

Silicified Anisian (Middle Triassic) spiriferinid brachiopods from Guizhou, South China

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A newly discovered silicified brachiopod interval from the Upper Member of the Guanling Formation (Late Anisian, Middle Triassic) in Guizhou Province (South China) is described for the first time. The most remarkable feature of this brachiopod assemblage, besides the very good preservation, is the very low taxonomic evenness and diversity. This impoverished, low diversity/high density assemblage is represented by more than 700 recovered specimens belonging to three species within two spiriferinid genera (*Pseudospiriferina multicostata*, *P. pinguis*, and *Punctospirella fragilis*). It is characterized by the overwhelming abundance of an endemic spiriferinid species, *P. multicostata*, which contributes to more than 90% of the community. Silicified valves of *P. multicostata* and *Punctospirella fragilis* allow detailed descriptions of the internal morphology based on direct observation. Brachiopod paleoecology, assessed by considering host-rock lithology, shell disarticulation, and shell size suggests that this endemic brachiopod fauna represents a favourable niche for development of dense brachiopod-dominated communities, i.e., high energy, hard substrate, nutrient rich environment.

Key words: Brachiopoda, Spiriferinida, Anisian, Triassic, China.

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Introduction

After a slow recovery from the end-Permian mass extinction during the Early Triassic, marine ecosystems experienced a rapid radiation in the Middle Triassic (Payne et al. 2004) as demonstrated by the benthic assemblages of shallow marine deposits (Erwin 1994; Hallam and Wignall 1997; Chen et al. 2005). Brachiopods commonly dominated the benthic life of the Anisian epicontinental seas (Komatsu et al. 2004). In these communities, spiriferinids were globally distributed before their demise in the Early Jurassic (Sandy and Blodgett 2000). Brachiopods are of high importance for any paleoecological and paleogeographic reconstructions, in some cases being also useful for biostratigraphic subdivisions (Benatov 2001; Komatsu et al. 2004) as demonstrated for the Western Tethys (Siblík 1972; Pálffy 1991, 2003; Urošević et al. 1992; Torti and Angiolini 1997; Benatov 2001), the Himalayas (Siblík 1975; Ching et al. 1976), and for the South China (Hsu and Tseng 1942; Hsu 1943; Hsu and Chen 1943; Yang and Xu 1966; Sun 1980).

Studies of Anisian brachiopods in South China hitherto have been restricted to central Guizhou. Pioneering work was carried out by Hsu and Tseng (1942) and Hsu (1943), who reported Anisian brachiopod faunas from the Machangping area of Fuquan County and Qingyan (Qingyen) area of Guiyang, central Guizhou Province. These authors, however, provided only taxonomic lists of the brachiopods neither with descriptions nor illustrations. A systematic work on

the brachiopod fauna from Qingyan was published by Yang and Xu (1966), who recognized 33 species belonging to 23 genera (including 28 new species of 14 new genera), which greatly enhanced our knowledge of Anisian brachiopods. Nevertheless, apart from central Guizhou, no other Anisian brachiopods have been reported from elsewhere in Guizhou Province.

In this paper, we report silicified Anisian spiriferinid brachiopods from the Upper Member of the Guanling Formation at the Yangjuan-Chupiwa section, Xinmin District, Panxian County, western Guizhou, South China. Biostratigraphically, these brachiopods lie within the bed Cy 3 (herein called the silicified spiriferinid interval; Fig. 1), about 10.4 m below the lithologic boundary between the Guanling Formation and the overlying Yangliujing Formation. The associated conodonts, including *Neogondolella bifurcata*, *Ng. constricta cornuta*, *Ng. constricta balkanica*, and *Ng. excentrica*, suggest the *Ng. constricta cornuta* Zone (Sun 2006) of the early Illyrian (Late Anisian, Middle Triassic). These well-preserved silicified brachiopod shells or valves allow detailed descriptions of the internal morphology based on direct observation, rather than from serial sections. Moreover, the community structure and possible paleoecology of this brachiopod interval are briefly discussed.

Institutional abbreviation.—GMPKU, Geological Museum of Peking University, Beijing, China.

Other abbreviations.—L, length; W, width; T, thickness.

