Small-sized cyrtospiriferids from the Upper Devonian (late Frasnian) of central Hunan, China

Malí cyrtospiriferidi ze svrchního devonu (pozdní frasn) centrálního Hunanu, Čína



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(8 figs)

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The late Frasnian brachiopods of central Hunan of south China were predominated by an atrypid-rhynchonellid-cyrtospiriferid assemblage. The cyrtospiriferid brachiopods are characterized by abundant small-sized forms which comprise four species belonging to at least three genera. Two new species (*Cyrtospirifer? variabilis* and *Mennespirifer yangqiaoensis*) are described.

Key words: Upper Devonian, Brachiopoda, cyrtospiriferids, Hunan, China

Introduction

Cyrtospiriferid brachiopods were a predominant group living in shallow tropical to subtropical seas during the Late Devonian. One of the most widespread cyrtospiriferid genera reported in Late Devonian brachiopod faunas is Cyrtospirifer Nalivkin, 1924. As many as 150 species or varieties (equivalent to species or subspecies in modern terminology) have been assigned to this genus during the twentieth century (Ma - Day submitted). In the later half of the 20th century efforts have been made to refine the genus and established a number of new genera or subgenera, e.g., Gatinaud (1949), Sartenaer (1982) etc. However, most new genera or subgenera were later considered by subsequent workers to be synonyms of Cyrtospirifer, for example by Pitrat (1965) and Carter et al. (1994). It should be noted that some synonyms of Cyrtospirifer in Pitrat (1965) were considered valid by Carter et al. (1994), e.g., Liraspirifer Stainbrook, 1950, Regelia Crickmay, 1952 and Sinospirifer Grabau, 1931. Therefore much work is needed to re-evaluate previously established cyrtospiriferid genera. In this paper we do not intend to tackle the validity of those genera. We would follow the revised classification of Carter et al. (1994).

The Upper Devonian is well developed in central Hunan Province of south China so that it is also known as the Hunan Series in China. Two Chinese stages were named after two famous localities in central Hunan, Shetienchiao (now spelled Shetianqiao) and Hsikuangshan (now spelled Xikuangshan) (Fig. 1) stages which are more or less equivalent to the Frasnian and Famennian respectively. Two most important early monographs on Devonian brachiopods of South China were published by Grabau (1931) and Tien (1938). These two workers' cyrtospiriferid species and a few others published by previous workers were gathered in Wang et al. (1964).

Grabau (1931) named about 20 species of *Sinospirifer* (commonly considered to be a synonym of *Cyrtospirifer* by most subsequent workers); most specimens (if not all) were bought from Chinese drug stores without locality and

horizon data. As Grabau (1931, p. 208) pointed out "The localities which furnish these specimens are, however, known only to the collectors and are kept secret so that even the dealers do not know of them". In this case some locations which were claimed to be a fossil locality might not be so (see Hou et al. 1996 about the locality of *Platyspirifer*). In the past few years abundant specimens were collected with precise locality and horizon data, and Ma and collaborators began a revision of the Upper Devonian cyrtospiriferids (e.g., Ma – Day 1999, 2000). It is almost undoubted that most of Grabau's cyrtospiriferid specimens came from the early Famennian of central Hunan.

Tien (1938) described a few species of "Tenticospirifer" and two species of Hunanospirifer from the Yunnanella bed (probably uppermost crepida to marginifera Zones). The Chinese Famennian "Tenticospirifer" described by Tien (1938) have been rejected from the genus Tenticospirifer established by himself based on the Russian type species, Spirifer tenticulum, from the Frasnian (Ma – Day 2000). Only three cyrtospiriferid species were described from Frasnian strata of central Hunan by Tien (1938): Sinospirifer sinensis Grabau, S. subextensus Martelli, and Tenticospirifer vilis (Grabau); all were collected from the (lower) Frasnian of the Chitzechiao (now spelled Qiziqiao) section. The former two forms are large in size. Observation of Tien's specimens shows that the two large forms merely represent one species.

In the type section of the Chinese Shetianqiao stage, there are abundant small-sized "*Cyrtospirifer*" in the upper Frasnian, which has been mentioned at many occasions (e.g., Zhao et al. 1978; Chen 1996; Ma – Day 2000). These cyrtospiriferids have not been described. They seem to be widely distributed in central Hunan. In this paper we would present our recent result on the taxonomy of these small-sized cyrtospiriferids.

