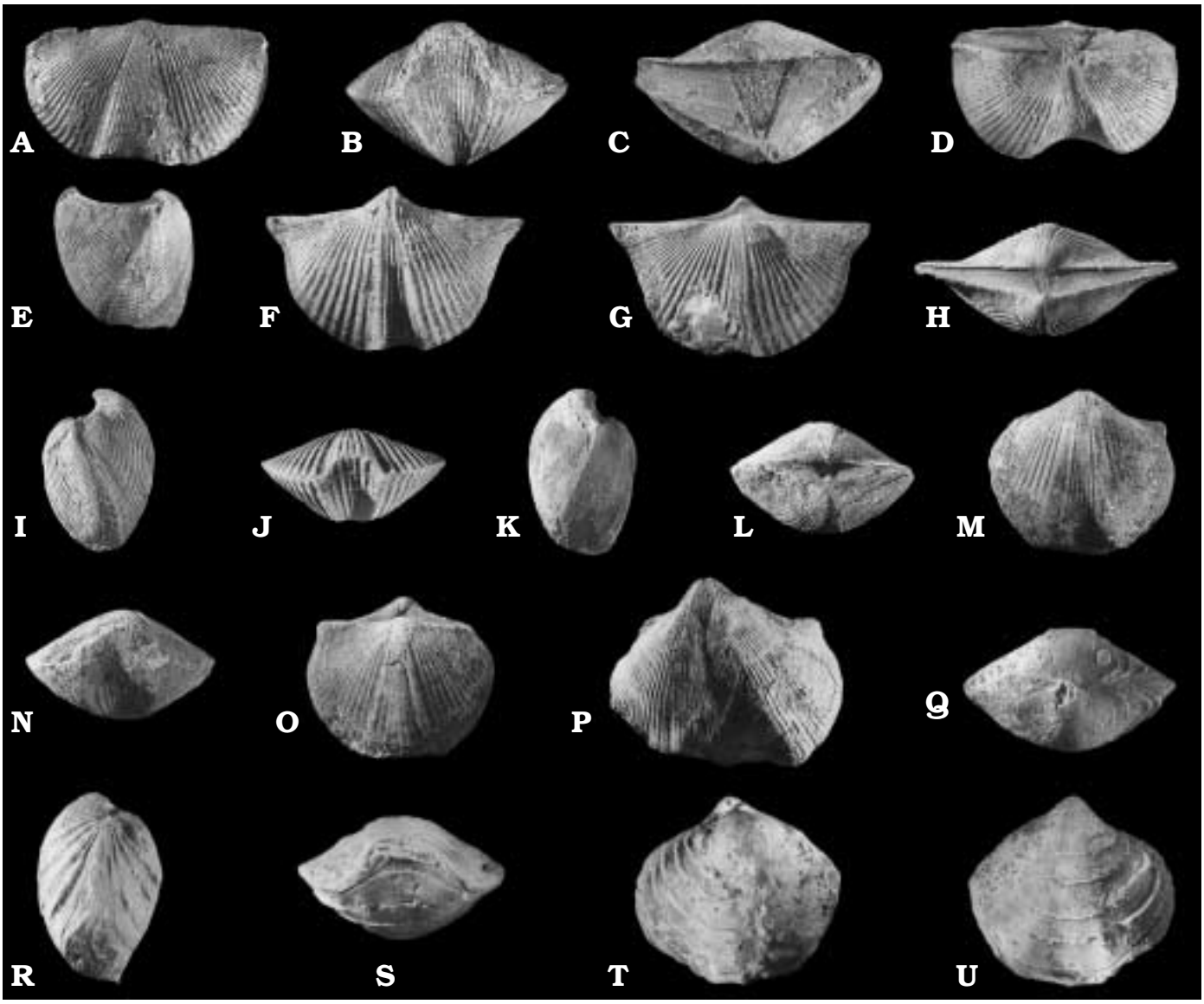

Fig. 13. **A–E**. *Cyrtospirifer* cf. *whitneyi* (Hall, 1858), sample S-Y-2, PUM 00011, dorsal, anterior, posterior, ventral and lateral views; × 1.5. **F–J**. *Cyrtospirifer*? *variabilis* Ma and Sun, 2001, sample S-25-2. **F–I**. Ventral, dorsal, posterior and lateral views of holotype PUM 00005; × 2. **J**. Anterior view of paratype PUM 00013, × 2. **K–O**. *Mennespirifer yangqiaoensis* Ma and Sun, 2001, sample S-H-0, lateral, posterior, ventral, anterior, and dorsal views of PUM 00036; × 2. **P**. *Sinospirifer* sp.1, sample C7, ventral view of PUM 00040, × 1. **Q–U**. *Athyris supervittata* Tien, 1938, sample S-Y-4, posterior, lateral, anterior, dorsal and ventral views of PUM 00047; × 3.