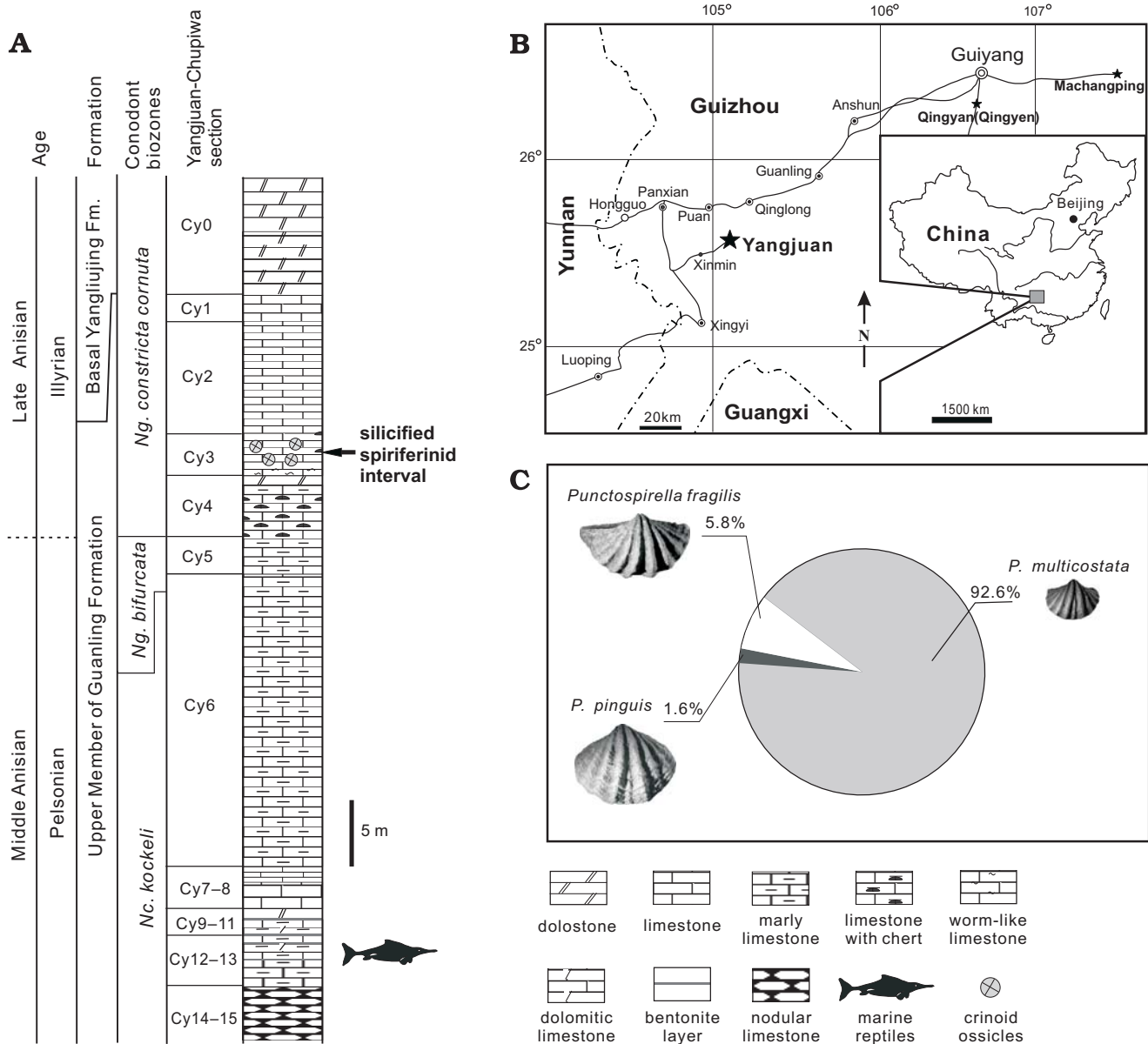


Fig. 1. Lithologic sequence (A) and geographic position (B) of the Yangjuan-Chupiwa section, and relative abundance of species in spiriferinid interval (C); position of the silicified spiriferinid interval is arrowed. Partly after Sun et al. (2006), simplified. *P.*, *Pseudospiriferina*; *Ng.*, *Neogondolella*; *Nc.*, *Nicoraella*.

Geological setting

During the Middle Triassic, the paleogeographic position of the brachiopod locality (the Yangjuan-Chupiwa section, Panxian County, Guizhou Province) was in the interior of the Yangtze Platform, a far distance away from the Nanpanjiang Basin (Lehrmann et al. 2005). Shallow-water carbonates with intermittent terrigenous influx dominated the Yangtze Platform sedimentation during the Middle Triassic (Enos et al. 1998). The Guanling Formation, generally thought to represent Anisian rocks of the interior of the Yangtze Platform, can be roughly correlated with its lateral equivalent, the Qingyan Formation of the basin-margin transition, and the basal facies of the Xinyuan Formation. The Yangtze Plat-

form is surrounded by the Jiangnan Massif in the East, the Songpanganzi fold system to the West, the Baoshan tectonic block to the Southwest, the Kangdian Massif to the South, and the Qinling fold belt to the North (Enos et al. 1998). The possible direct connection between the open ocean (represented by the Western Tethys and the Eastern Pacific) and the Yangtze Platform is the Nanpanjiang Basin. In central Guizhou Province, Anisian deposits of the Qingyan Formation at the margin of the Nanpanjiang Basin consist of normal marine, fossiliferous carbonates. In western Guizhou, however, the Anisian deposits of the Guanling Formation of the Yangtze Platform comprise poorly fossiliferous, shallow-water limestones, dolomites, evaporites and siliciclastics which represent a much more restricted environment (Lehrmann et al. 2005).