Geological setting

The Upper Devonian of central Hunan Province yields abundant benthic fossils. The Shetianqiao section was located in a platformal depression facies. The Frasnian strata



Fig. 1 Location map and late Frasnian stratigraphy of the Shetianqiao section. Size of dots represent relative abundance; data of open circles from the Xikuangshan section. Numbers 22–25 refer to bed number of Hou-Wang (1988).

have a thickness of 800-900 m, with about 130 m thick siliceous rocks in the lower part, 540 m thick thin-bedded silty marls characterized predominantly by a pelagic fauna in the middle part, and 225 m thick silty marls and argillaceous limestones characterized by a benthic faunal assemblage (Fig. 1). The Xikuangshan section was located in an outer littoral-shallow subtidal setting during the Frasnian featuring a benthic faunal assemblage. According to Wang et al. (1986), the Frasnian of the Xikuangshan section may be divided into three parts. The lower part is composed of 51 m thin-bedded clastics including sandstones and shales; the middle part consists of 194 m thick dark gray thin to thick-bedded limestones (the Qilijiang Member); and the upper part is made up of 50 m calcareous shale and argillaceous limestone interbeds (the lower part of the Changlungchieh Shale sensu Tien 1938).

Systematic paleontology

Family Cyrtospiriferidae Termier et Termier, 1949 Subfamily Cyrtospiriferinae Termier et Termier, 1949

Carter et al. (1994) recognized two subfamilies of the Cyrtospiriferidae: Cyrtospiriferinae Termier et Termier, 1949 and Cyrtiopsinae Ivanova, 1972. As commented by Carter et al. (1994, p. 335), "The assignment of at least 19 genera to one of two subfamilies on the basis of shell

shape is inadequate". Adequate documentation of both external and internal structures of key genera is needed before a plausible classification of the Cyrtospiriferidae is reached.

Genus Cyrtospirifer Nalivkin, 1924 (in Fredericks, 1924)

Cyrtospirifer cf. *whitneyi* (Hall, 1858) Fig. 2A–B

1938 Spirifer (Tenticospirifer) vilis (Grabau); Tien, p. 123, Pl. 16, Figs 8–9.

M a t e r i a l : Over 60 complete shells of different growth stages. Central Hunan Province in the Shetianqiao section, present in several horizons; late Frasnian.

Description: Characterized by small size, slightly extended to rounded cardinal extremities, up to 20 plications per flank, sinal plications average 10, numerous micro-pustules present both in grooves and on plications. Internally a myophragm is developed on floors of both valves; thin extrasinal dental plates; delthyrial plate welldeveloped, covering the whole delthyrial cavity; posterior region of dorsal interior filled by secondary shell; comblike cardinal process with 10 to 14 vertical lamellae.

Comparison and discussion: This species is almost identical to *C. whitneyi* in terms of relatively large ventral interarea, overall shell outline, micro-ornament,

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Fig. 2 A–B – *Cyrtospirifer* cf. *whitneyi* (Hall, 1858) from the late Frasnian of Hunan, China. Sample S-Y-2: A1–A5 – ventral, dorsal, posterior, anterior and lateral views showing a slightly curved, large catacline ventral interarea, x1.5, PUM 00011, B1–B5 – posterior, anterior, lateral, ventral and dorsal views; note traces of the pseudodeltidium and the curved ventral interarea; all x2 except B4 and B5, x1.5, PUM 00012; C–H – *Cyrtospirifer? variabilis* sp. nov. from the late Frasnian of Hunan, China; all of sample S-25-2 except PUM 00006, sample S-Y-4: C1–C5 – ventral, dorsal, posterior, anterior and lateral views, x2, holotype (PUM 00005): D – ventral view, x1.5, paratype (PUM 00010); E1–E4 – ventral, dorsal, anterior and lateral views, x2, paratype (PUM 00006), F1–F5 – ventral, dorsal, lateral, posterior and anterior views, x2, paratype (PUM 00006), H1–H3 – ventral, lateral and dorsal views showing its outline mimicing early Famennian *S. subextensus*, x3, paratype (PUM 00007).





