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PARALLEL EVOLUTION OF JUGAL STRUCTURES IN DEVONIAN ATHYRIDIDE BRACHIOPODS

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Abstract: Here, we describe *Sinathyris crassa* gen. et sp. nov., a new early Emsian (Early Devonian) athyridide brachiopod with a double spiralium from the Guangxi Province of southern China. Unlike the majority of genera of the subfamily Helenathyridinae, which possess accessory spiral lamellae developed directly from the jugal branches, the form described here shows these lamellae arising from a distally bifurcating jugal stem. These differences suggest that the double spiralium in *S. crassa* might have appeared independently from the double spiralium of the helenathyridins. To test the subfamily assignment of *Sinathyris* gen. nov., we carried out phylogenetic analyses, which indicate that the new genus is more appropriately referred to the Didymothyridinae. The cladistic analyses of the athyridides indicate that double spiralia have developed independently among these brachiopods at least five times during their evolutionary history.

Key words: *Sinathyris*, Athyridida, double spiralium, Devonian, phylogenetic analyses, China.

AMONG brachiopods grouped within the order Athyridida, there are a few small but distinct groups of genera that developed elaborate support of the lophophore in the form of two pairs of separated, parallel spiral coils (double spiralia). The first athyridides with double spiralia appeared in the Early Devonian within two subfamilies. One of them, Helenathyridinae, is included within superfamily Athyridoidea and was represented by two genera, *Helenathyris* Alekseeva, 1969, and *Sphaerathyris* Baranov, 1994. The second subfamily, Coelospirinae, belongs to superfamily Anoplothecoidea and was represented by a single genus with double spiralia, *Coelospira* Hall, 1863 (Campbell and Chatterton 1979). During the Mid-Devonian, three new genera with double spiralia appeared. Two of them, Givetian *Eobiernatella* Baliński, 1995, and Givetian–Frasnian *Biernatella* Baliński, 1977, are helenathyridins (Baliński 1995). The third genus, *Kayseria* Davidson, 1882, which is included in the superfamily Anoplothecoidea, lived through the Eifelian and Givetian (Copper 1973). During the late Frasnian, the last helenathyridins, represented by *Biernatella* and *Neptunathyris* Mottequin, 2008, disappeared from the fossil record (Baliński 1995; Mottequin 2008). The double-spired athyridides reappear as late as the Mid-Triassic, and they were represented by two groups: suborder Koninckinidina and family Diplospirellidae (Alvarez and Rong 2002; MacKinnon 2002). In the Late Triassic, a single, double-spired representative of the suborder Retziidina, *Hungarispira* Dagys, 1972, appears (Dagys 1974). The last athyridides with double spiralia, represented by the koninckinidines, disappear from the fossil record in the Early Jurassic. The fossil record of the athyridides with double spiralia shows that this elaborate brachidium must have developed independently several times during their evolutionary history (Boucot *et al.* 1964; Copper 1973; Baliński 1977, 1995).

The Early Devonian material described here represents a new genus that is one of the oldest occurrences of an athyridide with double spiralia. Moreover, this is the first record of the double-spired group of brachiopods in China. Sufficiently good preservation of the material permitted a detailed study of the brachidium through serial sectioning, including an examination of the structure of the jugum and the origin of the accessory lamellae. These observations revealed that, as presently understood within the helenathyridins, the development of double spiralia in various genera was distinctly different, indicating that the group is most likely not monophyletic. Therefore, we propose to include only those genera that possess a jugum with two pairs of jugal branches in the subfamily Helenathyridinae. On the other hand, according to the cladistic analysis in this study, *Sinathyris* gen. nov. with one pair of jugal branches and a long, bifurcated jugal stem belongs to the subfamily Didymothyridinae.

Although the presence of a bifurcated jugal stem in *Sphaerathyris* Baranov, 1994, is equivocal (see Discussion below), it is probable that the genus may not belong to the subfamily Helenathyridinae. The data presented here provide new evidence for the evolutionary relationship between Devonian, double-spired athyridoids.

The functional morphology of double spires in the athyridide brachiopods was discussed broadly in several previous studies, such as Williams (1960), Williams and Rowell (1965), Campbell and Chatterton (1979), Alvarez and Brunton (1990), Baliński (1995) and Williams *et al.* (1997).