side of the fold extended into the ventral valve at various degrees in different individuals. Externally this species is very similar to *Pachyplaxoides postgyralea* Grunt, 1998. The latter genus has no dental plates (Grunt in Grunt and Racki 1998). We would rather leave the Chinese species in the genus *Athyris* before its internal structure is revealed. Our specimens are also very similar to *Athyris oehlerti* Rigaux, 1908 figured in Brice (1988: pl. 43: 6–10) except that the Hunan specimens are somewhat smaller. Further comparison is needed when more specimens are available.

Occurrence.—Qiziqiao Section, middle Frasnian; in the Shetianqiao and Jiangjiaqiao sections, late Frasnian (early *Pa. linguiformis* Zone).

Order Spiriferida Waagen, 1883
Suborder Spiriferidina Waagen, 1883
Superfamily Cyrtospiriferoidea Termier and Termier, 1949
Family Cyrtospiriferidae Termier and Termier, 1949

Remarks.—Grabau (1931) described over 20 species or varieties of *Sinospirifer* and seven species of *Cyrtiopsis* from the Upper Devonian of South China (for recent revision see Ma and Day 1999). Tien (1938) designated *S. sinensis* as the type species of *Sinospirifer* and in the meantime renamed two genus group names: *Tenticospirifer* (type: *Spirifer tenticulum*), and *Hunanospirifer* (type: *H. wangi*). *Hunanospirifer* and