Material and methods

All studied specimens come from an about 3.2 m-thick fossiliferous interval of the bed Cy 3 in the Yangjuan-Chupiwa section, near Chupiwa village (Xinmin District, Panxian County, Guizhou Province, South China). The host-rocks are composed of grey, medium-bedded, coarse-grained, slightly silicified biotrital limestone alternating with 0.5 m-thick vermicular dolomitic limestone at the base. They are densely packed with brachiopods and crinoid ossicles. In the lab, the bulk samples of biotrital limestones, each about 5 kg in weight, were dissolved in 7–8% acetic acid and the residues were sieved with a sieve of 200 grids/per cm². The residues yielded silicified brachiopods, associated with abundant conodonts, crinoid ossicles, and rare holothurian sclerites, gastropods, bivalves, and shark teeth. The macrofossils were picked out directly from the residues with small tweezers. The microfossils, such as conodonts and shark teeth, were picked using a fine writing brush under a binocular microscope Nikon SMZ645.

Systematic paleontology

We adopted the terminology and classification of spiriferinids given by Carter and Johnson (2007) in the Treatise on Invertebrate Paleontology Part H, Brachiopoda, revised (Williams et al. 1997–2007).

Phylum Brachiopoda Duméril, 1806

Order Spiriferinida Ivanova, 1972

Family Spiriferellinidae Ivanova, 1972

Genus *Pseudospiriferina* Yang and Xu, 1966

Type species: Pseudospiriferina variabilis Yang and Xu, 1966; Middle Triassic of Guizhou (South China).

Pseudospiriferina multicostata Yang and Xu, 1966

Figs. 2, 3A–H.

1966 *Pseudospiriferina multicostata* sp. nov.; Yang and Xu 1966: 45–47, pl. 6: 2, 3.

Material.—27 articulated shells, 278 ventral and 387 dorsal valves.

Dimensions.—L = 12.0 mm; W = 16.0 mm; H = 8.0 mm (GMPKU-P-6145, Fig. 3A₁–A₃).

Emended diagnosis (modified from Yang and Xu 1966).—This species differs from all other representatives of the genus *Pseudospiriferina* and the other spiriferellinid genera by its small size (rarely exceeding 10 mm), fold with median groove, sulcus with median costa, and more numerous and finer costae on the flanks.

Description.—Shell small to medium-sized, generally up to 10 mm in length, with the width-to-length ratio of about 1.3 (Fig. 2), transversely spiriferoid and ventribiconvex in outline. The maximum width of the shell at the hinge line or

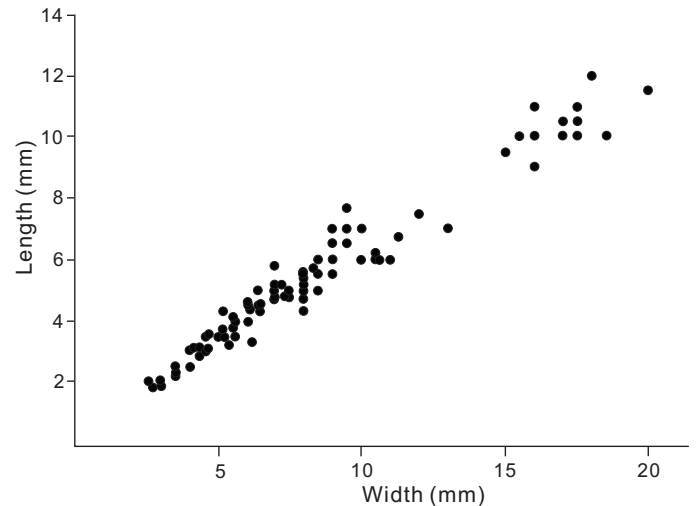


Fig. 2. Length vs. width diagram for 128 dorsal valves of *Pseudospiriferina multicostata* Yang and Xu, 1966 from the bed Cy 3 of the Yangjuan-Chupiwa section, near Chupiwa village, Xinmin District, Panxian County, Guizhou, China.

slightly posterior to it, which is straight. Cardinal extremities usually subangular (Fig. 3B₁, D₁, E₁), occasionally obtuse.

Ventral valve moderately convex, varying from broadly triangular to semicircular in outline, with a small acute, incurved beak. Ventral interarea transverse triangular, apsacline, with numerous transverse striations with the exception of narrow and slightly concave triangular areas flanking delthyrium. Delthyrium open, its width attaining about 1/4 of the hinge line. Anterior commissure sulcinate, with a distinct tongue (Fig. 3B₂). Sulcus well developed, twice as wide as the interspaces between costae on flanks, with one intercalated median costa (Fig. 3A₁, B₁, C₁).

Dorsal valve gently convex with semicircular outline. Dorsal interarea very low, about 2 mm in height, orthocline. Fold moderately developed, slightly higher than costae on the flanks, much more prominent near the anterior margin, with a characteristic narrow median groove dividing the fold into two plicae (Fig. 3A₂, A₃, C₂, C₃, D₁, E₁, F₁).