Fig. 3 Transverse serial sections of *Cyrtospirifer*? *variabilis* sp. nov. from the Shetianqiao section (sample S-H-0). PUM 00112. Numbers refer to distance in mm from the ventral apex. Arrows indicate enlargement. Note the thickened dental plates and there is no true delthyrial plate. Images of shell outline x1.7.

internal structures (the presence of a myophragm in both valves, thin extrasinal dental plates and delthyrial plate etc.). The only significant differences are the prominent thickening of dorsal notothyrial cavity and fewer vertical lamellae of the cardinal process and medially depressed cardinal process shelf in *C*. cf. *whitneyi*.

It is also quite similar to the upper Frasnian *Cyrtospirifer* sp. described by Alekseeva et al. (1996, p. 183, Pl. 20, Figs 5a–c) from northeastern Siberia. The Siberian species differs by its wider delthyrium.



1994 Cyrtospirifer archiaciformis (Grabau); Ma, p. 202, Pl. 39, Fig. 9.

Holotype: Specimen PUM 00005, figured here as Figs 2C1-2C5. Paratypes: Specimens PUM 00006 (Fig. 2E1-E4), PUM 00007 (Fig. 2H1-H3), PUM 00009 (Fig. 2G), PUM 00010 (Fig. 2D), and PUM 00013 (Fig. 2F1-F5).

Type horizon: Upper part of the Shetianqiao Formation at a horizon corresponding to upper part of bed 24 (Hou – Wang 1988, p. 132), latest Frasnian (probably late Upper *rhenana* Zone).



Fig. 4 Transverse serial sections of *Cyrtospirifer* cf. *variabilis* sp. nov. from the Shetianqiao section (sample S-Y-4). PUM 00113. Numbers refer to distance in mm from the ventral apex. Arrow indicates enlargement. There is only a trace of delthyrial plate at the very posterior end of the ventral valve. Numbers in the image of lateral shell profile refer to position of the first four serial sections.



Fig. 5 A–E – *Mennespirifer yangqiaoensis* sp. nov. from the late Frasnian of Hunan, China. Sample S-H-0: A1–A5 – ventral, anterior, posterior, dorsal and lateral views of paratype PUM 00037, note its short hinge line and rounded cardinal extremities, x3, A6 – enlarged ventral portion of paratype PUM 00037 showing the micro-ornament, x19, B1–B5 – dorsal, ventral, lateral, anterior and posterior views of holotype PUM 00045, x3, C1–C2 – dorsal and ventral views of paratype PUM 00036, x2, D – interarea view showing the pseudodeltidium of paratype PUM 00044, x3.5, E – interarea view showing the rod-like left tooth of PUM 00043, x3.

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

Etymology: Indicates great variation of the hinge width.

Material: 100 specimens, generally in good state of preservation. Central Hunan Province in the Shetianqiao section; late Frasnian.

D i a g n o s i s : Small sized *Cyrtospirifer*? characterized by 6–7 sinal plications, very short delthyrial plate or replaced by thickening of dental plates.

Description: Shell small, generally 2 cm in width; greatest width generally at hinge, cardinal extremities acute. Ventral interarea low, generally apsacline; beak curved; delthyrium open in some specimens but not observable in most specimens due to rock cover; traces of pseudodeltidium observed in some specimens. Surface marked by 35 to 40 rounded simple plications, with about 16 on each flank; interspaces equal to or wider than lateral shell plications; sinus generally with 4 to 8 plications: zero to one simple lateral sinal plication on each side; primary sinal plications also simple; median sinal plications generally bifurcating once or rarely twice, ranging from 2 to 5. Micro-ornament of dense, very delicate striae in interspaces and on plications (commonly preserved in interspaces).

Internally ventral valve with a pair of extrasinal dental plates strongly thickened medially to form "delthyrial plate"; dorsal valve with thickened notothyrial cavity to give a false median septum, with comb-like cardinal process, crura slender.

V a r i a b i l i t y : Width of hinge greatly varied from slightly shorter than greatest width to greatly extended similar to *Cyrtospirifer chemungensis* or *Regelia glaucus* of North America in rare cases; in any case, however, cardinal ex-

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Fig. 6 Sinal plication patterns of some representatives of *Mennespiri-fer yangqiaoensis* (all drawn from shells with wider hinge similar to the one figured by Fig. 5C).

tremities are acute. And the holotype and paratype PUM 00006 would represent the typical shape of this species.