GEOLOGICAL SETTING

The studied material was collected from the upper part of the Lower Devonian Yilan Formation exposed along the highway from Nandan County to Tian'e County near Mode village, Nandan, in the Guangxi Province of China (Fig. 1A–B). In this section, the Yilan Formation is faulted near its base and overlain by black to dark grey shale of the Lower and Middle Devonian Tangding Formation. In Tangding village, the type locality of the Yilan Formation, the formation overlies the lowermost Devonian sandstones. The thickness of the exposed portion of the Yilan Formation in the studied section at Mode is approximately 70 m and can be divided from the bottom to the top into three lithological units (Fig. 1C): purple to brownish-yellow calcareous mudstone (*c.* 14 m thick), grey marl and nodular limestone (*c.* 21 m thick) and dark grey mudstone with some lenses of marl and calcareous concretions (*c.* 35 m thick). The lower and middle units of the formation contain abundant brachiopods that are characteristic of the *Rostrospirifer–Dicoelostrophia–Cymostrophia* fauna, a diverse neritic, early Emsian fauna widely distributed in southern China (Wang 1956; Hou and Xian 1975; Bai and Hao 1982; Wang and Rong 1986). The succeeding brachiopod fauna of the upper unit is of rather low diversity and is dominated by *S. crassa* gen. et sp. nov. described in this paper and accompanied by the very rare orthide *Eosophragmophora sinensis* Wang *in* Wang *et al.*, 1974 (four specimens), atrypides (four specimens) and the athyridide *Athyris pauca* Wang and Rong, 1986 (which most likely belongs to *Brimethyris*; one specimen) that together constitute 1% of the brachiopod fauna. In addition to brachiopods, the benthic fauna is represented by solitary rugose corals (about 7% of the whole fauna) and sporadic trilobites. Other co-occurring fauna includes nautiloids, gastropods, conodonts and thin-shelled tentaculitids. Among the collected *S. crassa* specimens, those with conjoined valves predominate, while those with single valves only constitute approximately 7.6% of all specimens. Pyrite is abundant in the sediment and often within the interiors of the brachiopod shells. The facies and taphonomic characteristics suggest that *S. crassa* lived in a quiet, relatively deep marine setting with probable intermittent dysoxic conditions. The co-occurring conodont fauna suggests an early Emsian age for the range of the species (Fig. 1C).

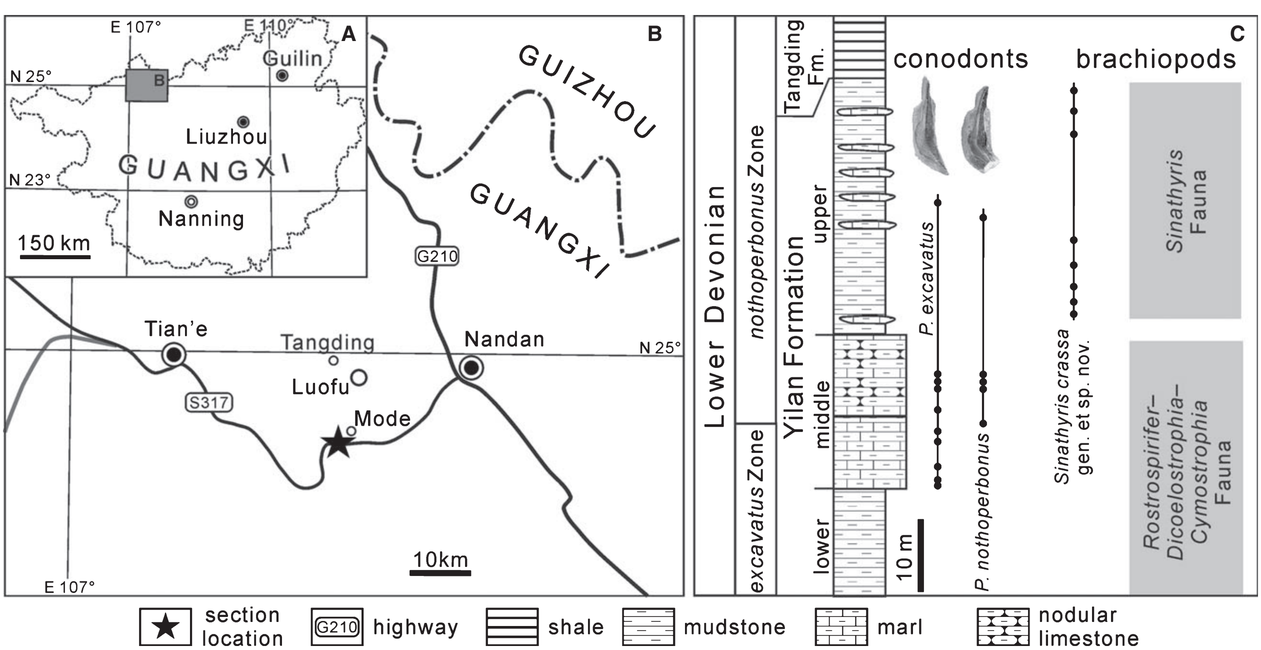


FIG. 1. Geographical location and stratigraphy of collection site. A, regional map of Guangxi Province. B, detailed map of study area near the village of Mode, Nandan County. C, stratigraphical column at the collection locality with brachiopod and conodont ranges.