Costae begin near the umbo, widen anteriorly. Costae on the flanks narrow, triangular in cross section, separated by interspaces of similar width; usually about 6 costae on each flank. Costa close to the fold or the sulcus occasionally bifurcating anteriorly (Fig. 3B₁, E₁). Growth varices subimbricate, which are crowded near the anterior margin of both valves (Fig. 3A₁, A₃, B₁, C₃, D₁, E₁), occasionally throughout the whole valve (Fig. 3F₁).

Ventral interior with the blade-like median septum originating from the umbonal thickening and extending to about one-third of the valve length (Fig. 3B₃, B₄). Dental plates divergent, reaching the floor of the valve near the beak, and continuing anteriorly as about 1 mm deep dental flanges. Dental plates and median septum discrete, posteriorly much thickened with callus (Fig. 3B₄).

Dorsal valve interior with small-sized and trough-like sockets (Fig. 3D₂, D₃, F₂, F₃, H). Inner socket ridges together

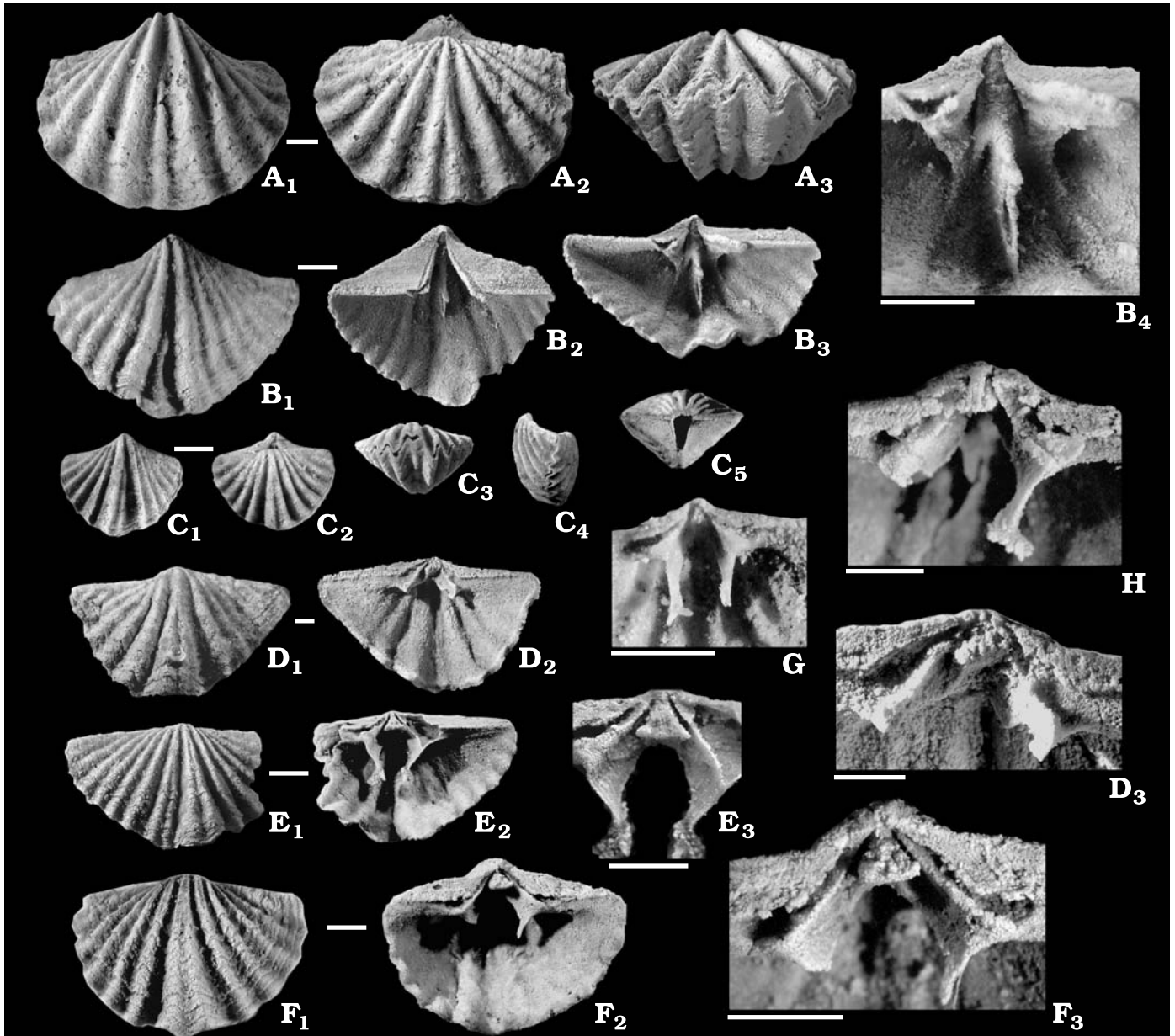


Fig. 3. Spiriferinid brachiopod *Pseudospiriferina multicosata* Yang and Xu, 1966 from the bed Cy 3 of the Yangjuan-Chupiwa section, near Chupiwa village, Xinmin District, Panxian County, Guizhou, China. **A.** Complete shell GMPKU-P-6145, in ventral (A₁), dorsal (A₂), anterior (A₃) views. **B.** Ventral valve GMPKU-P-6148, in ventral (B₁), posterior (B₂), internal (B₃) views, and enlargement of posterior internal structures showing the median septum and dental plates (B₄). **C.** Shell GMPKU-P-6146, in ventral (C₁), dorsal (C₂), anterior (C₃), lateral (C₄), and posterior (C₅) views. **D.** Dorsal valve GMPKU-P-6172 in external (D₁), internal (D₂) views, and enlargement of cardinalia (D₃). **E.** Slightly damaged dorsal valve GMPKU-P-6149, in external (E₁), internal (E₂) views, and enlargement showing cardinalia (E₃). **F.** Dorsal valve GMPKU-P-6156, in external (F₁), internal (F₂) views, and enlargement showing cardinalia (F₃). **G.** Posterior internal structures (cardinalia) of dorsal valve GMPKU-P-6151, showing crura. **H.** Posterior internal view of dorsal valve GMPKU-P-6152, showing cardinalia and one of crus with start of spirillum. Scale bars 2 mm.

with crural bases form subtriangular plates that connect with each other behind the ctenophoridium (i.e., cardinal process). Ctenophoridium is relatively large and well developed as an outgrowth of the secondary shell apically between the inner socket ridges. It is striated, triangular in cross section, and swollen anteriorly (Fig. 3E₂, E₃, F₂, F₃). Dorsal median septum and septalium not developed. Crura rather short, subparallel to slightly medially convergent, frequently with preserved short, broken, submedially directed jugal processes (Fig. 3E₂, G, H).