Comparison: This species is characterized by small size, variable hinge width, apsacline low ventral interarea, few sinal plications, and internally with ventral posterior thickening of dental plates instead of a true delthyrial plate. The last two characters (few sinal plications and ventral posterior thickening) are different from true Frasnian Cyrtospirifer which have a well-developed delthyrial plate of considerable length (Brice 1988; Ma - Day submitted). It is in these two characters similar to Regelia glaucus (Crickmay, 1952), the type species of Regelia. However, the present species is rather small and has an apsacline ventral interarea, which is large and catacline in Regelia. Further study is needed to evaluate relationships between the new species and species of Regelia. It is different from Cyrtospirifer cf. whitneyi in its thickened delthyrial cavity, low ventral interarea, and capillate-radially striate micro-ornament (versus pustules in Cyrtospirifer cf. whitneyi). It differs from Cyrtospirifer extensa Ching – Liu (in Wang et al. 1982) in that the latter has a trapezoidal shape and more sinal and lateral shell plications.

D i s c u s s i o n : Specimens from the Xikuangshan section had previously been classified as *C. archiaciformis* (Grabau). However, in comparison with Grabau's species, Ma (1993) also pointed out that the present species is smaller and that there is no median furrow on fold. Study of Grabau's type specimens housed in Nanjing Institute of Geology and Palaeontology shows that that species is characterized by larger size, pustulose micro-ornament, presence of a median furrow or flat top on fold and corresponding underdevelopment of median sinal plications.

Genus Mennespirifer Lyashenko, 1973

Mennespirifer yangqiaoensis sp. nov. Figs 5A–E, 6, 7, 8

Holotype: Specimen PUM 00045, figured here as Fig. 5B1–B5. Paratypes: Specimens PUM 00036 (Fig. 5C1–C2), PUM 00037

- (Fig. 5A1–A6), PUM 00043 (Fig. 5E), and PUM 00044 (Fig. 5D). Ty pe horizon: Upper part of the Shetianqiao Formation at a horizon corresponding to middle part of bed 23 (Hou – Wang 1988,
- p. 132), latest Frasnian (probably Upper *rhenana* Zone).
 Type locality: About 50 m south of Daoshitang, Heyi village, Yangqiao Township, Shaodong County, central Hunan Province.



Fig. 7 Scatter diagram of Mennespirifer yangqiaoensis.

E t y m o l o g y : A small local township name where the type specimens were collected.

M a t e r i a l : About 250 complete specimens. Shetianqiao section; late Frasnian (*rhenana* Zone).

D i a g n o s i s : Small sized cyrtospiriferids with hinge shorter than greatest width, small ventral interarea, few sinal plications; internally with a short delthyrial plate in ventral valve, extrasinal dental plates, comb-like cardinal process.

Description: Shell small sized, slightly wider than long, oval or sub-oval in ventral view, uniplicate in anterior view, about equi-biconvex in lateral view. Hinge straight, its width variable from nearly equal to greatest width to much shorter. Cardinal extremities slightly pointed to rounded.

Ventral interarea small, curved, apsacline; beak ridges rounded. Delthyrium generally open, but traces of pseudodeltidium observed at least in a few shells. Sinus generally shallow and rounded, rarely sharp-bottomed. Sinal plications 3 to 7, generally 4 to 5, with one simple primary plication on each side, median sinal plications 1 to 4, generally 2 to 3, lateral sinal plication zero to one. Bounding plications of sinus relatively coarse; lateral shell plications around 15, low and rounded, separated by interspaces of about equal or greater width.

Micro-ornament of very fine striae intercepted by very weak growth lines making the striae an intermittent appearance (Fig. 5A6).

Internally with a very short delthyrial plate in ventral valve; dental plates thickened posteriorly. In dorsal valve, posterior thickened around crural bases, still leaving a fissure medially; comb-like cardinal process with several vertical lamellae, crural bases short and thin.