MATERIALS AND METHODS

The internal shell structures of *S. crassa* were studied in serial sections. Before sectioning, the interiors of the selected specimens were first checked for the presence of double spiralia by X-ray microtomography (Institute of Paleobiology, Warsaw, Poland) because only a small number of the studied shells appeared to have sufficiently well-preserved internal structures. In addition to peels, each section was photographed using a Nikon SMZ 1500 binocular equipped with a Nikon D800 digital SLR camera. The images were then redrawn using CorelDraw X3 software.

A heuristic search strategy for the cladistic analysis was conducted on a personal computer using the PAUP* 4.0 Beta 10 software (Swofford 2002) with the following search settings: optimality criterion = parsimony, starting tree(s) obtained via stepwise addition, random for the addition sequence and 1000 replicates, outroot = paraphyl.

Institutional abbreviations. PKUM, Geological Museum of Peking University, Beijing, China; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

DISCUSSION

Jugal structure in helenathyridins and Sinathyris

A characteristic feature that distinguishes the new genus from all helenathyridins, with the possible exception of the Early Devonian *Sphaerathyris* Baranov, 1994, is the structure of its jugum and the development of the spiral accessory lamellae. In *Sinathyris* gen. nov., the accessory lamellae arise through distal bifurcation of the posteroventrally directed jugal stem (Fig. 2A–B). On the contrary, in the Early Devonian *Helenathyris* Alekseeva, 1969, and the Givetian–Frasnian *Eobiernatella* Baliński, 1995, and *Biernatella* Baliński, 1977, these lamellae stretch from the dorsally directed jugal outgrowths (Fig. 2C). Although the serial sections of the Frasnian *Neptunathyris* Mottequin, 2008 (see Mottequin 2008, fig. 33), do not show the details of the development of the accessory lamellae (they are usually extremely thin and delicate and easy to overlook in the serial sections even when preserved), their most probable origin is comparable to that in *Helenathyris* and *Biernatella*, for example. This assumption is also supported by the absence in the *Neptunathyris* sections of a long, more posteriorly directed and distally bifurcated jugal stem.

In the serial sections of *Sphaerathyris repetina* Baranov, 1994 (the type species of the genus; Baranov 1994), from the Emsian of north-east Russia, neither the jugal stem nor the beginning of the accessory lamellae is revealed.

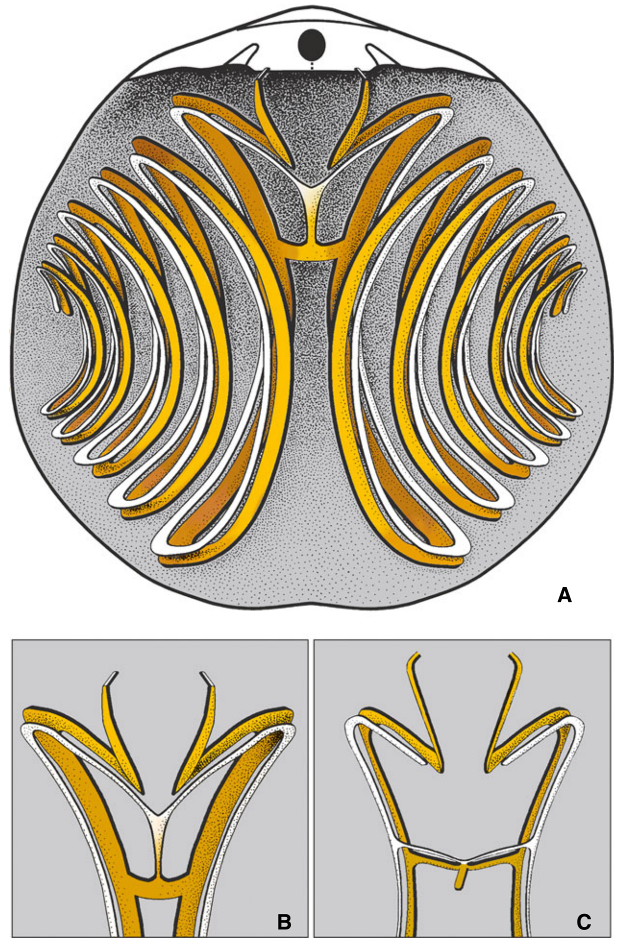


FIG. 2. Reconstruction of the double spiralium in *Sinathyris crassa* gen. et sp. nov. (A) and comparison of the jugal structure of *S. crassa* (B) and helenathyridin *Biernatella polonica* Baliński, 1977 (C; modified from Baliński 1977, 1995).

Although the serial sections of another species of *Sphaerathyris*, *S. spicata* Baranov, 1994, from the Pragian of north-east Russia also do not show the jugal stem, they reveal the presence of a pair of closely set blades in the mid-ventral region (Baranov 1994, fig. 5, drawings 11 and 12), which strongly suggests the configuration observed in *Sinathyris*, that is the origin of the accessory lamellae by distal bifurcation of the jugal stem.