Remarks.—Our examined specimens are evidently conspecific with *Pseudospiriferina multicosata* Yang and Xu, 1966 in their relatively small shell size, having median costa in the sulcus and median groove on the fold, and more numerous and finer costae on flanks in comparison to other species of *Pseudospiriferina*. These characters also allow us to distinguish them from other co-occurring species of *Punctospirella*. It is noteworthy that *P. multicosata* was originally established by Yang and Xu (1966) on only three articulated

shells and four fragments coming from the Middle Guanling Formation at the Qingyan section of Guiyang, while the very abundant and well-preserved silicified valves herein substantially added the knowledge of the internal features of *P. multicosata* as described above. Morphological changes in the growth varices, the cardinal extremities, and the bifurcation of the costa near the fold (Fig. 3B₁, E₁) are interpreted as intraspecific variations.

Stratigraphic and geographic distribution.—Middle and Upper Member of the Guanling Formation, Middle Anisian, from Qingyan, Guiyang, central Guizhou, and Xinmin, Panxian, western Guizhou, China.

Pseudospiriferina pinguis Yang and Xu, 1966

Fig. 4.

1966 *Pseudospiriferina pinguis* sp. nov.; Yang and Xu 1966: 45, pl. 5: 5; pl. 6: 1.

1974 *Pseudospiriferina* cf. *pinguis* Yang and Xu, 1966; Liao and Sun 1974: 352, pl. 184: 11–14.

1978 *Pseudospiriferina pinguis* Yang and Xu, 1966; Feng and Jiang 1978: 292, pl. 104: 5.

Material.—7 articulated shells and 4 dorsal valves.

Dimensions.—L = 15.5 mm; W = 19.0 mm; H = 12.0 mm (GMPKU-P-6168, Fig. 4A–D).

Description.—Shell medium-sized, strongly ventribiconvex, with subcircular outline and rounded cardinal extremities. Greatest width attained near midlength. Anterior commissure uniplicate. Ventral interarea moderately high, apsacline. Beak relatively stout, slightly incurved. Delthyrium open, its width attaining about one-third of the hinge line. Ventral sulcus, gently developed, only slightly wider than interspaces between costae, occasionally with weak median costa. Dorsal fold low, slightly higher than costae on flanks. Shell ornamented on flanks with strong costae, rounded in cross

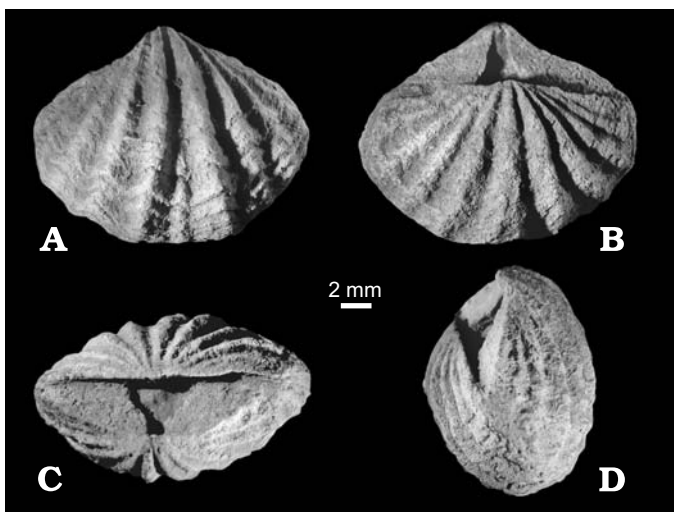


Fig. 4. Spiriferinid brachiopod *Pseudospiriferina pinguis* Yang and Xu, 1966 from the bed Cy 3 of the Yangjuan-Chupiwa section, near Chupiwa village, Xinmin District, Panxian County, Guizhou, China. Complete shell GMPKU-P-6168, in ventral (A), dorsal (B), posterior (C), and lateral oblique (D) views. Scale bars 2 mm.