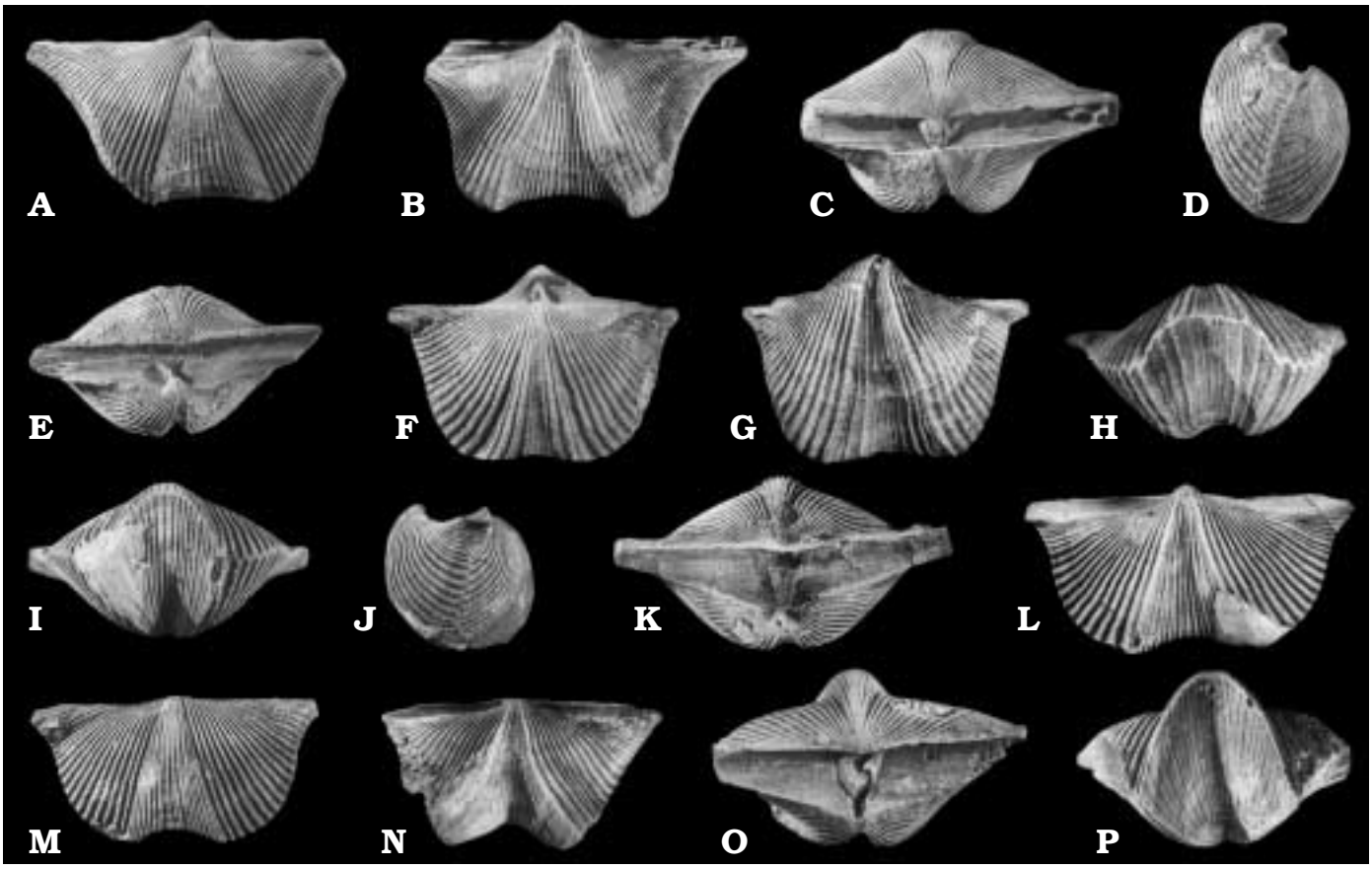

Fig. 14. **A–C**. *Sinospirifer gortanioides* Grabau, 1931, sample C-H, dorsal, ventral, and posterior views of PUM 98014; × 1.3. **D–H**. *Lamarckispirifer hayasakai* (Grabau, 1931), sample C-H, lateral, posterior, dorsal, ventral and anterior views of PUM 00025; × 1.3. **I–M**. *Sinospirifer subarchiaci* (Martelli, 1902), sample C-H, anterior, lateral, posterior, ventral and dorsal views of PUM 98001; all × 1.3 except **K** and **L**, × 1.5. **N–P**. *Sinospirifer pekinensis* Grabau, 1931, sample C-H, ventral, posterior and anterior views of PUM 980152; × 1.5.

Chinese "*Tenticospirifer*" are present in the *Yunnanella* bed of middle Famennian age. They are beyond the scope of this paper (for discussion on Chinese Famennian "*Tenticospirifer*" see Ma and Day 2000). Gatinaud (1949) proposed a radical subdivision of the *Cyrtospirifer* group chiefly based on Grabau's 1931 work. Of the available names *Tenticospirifer* (*Lamarckispirifer*) may be valid. Wang et al. (1964), Pitrat (1965) and all subsequent workers consider that *Sinospirifer* to be a synonym of *Cyrtospirifer*. However, Carter et al. (1994) listed it as a valid genus.

Before a detailed study of the Chinese early Famennian cyrtospiriferids we would rather use *Sinospirifer* for the time being. Most of Grabau's Famennian *Sinospirifer* species will be addressed in another paper (Ma and Day in preparation). And the late Frasnian small-sized cyrtospiriferids are described in Ma and Sun (2001). Those species will not be described or discussed in this paper except for their illustrations, including *Cyrtospirifer* cf. *whitneyi* (Fig. 13A–E), *Cyrtospirifer*? *variabilis* that features rare pustules both on plications and in grooves in some specimens (Fig. 13F–J), *Mennespirifer yangqiaoensis* (Fig. 13K–O), *Lamarckispirifer hayasakai* (Figs. 14D–H and 15P, Q), *Sinospirifer gortanioides* (Figs. 14A–C and 15R), *S. pekinensis* (Fig. 14N–P), *S. subarchiaci* (Fig. 14I–M), *S. subextensus* (Fig. 15K–O), and *S*. sp .1 (Fig. 13P).

Genus *Cyrtiopsis* Grabau, 1923

Cyrtiopsis? cyrtiopsiformis (Yang, 1977)

Figs. 15F–J, 16.