C o m p a r i s o n : Zhao (in Yang et al. 1977) established a new genus, *Changshaispirifer* whose familiar status was then set uncertain. Carter et al. (1994) put it in the syn-



Fig. 8 Transverse serial sections of *Mennespirifer yangqiaoensis* from the Shetianqiao section (sample S-H-0). Numbers refer to distance in mm from the ventral apex. Arrow indicates enlargement. There is only a very short delthyrial plate at the very posterior end of the ventral valve. A – Specimen PUM 00114. B – Specimen PUM 00115.

onymy of *Adolfia*. The present new species is very similar to the type species of *Changshaispirifer*, *C. lianhuaqiaoensis*, in shell shape. However, the latter species has a V-shaped sinus in cross section, only one weak plication on each lateral slope of sinus, and internally a pair of delicate dental plates. In addition, it cannot be certain whether *C. lianhuaqiaoensis* has a delthyrial plate from the illustration of its posterior serial sections. The present species is different from "*Cyrtospirifer*" sichuanensis Chen in Xu et al. (1978) in that the latter species is larger in size, has a nearly orthocline ventral interarea and more sinal and lateral shell plications (25 to 28).

This species is also externally somewhat similar to Rigauxia acutosina (Rigaux, 1908) figured and described by Brice (1988). However, the latter species possesses pustulose micro-ornament, stronger plications and narrower and deeper interspaces. R. acutosina is unique in having Cyrtospirifer-type fold and sinus (Ma - Day 2000) but lacking a delthyrial plate. Tenticospirifer columnaris Roberts, 1971 from the Australian Frasnian is apparently a mixture of probably four different species belonging to different genera (Ma – Day 2000, p. 447). The holotype of *T. columnaris* is not a *Tenticospirifer*; it is very similar to the new species herein. Differences include a larger interarea and sharper beak ridges in the Australian species. Other features are difficult to compare because one is not sure to which type of specimens Roberts (1971, p. 199-200, Figs 56 and 57) referred in the figures of transverse serial sections. The present species differs from the type species of *Mennespirifer*, M. menneri (Lyashenko) (see Lyashenko 1959, p. 129,

Pl. 17, Fig. 12), in its smaller size, fewer sinal plications, wider interspaces, and narrower shell plications.

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D i s c u s s i o n : This species can be divided into two morphological groups. The first group is represented by the holotype (Fig. 5B) characterized by short hinge and rounded to obtuse cardinal extremities and the second is represented by paratype PUM 00036 (Fig. 5C) characterized by longer hinge and rectangular to slightly pointed cardinal extremities. Specimens of both groups have the same micro-ornament, sinal plication pattern, size (Fig. 7) etc. Differences in hinge width and shape of cardinal extremities are considered to be intraspecific growth variations.

Concluding remarks

There are only about five cyrtospiriferid species in the late Frasnian of central Hunan, including *Tenticospirifer tenticulum*, *Mennespirifer yangqiaoensis* sp. nov., *Cyrtospirifer* cf. *whitneyi*, *Cyrtospirifer*(?) *variabilis* sp. nov., and *Cyrtospirifer "sinensis*". Except for the last one, all the former four taxa are small-sized. Although *Cyrtospirifer* is a well-known Late Devonian genus in the world, it still needs revision since so many different-shaped species have been included in the genus from the late Givatian throuth late Famennian. For example, Sidyachenko (1962) described 29 species and subspecies of *Cyrtospirifer* from the Famennian (Late Devonian) of central and southeastern Karatau, Kazakhstan.

Mennespirifer yangqiaoensis is very similar to Australian Frasnian "*Tenticospirifer*" columnaris Roberts. In addition there are also similar atrypids between Austra-

lia and South China, e.g., the presence of Australian *Desquamatia (Synatrypa) kimberleyensis* (Coleman, 1951) in South China (Ma 1998). This may suggest a close geographic affinity between the two regions. In fact Hao – Gensel (1998) recognized a northeastern Gondwana phytogeographic unit during the early Devonian comprising Australia and the South China block.

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Malí cyrtospiriferidi ze svrchního devonu (pozdní frasn) centrálního Hunanu, Čína

V brachiopodových faunách pozdního frasnu v centrálním Hunanu (jižní Čína) dominují atrypido-rhynchonellido-cyrtospiriferidní společenstva. V nich přítomní cyrtospiriferidní brachiopodi jsou typičtí drobnou velikostí. Náleží čtyřem druhů, patřícím nejméně třem rodům. Z nich jsou popsány dva druhy jako nové (*Cyrtospirifer* (?) variabilis a Mennespirifer yangqiaoensis).