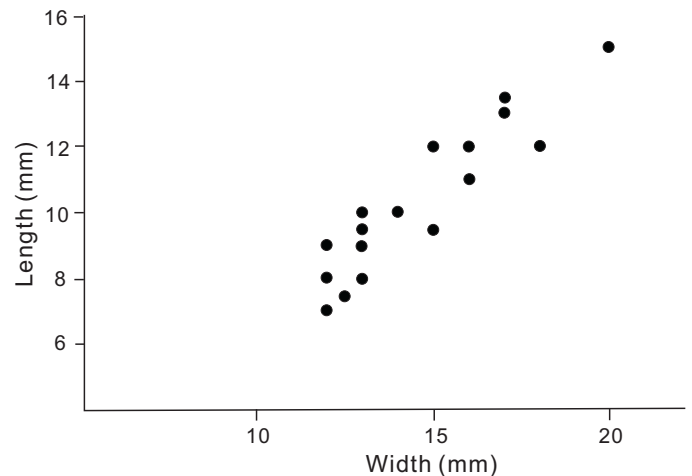


Fig. 5. Length vs. width diagram for 17 specimens of *Punctospirella fragilis* (Schlotheim, 1814) from the bed Cy 3 of the Yangjuan-Chupiwa section, near Chupiwa village, Xinmin District, Panxian County, Guizhou, China.

section. Concentric lamellae crowded near the anterior margin, commonly about four lamellae per 1 mm.

Remarks.—*Pseudospiriferina pinguis* Yang and Xu, 1966 is characterized by subcircular shell outline, strongly biconvex shell with crowded concentric lamellae near its anterior margin. Our material generally agrees with these features as observed on the holotype by Yang and Xu (1966). However, some specimens of the studied collection display variation especially in the relatively transverse outline and larger size.

Stratigraphic and geographic distribution.—Guanling Formation, Anisian, Machangping, Fuquan, central Guizhou, and Xinmin, Panxian, western Guizhou, China.

Subfamily Punctospirellidae Dagys, 1974

Genus *Punctospirella* Dagys, 1974

Type species: *Terebratulites fragilis* Schlotheim, 1814; Middle Triassic of Germany.

Punctospirella fragilis (Schlotheim, 1814)

Figs. 5, 6A–D.

- 1814 *Terebratulites fragilis* sp. nov.; Schlotheim 1814: pl. 2: 4.
 1972 *Spiriferina fragilis* (Schlotheim, 1814); Siblík 1972: table 61, fig. 2.
 1974 *Punctospirella fragilis* (Schlotheim, 1814); Dagys 1974: 136–137, pl. 39: 2, 3; fig. 91.
 1988 *Punctospirella fragilis* (Schlotheim, 1814); Usnarska-Talerzak 1988: 688, pl. 2: 2.
 1992 *Punctospirella fragilis* (Schlotheim, 1814); Urošević et al. 1992: 473, pl. 1: 4–6.
 1993 *Punctospirella fragilis* (Schlotheim, 1814); Urlichs 1993: 211, fig. 2.
 1997 *Punctospirella fragilis* (Schlotheim, 1814); Torti and Angiolini 1997: 165, pl. 1: 25–27.
 1997 *Punctospirella fragilis* (Schlotheim, 1814); Kaim 1997: fig. 19B.
 2003 *Punctospirella fragilis* (Schlotheim, 1814); Pálffy 2003: 145, pl. Br-1: 13, 14.

Material.—12 shells, 6 ventral and 8 dorsal valves.