Arctospirifer cyrtiopsiformis Yang (sp. nov.); Yang et al. 1977: 434, pl. 172: 5

Material.—Fifteen complete specimens.

Remarks.—This species is characterized by a shell form almost identical with that of *Cyrtiopsis graciosa* Grabau, 1931. They are similar in shell micro-ornamentation and shell outline and lateral profile. They are also identical in the structure of cardinalia, i.e., with a median cavity anterior to the cardinal process (compare fig. 16 with fig. 10 of Ma and Day 1999: 618). Differences lie in that the present species has a short delthyrial plate and has no pseudodeltidium. If there were sexual dimorphism in shell morphology of modern brachiopods, by analogy these two Devonian species would be taken as such an example. There have been indeed some reports of sexual dimorphism in fossil brachiopods such as *Leiorhynchus* (Harrington 1969).

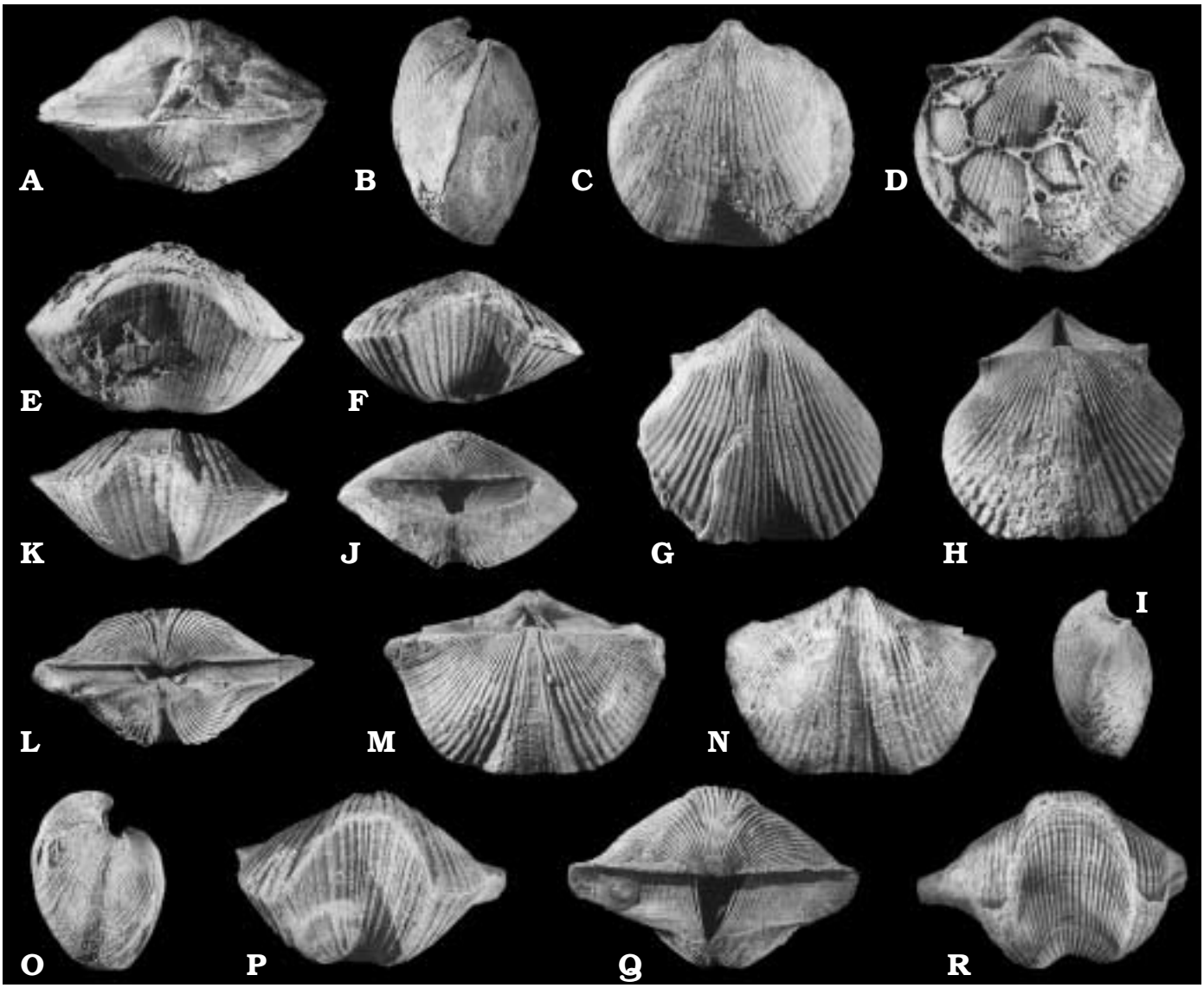

Fig. 15. **A**–**E**. *Platyspirifer paronai* (Martelli, 1902), sample C-H. **A**. Interarea view of PUM 00026 showing the convex pseudodeltidium, × 2.75. **B**, **C**. Lateral and ventral views of PUM 00022; × 1.5. **D**, **E**. Dorsal and anterior views of PUM 00038; × 1.2. **F**–**J**. *Cyrtiopsis*? *cyrtiopsiformis* (Yang, 1977), sample C-H, anterior, ventral, dorsal, lateral, and posterior views of PUM 97011; all × 2 except **I** × 1.5. **K**–**O**. *Sinospirifer subextensus* (Martelli, 1902), sample C-H, anterior, posterior, dorsal, ventral and lateral views of PUM 00023; × 1.3. **P**, **Q**. *Lamarckispirifer hayasakai* (Grabau, 1931), sample C-H, anterior and posterior views of PUM 00028; × 1.3. **R**. *Sinospirifer gortanioides* Grabau, 1931; sample C-H, anterior view of PUM 98014, × 1.3.