Taxonomic significance of the jugal structure

As outlined above, within the Devonian smooth-shelled athyridids with double spiralia, there are two groups of genera differentiated by their jugal structures and the origin of their accessory lamellae. The accessory lamellae of *Helenathyris*, *Eobiernatella*, *Biernatella* and, most likely, *Neptunathyris* arise from the dorsally projecting, very thin outgrowths of the jugum. These outgrowths or branches stretch from the median tip of the jugal arch and are more or less parallel to the main jugal branches that join the primary lamellae. Thus, in these helenathyridins, the jugum consists of four branches; the stronger two connect the primary lamellae, and the other two, which are very thin, join the accessory lamellae. All four branches are fused on the ventral (median) tip of the jugal arch. In *Sinathyris* gen. nov., and most likely *Sphaerathyris*, these lamellae originate by the distal bifurcation of the postero-ventrally projecting jugal stem. As a consequence, only one pair of the jugal branches is present, that which connects the primary lamellae.

The difference in the jugal structure between these two groups of genera seems quite significant. In the former group, each of the accessory spiral lamellae has two sections: a short one, posteriorly directed from the jugum, that terminates near the crural ends, and a second that runs anteriorly and then intercoils until it reaches the ends of the spiralia. In the second group, each of the accessory lamellae represents a continuous single blade that extends from the tip of the jugal stem. An important issue arising from these differences in the structure of the brachidium is their taxonomic significance. To include all smooth-shelled, double-spired genera within one subfamily assumes a great variability in the structure of the brachidium within the group. However, if this differently structured jugum and brachidium appeared independently, which seems credible, this subfamily would not be a natural group.

It should be noted that the four-branched jugum, which is characteristic of *Helenathyris*, *Eobiernatella*, *Biernatella* and, most likely, *Neptunathyris*, is unique among athyridides, except in koninckinidines whose taxonomic position is somewhat equivocal (see the Discussion in MacKinnon 2002). The majority of athyridides possess secondary lamellae (short or long) arising from the distal bifurcation of the jugal stem. This condition is also the characteristic of *Sinathyris* gen. nov. and, most likely, *Sphaerathyris*. In these two genera, the origin of the accessory spiralia may be elucidated as simple prolongations of the umbonal accessory blades. From this point of view, the two genera are distinguishable from the helenathyridins, *Helenathyris*, *Eobiernatella* and *Biernatella*, on the basis of their differently structured jugum and accessory spiralia.

Phylogenetic position of Sinathyris *among athyridides*

To test the phylogenetic position of *Sinathyris* gen. nov. among athyridides, cladistic analyses were performed based on a data matrix developed by Alvarez *et al*. (1998) for the suprageneric classification of the athyridide brachiopods; a minor emendation was made to the outgroup selection and character coding and states related to characters 29 (brachidium), 33 (jugal saddle) and 36 (accessory jugal lamellae). In their original analysis, Alvarez *et al*. (1998) selected two rhynchonellides (Ancistrorhynchidae and Trigonirhynchidae) as outgroups. Although there is no doubt that Rhynchonellida can be placed at the base of the crown group of rhynchonelliformean brachiopods, both Ancistrorhynchidae and Trigonirhynchidae look somewhat distinct and specialized, which may affect the polarity of some characters. Some previous phylogenetic studies on the spiralium-bearing brachiopods revealed that the athyridides have a closer relationship to the atrypides (especially the smooth lissatrypidines that bear planospiral brachidium with short, separated jugal processes located dorsomedially) than to the rhynchonellides (Alvarez and Carlson 1998; Popov *et al.* 1999). Thus, besides the two rhynchonellide families mentioned above, we also added the lissatrypidine family Cyclospiridae as an outgroup in the analysis. Consequently, a new state (brachidium with spiral tips directed medially) is added for coding character 29 in the new outgroup. Alvarez *et al.* (1998) previously coded jugal saddle (character 33) as being anteriorly directed in Didymothyridinae. However, only two genera, *Didymothyris* Rubel and Modzalevskaya, 1967, and *Collarothyris* Modzalevskaya, 1970, have this structure anteriorly directed; in the other seven, there is no jugal saddle; and such a structure is unknown in the remaining one. Thus, we assigned two states, absent (0) and anteriorly directed (1), to the coding of this character for Didymothyridinae. For character 36 (accessory jugal lamellae), we modified the original character state 5 (free, intercalated with spiralia to apex) to create two different states (new states 5 and 6) to distinguish the origination of accessory jugal lamellae among the groups bearing double spiralia. The new state 5 (arising by bifurcation from jugal stem, free, intercalated with spiralia to apex) is present in Diplospirellinae, Hungarispirinae and *Sinathyris*, while the new state 6 (arising from jugal arch, free, intercalated with spiralia to apex) is present in Helenathyridinae and Koninckinoidea.