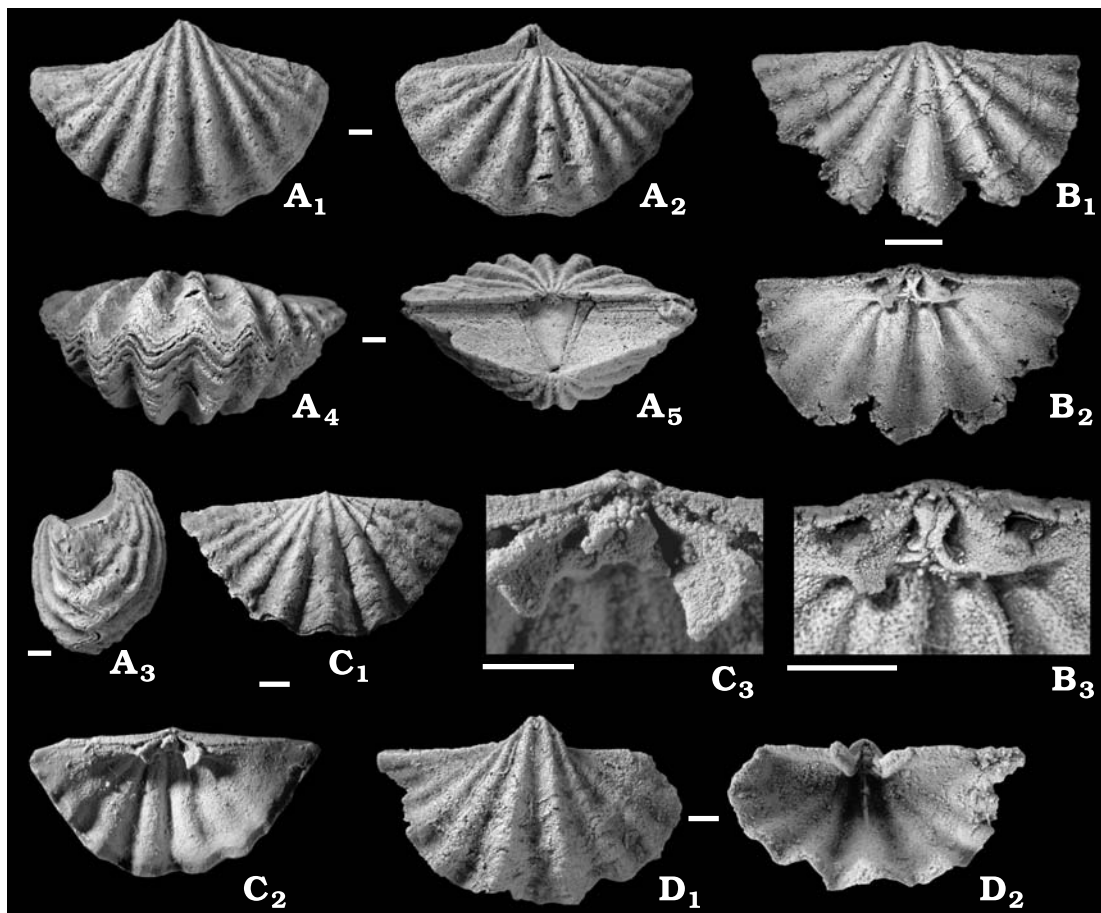


Fig. 6. Spiriferinid brachiopod *Punctospirella fragilis* (Schlotheim, 1814) from the bed Cy 3 of the Yangjuan-Chupiwa section, near Chupiwa village, Xinmin District, Panxian County, Guizhou, China. A. Complete shell GMPKU-P-6164, in ventral (A₁), dorsal (A₂), lateral (A₃), anterior (A₄), and posterior (A₅) views. B. Slightly damaged dorsal valve GMPKU-P-6169 in external (B₁), internal (B₂) views, and enlargement of cardinalia (B₃). C. Dorsal valve GMPKU-P-6166 in external (C₁), internal (C₂) views, and enlargement of cardinalia (C₃). D. Ventral valve GMPKU-P-6173, in ventral (D₁) and internal views (D₂). Scale bars 2 mm.

Dimensions.—L = 10.0 mm; W = 15.0 mm; H = 6.8 mm (GMPKU-P-6164, Fig. 6A₁–A₅).

Description.—Shell medium-sized, transversely semicircular in outline, with a width-to-length ratio of about 1.45 (Fig. 5), ventribiconvex. Hinge line straight, corresponding to the greatest width of shell or slightly shorter. Cardinal extremities subangular to nearly rounded. Anterior margin subrounded. Costae strong, rounded, 4–6 on each flank (Fig. 6A₁, A₂, B₁, C₁, D₁).

Ventral valve convex. Interarea moderately high and concave (Fig. 6A₃, A₅). Beak pointed, incurved. Delthyrium open. Sulcus poorly developed, only slightly wider than interspaces between bordering costae. Dorsal valve weakly convex. Fold nearly as wide as bordering costae.

Ventral interior with strongly reduced to absent dental plates. Dental flanges incurved, nearly 1 mm high, joining the median septum near the apex (Fig. 6D₂). Median septum high, extending one-third of the valve length.

Dorsal interior with knoblike, weakly striated, and probably bifurcating ctenophoridium (Fig. 6B₂, B₃, C₂, C₃). Cardinalia massive with cone-shaped sockets and well-devel-

oped and strongly incurved inner socket ridges (Fig. 6B₃, C₃). Septalium and inner hinge plates absent.

Remarks.—Diagnostic characters of *Punctospirella fragilis* are the transverse outline, the wide median sulcus and fold, the presence of 10–12 costae (generally 10 on the ventral valve and 11 on the dorsal valve), and the high ventral median septum (see also Urošević et al. 1992; Torti and Angiolini 1997). Our specimens share these characters, except for the less developed sulcus and fold. As pointed out by Pálffy (2003), specimens from the Muschelkalk faunas of the Germanic Basin yield less prominent median rib (= dorsal fold) and corresponding interspace (= ventral sulcus), which correspond well with our material. *Punctospirella fragilis* is widely distributed both in the Alpine and Germanic Anisian deposits. In South China, *Spiriferina* (= *Punctospirella*) *fragilis* (Schlotheim, 1814) was first reported by Hsu and Chen (1943) from the Qingyan Formation (correlated with the Guanling Formation), central Guizhou Province, but with neither description nor illustration.