Originally Yang et al. (1977) assigned this species to *Arctospirifer* Stainbrook, 1950. However, *Arctospirifer* has no delthyrial plate (Carter et al. 1994: 333 and X. P. Ma's observations of Stainbrook's type specimens) and has a median primary sinal plication instead of *Cyrtospirifer*-type sinal plications characteristic of the Cyrtospiriferidae (Ma and Day 2000: 445). Therefore *Arctospirifer* is not a cyrtospiriferid and Carter et al. (1994) reassigned it to the Echinospiriferidae of the Spinelloidea.

Occurrence.—Xinhua County (Upper Devonian); in the Jiangjiaqiao section (Qidong County), early Famennian.

Genus *Platyspirifer* Grabau, 1931
Platyspirifer paronai (Martelli, 1902)

Fig. 15A–E.

Schizophoria Paronai sp. nov.; Martelli 1902: 365–367, pl. 14: 21–24.

Platyspirifer paronai (Martelli, 1902); Grabau 1931: 355–357, pl. 37: 2–4;

Platyspirifer paronai (Martelli, 1902); Hou et al. 1996a: 161, pl. 1: 4–6, pls. 5–6, text-fig. 4.

Material.—Thirty well preserved complete specimens.

Remarks.—This species is characterized by short hinge, low and flat plications, very narrow interspaces, shallow sinus and internally with a long, thick delthyrial plate in ventral valve and a well developed large comb-like cardinal process (Hou et al. 1996a: 160, text-fig. 4). All previous authors have recorded the delthyrium as open without a pseudodeltidium. We have found that this structure is present in some speci-