Two series of analyses were performed to compare the results under different sets of character weights, character emendation and taxon addition. In the first series, character ordering and weighting strictly followed those of Alvarez *et al.* (1998): four characters (numbers 6, 22, 23 and 26) were ordered; four characters (numbers 3, 5, 6 and 25) were weighted three times greater than the others; three characters (numbers 22, 23 and 26) five times greater; and the character (punctate or impunctate) of the shell structure (number 37) 13 times. Outgroup selection follows Alvarez *et al.* (1998), but Cyclospiridae (if added in the analysis) is also selected. Under such a weighting strategy, respectively, three and four equally most parsimonious trees were obtained in the analyses irrespective of whether Cyclospiridae was excluded or not. The number of most parsimonious trees obtained and the topology of the cladograms from the analyses excluding Cyclospiridae strongly agree with those of Alvarez *et al.* (1998). Among the four cladograms that resulted from the analyses including Cyclospiridae, three agree with those of Alvarez *et al.* (1998) in topology and one does not. In this latter cladogram, Koninckinoidea is placed below Cyclospiridae (see Guo *et al.*, appendix S4, fig. 2C), and its phylogenetic relationship is unresolved at the base of the athyridides in the strict consensus tree (Fig. 3B). Modifying the coding of character 36 (i.e. using the original data of Alvarez *et al.* or using our new data with the above-