Stratigraphic and geographic distribution.—Middle Triassic of the Western Tethys and South China.

Discussion

Three species of two spiriferinid genera, *Pseudospiriferina multicosata*, *P. pinguis*, and *Punctospirella fragilis*, were identified from more than 700 specimens including both articulated shells and disarticulated valves. *Pseudospiriferina multicosata* and *P. pinguis* are typically endemic forms restricted to the Middle Triassic of South China. They were originally erected by Yang and Xu (1966) based on specimens from the Qingyan Formation from two localities in central Guizhou Province: the Qingyan locality near Guiyang, and the Machangping locality near Fuquan, respectively. In the bed 5 (Kch 263–267) of the Middle Qingyan Formation at the Qingyan locality, only 7 specimens (including three articulated shells and four fragments) of *P. multicosata* were recorded among 301 specimens of collected brachiopods (Yang and Xu 1966). The host-rocks consist of grey marl shales alternating thin-bedded fine grained limestones and marl limestones. This very low abundance is in contrast to the locality described in this paper, where *P. multicosata* contributes to more than 90% of the fauna (Fig. 1). *P. pinguis* is also exclusively known from the Anisian deposits of South China (Yang and Xu 1966; Liao and Sun 1974; Feng and Jiang 1978). *Punctospirella fragilis*, in fact the first described Middle Triassic brachiopod species (see Pálffy 2003), is a typical Tethyan form. It is known from the Anisian and Ladinian of the southern Alps and the Germanic Basin (Siblík 1975; Pálffy 1991, 2003; Urlichs 1993; Kaim 1997; Torti and Angiolini 1997).

The most remarkable feature of this brachiopod community is its very low evenness and taxonomic diversity, besides its very good preservation. It is dominated by the endemic species *Pseudospiriferina multicosata* and can be considered as an impoverished, low diversity-high density fauna. The lithology of host-rocks, i.e., coarse-grained, slightly silicified biodetrital limestone densely packed with brachiopods and crinoid ossicles, indicates a relatively high-energy environment. This is also confirmed by the very high contribution of disarticulated valves (93%) to this brachiopod assemblage. The high mean shell size (see Figs. 2 and 5) and the overwhelming abundance of an opportunistic species, *Pseudospiriferina multicosata*, hint the presence of a specific brachiopod favourable niche, i.e., well-agitated water, ample nutrient supply and widely available hard substrate for attachment. Thus, brachiopod paleoecology, assessed by considering host-rock lithology, shell disarticulation, and shell size (Pálffy 1991), is suggestive of high energy, hard substrate, nutrient rich environment. The community structure and possible paleoecology of this silicified spiriferid paleocommunity are different from those of the Anisian Qingyan brachiopod fauna (Yang and Xu 1966). The latter is highly diverse (including 33 species of 23 genera) and characterized by a predominance of the most common and opportunistic forms, thriving in a warm shallow marine facies on the upper part of the slope at the southern margin of the Yangtze platform (Chen and Tong 2006).

A similar occurrence of low vs. high diversity Middle Triassic brachiopod assemblages was observed in the Balaton Highland (35 species from four localities) and Mecsek Mountains (7 species) in Hungary (Pálffy and Török 1992). The former represents good life conditions for brachiopods with well-agitated shallow water and firm substrate whereas the impoverished fauna indicates extreme environmental factors such as varying salinity and fluctuating water energy (Pálffy and Török 1992). Brachiopod beds characterized by occurrence of low-diversity brachiopod association dominated by one species of *Punctospirella* (so called *Spiriferina*-Bank) is well known from the Upper Muschelkalk of Europe (e.g., Hagdorn and Mundlos 1982; Urlichs 1993; Hagdorn and Simon 1993; Kaim 1997).

Conclusion

A newly discovered Illyrian (Late Anisian, Middle Triassic) silicified brachiopod interval from the Upper Member of the Guanling Formation at the Yangjuan-Chupiwa section, Guizhou Province, South China is described for the first time. Three species of two spiriferinid genera (*Pseudospiriferina multicosata*, *P. pinguis*, and *Punctospirella fragilis*) are recorded, which are also found from the coeval Qingyan brachiopod fauna.

This silicified brachiopod interval represents an impoverished, low diversity-high density assemblage, with 3 species of 2 spiriferinid genera accounting for more than 700 specimens. It is characterized by the overwhelming abundance of an endemic spiriferid species, *Pseudospiriferina multicosata*.

Brachiopod paleoecology, assessed by considering host-rock lithology, shell disarticulation, and shell size are suggestive of good condition for development of dense brachiopod-dominated communities, i.e., high energy, hard substrate, nutrient rich environment for this paleocommunity.

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