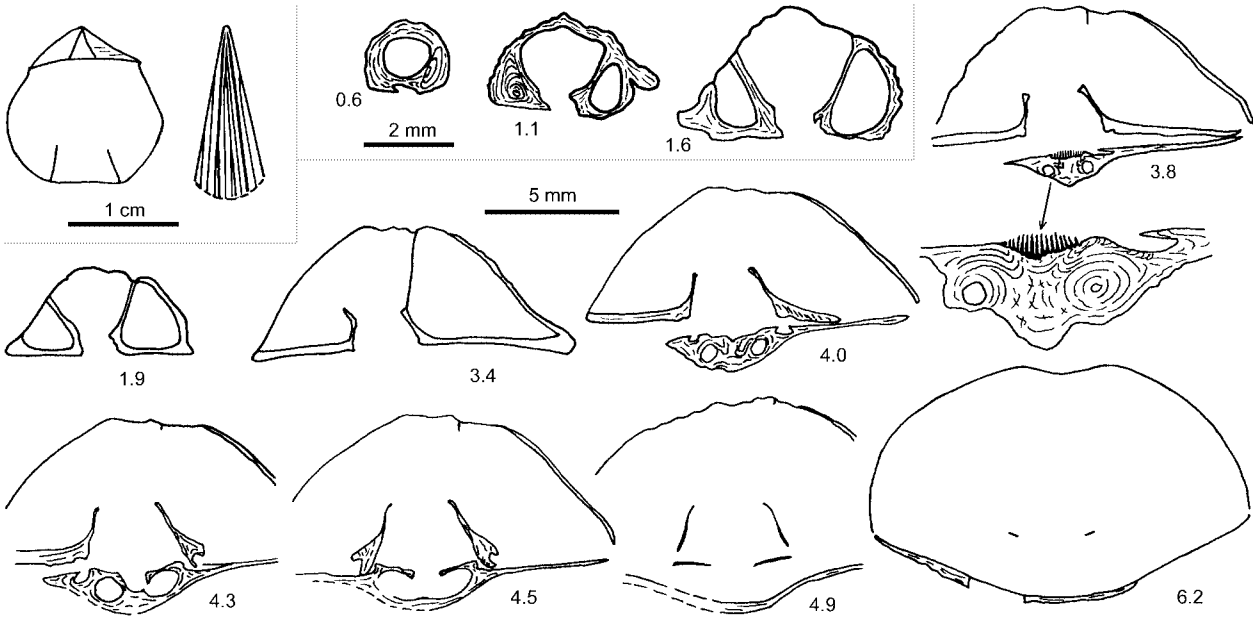

Fig. 16. Transverse serial sections of *Cyrtiopsis*? *cyrtiopsiformis* from the Jiangjiaqiao section (sample C-H). Numbers refer to distance in mm from the ventral apex. Arrow indicates enlargement. Note the presence of a very short delthyrial plate and absence of a pseudodeltidium at the very posterior end of the ventral valve. Specimen PUM 00071 (97D).

mens and hence it would have been present in all specimens when they were alive.

Wang et al. (1964: 470) pointed out that a young specimen of *P. paronai* (Cat. No. 784) is very similar to *P. subparonai* Grabau, 1931 in shell indices, outline, and bifurcation pattern of plications. Whereas Hou et al. (1996a: 161) suggested that "*Platyspirifer subparonai* Grabau, 1931 may be rejected from genus *Platyspirifer* because its cardinal angles truncate and project sharply beyond the shell margins". Based on our observations we concur with the opinion of Hou et al. (1996a).

Occurrence.—Shaanxi Province (Martelli 1902), but not proved by recent geological investigation; in the Jiangjiaqiao section (Qidong County), early Famennian.

Conclusions

Our study shows that major benthic fossil groups were all affected by the F–F extinction event. The most severely affected group is the order Rugosa. The rugose corals suffered near-total extinction just after achieving their peak abundance and diversity during the late Frasnian.

Ostracods need further taxonomic revision. Preliminary data from the Xikuangshan section show that late Frasnian ostracod fauna was very abundant and diverse and that most taxa disappeared near the F–F boundary. The early Famennian ostracod fauna is of low diversity, but certain species are abundant in various early Famennian horizons.

The late Frasnian brachiopod fauna is characterized by atrypids, *Hunanotoechia* (rhynchonelloid), small-sized cyrtospiriferids, and rare pentamerids (*Gypidula*), whereas the early Famennian brachiopod fauna mainly consists of diverse and abundant cyrtospiriferids, abundant *Yunnanellina* (rhynchonelloid), with common productoids. Preliminary observation of Ma and Day (personal communication) suggests that all but one possible early Famennian cyrtospiriferid are new forms distinct from late Frasnian species.

Acknowledgments

This work is supported by the Major Basic Research Projects of the Ministry of Science and Technology, China (G2000077700), the Foundation for University Key Teachers of the Chinese Ministry of Education, and the National Natural Science Foundation of China (40172006 and 49872007). We thank Prof. Denise Brice (France), Dr. Ewa Olempska (Poland), and an anonymous reviewer for their constructive comments in their reviews of this paper. Dr. Jed Day (USA) carefully read the manuscript, polishing the text throughout and addressed the taxonomic problem of the Frasnian chonetids. C.Y. Zhou took some of the pictures and did the printing job. G.M. Shu took the SEM photographs of the ostracods.

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