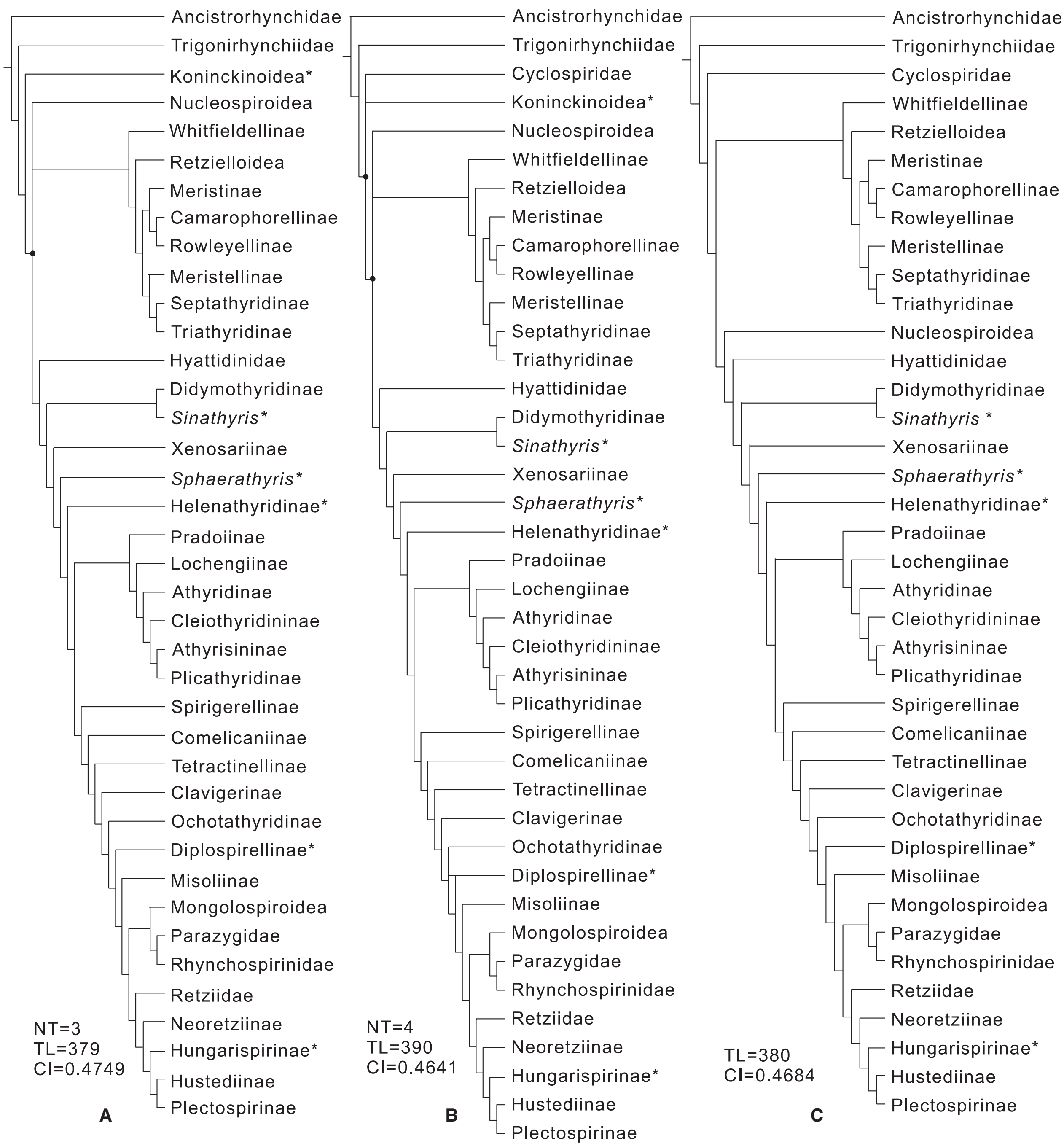


FIG. 3. Cladograms showing hypothesized phylogenetic relationships between *Sinathyris* gen. nov. and the suprageneric taxa of the Athyridida s.l. obtained from the data matrix in Guo *et al.* (2014, appendix S2). A–B, strict consensus trees obtained in the analyses with the Cyclospiridae outgroup excluded and included, respectively. C, single most parsimonious tree obtained in the analysis with Koninckinoidea excluded and the Cyclospiridae outgroup included. Double spiralia-bearing taxa are marked with an asterisk. Unresolved nodes are indicated with heavy dots. NT, number of trees; TL, tree length; CI, consistency index.

mentioned modifications) and adding another taxon, *Sphaerathyris*, do not affect the pattern. In all cases, the new genus, *Sinathyris,* is consistently grouped with Didymothyridinae (Fig. 3A–B), and *Sphaerathyris*, if added, occurs as an independent lineage at a level more derived than Xenosariinae and more primitive than Helenathyridinae (Fig. 3B). Because the position of the enigmatic Koninckinoidea became unresolved after Cyclospiridae was added, we deleted the Koninckinoidea and repeated the analysis. Although only a single most parsimonious tree was obtained from each of the experiments, the phylogenetic position of Nucleospiroidea was resolved either between the Meristelloidea and Hyattidinidae group (Fig. 3C) or between the two rhynchonellide outgroups in the analyses with and without Cyclospiridae (see Guo *et al.*, appendix 4, figs 5–6). The former result is more reasonable and acceptable than the latter. The pattern of the other in-groups in the cladograms is not changed.

The results strongly suggest that *Sinathyris* gen. nov. has closest relationship to subfamily Didymothyridinae and not to Helenathyridinae, and the double spiralium has independently developed among athyridide brachiopods at least five times (Fig. 3) during their evolutionary history. Thus, based on these cladistic analyses, we tentatively interpret *Sinathyris* to be a member of subfamily Didymothyridinae.

A second series of experimental analyses were tried to assess the effects of modifying character 36 (accessory jugal lamellae) and adding or deleting *Sphaerathyris* and Cyclospiridae under the condition of equal weights for all characters (see Guo *et al*. 2014, appendix 4). The most parsimonious trees obtained are highly unstable and contain multiple polytomies (see Guo *et al*. 2014, appendix 4). The results of these experiments reveal that the topology of the cladograms is variable whether character 36 is modified and whether new taxa are added; in the strict consensus tree of each experiment, the relationships between many taxa remain unresolved. The conflicting results from the analyses with or without giving certain characters greater weight, as well as the weakness of phylogenetic interpretation with equal character weighting, imply that the relationships between the suprageneric groups of the athyridides are far from understand and that cladistic analyses for such groups remain in their infancy. However, the weighted strategy suggested by Alvarez *et al.* (1998) provides a tentative and relatively stable framework that is consistent with the traditional classification.

SYSTEMATIC PALAEONTOLOGY

This published work and the nomenclatural acts it contains have been registered in Zoobank: http://zoobank.org/References/147C01C5-6C47-4628-B0F2-F8469DB501B1

Repository. All illustrated and sectioned specimens (holotype and paratypes) are housed in the PKUM, Beijing, China; part of the type material (paratypes) is housed at ZPAL in the Institute of Paleobiology, Warsaw, Poland.

Order ATHYRIDIDA Boucot, Johnson and Staton, 1964
Suborder ATHYRIDIDINA Boucot, Johnson and Staton, 1964
Superfamily ATHYRIDOIDEA Davidson, 1881
Family ATHYRIDIDAE Davidson, 1881
Subfamily DIDYMOTHYRIDINAE Modzalevskaya, 1979

Genus SINATHYRIS gen. nov.

LSID. urn:lsid:zoobank.org:act:C4C230C1-E59E-4FF5-83DB-18D0B45543F9

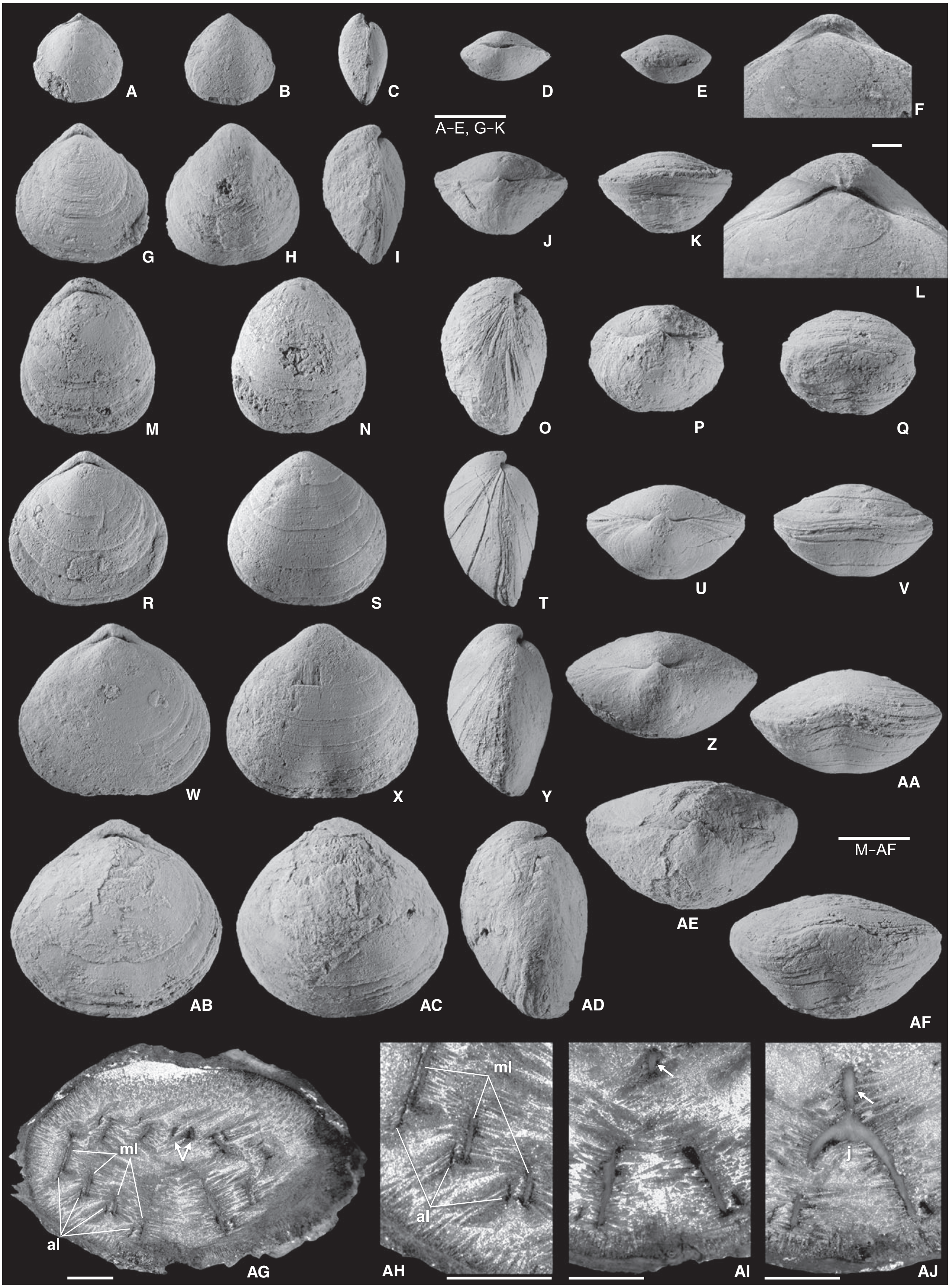
Derivation of name. Combination of *Sin-* (from Greek prefix *Sino-* referring to China) and the genus name *Athyris*.

Type species. Sinathyris crassa gen. et sp. nov.; lower Emsian, Guangxi Province, southern China.

Species assigned. Type species only.

Diagnosis. Shell medium-sized, ventribiconvex; ventral beak incurved, palintrope distinct, curved; ventral sulcus shallow and narrow, originating posteriorly to mid-length; dorsal fold absent to very weak in proximity to the anterior margin; anterior commissure weakly uniplicate to almost rectimarginate. Dental plates absent or, exceptionally, buried by secondary shell; ventral muscle field deeply impressed; dorsal cardinalia with thickened cardinal plate;

FIG. 4. *Sinathyris crassa* gen. et sp. nov., Mode village, Nandan County, Guangxi Province, southern China, Lower Devonian, upper part of the Yilan Formation, early Emsian. A–E, paratype PKUM02-645, dorsal, ventral, lateral, posterior and anterior views of juvenile shell. F, paratype PKUM02-651, umbonal region of relatively small shell in dorsal view. G–K, M–Q, two paratypes PKUM02-646–647, dorsal, ventral, lateral, posterior and anterior views of relatively small shells. L, paratype PKUM02-652, umbonal region of large shell. R–V, paratype PKUM02-648, dorsal, ventral, lateral, posterior and anterior views of shell with well-preserved concentric growth lamellae. W–AA, holotype PKUM02-649, dorsal, ventral, lateral, posterior and anterior views. AB–AF, paratype PKUM02-650, dorsal, ventral, lateral, posterior and anterior views of large shell. AG–AJ, paratype PKUM02-653, transverse sections of shell showing double spiralia and jugum (compare with Fig. 6A); al, accessory lamella; ml, main lamella; j, jugum, arrows indicate distally bifurcate jugal stem (AG), distal end of the jugal stem prior to bifurcation (AI), and proximal part of the jugal stem (AJ). Scale bars represent 5 mm (A–E, G–K, M–AF) and 1 mm (F, L, AG–AJ).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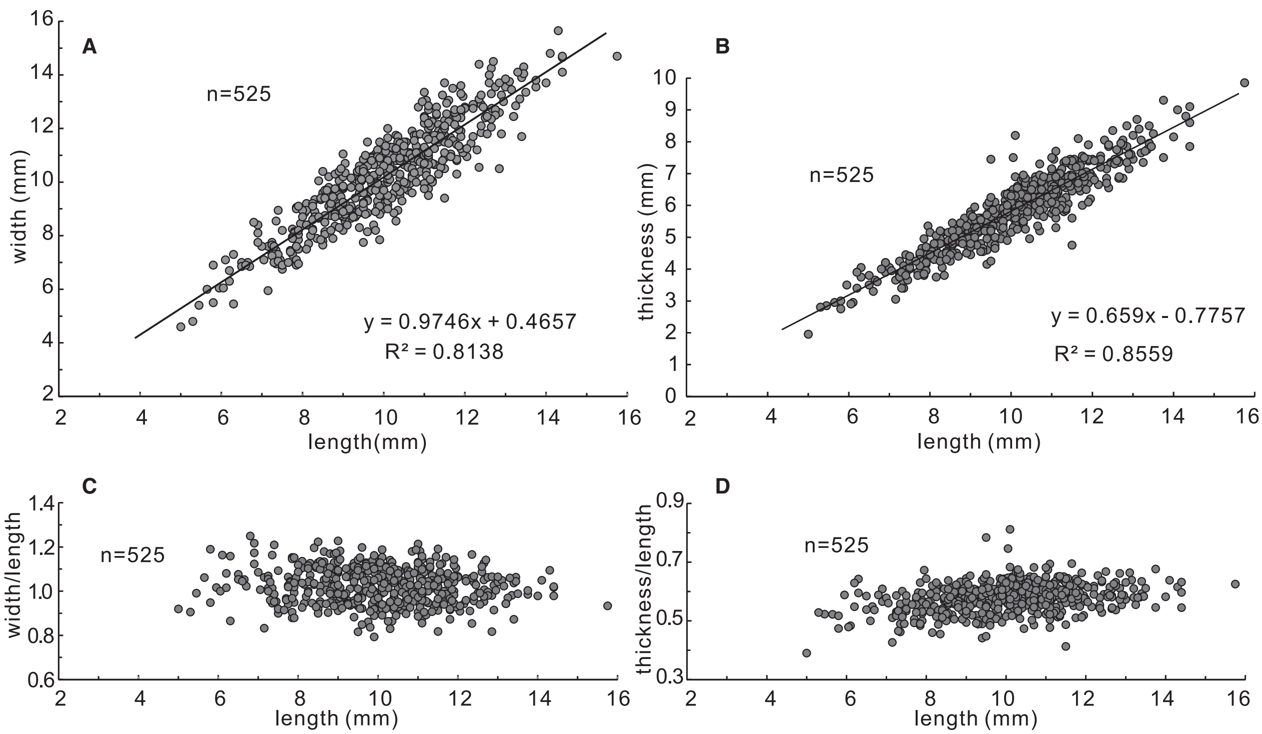

FIG. 5. Bivariate plots of the main shell measurements in *Sinathyris crassa* gen. et sp. nov. A, length to width. B, thickness to length. C, width index to length. D, thickness index to length.

dorsal median septum absent; jugal arches U-shaped, jugal stem postero-ventrally directed, distally bifurcating giving rise to accessory lamellae; accessory lamellae intercoiled with primary lamellae to the apices of spiral cones. Shell substance greatly thickened at posterior. Shell surface smooth except rare growth lamellae.

Remarks. The new genus differs from *Helenathyris* Alekseeva, 1969, by having weakly uniplicate, more robust shell with rather subpyriform outline contrary to the circular, rectimarginate and lenticular outline in the latter genus. The interior of *Sinathyris* gen. nov. is distinguished from that of *Helenathyris* by the absence of well-developed dental plates and by the presence of long, postero-ventrally directed jugal stem. From *Sphaerathyris*, the new genus differs by the absence of dental plates and by having a greatly thickened cardinal plate and shell (thin and delicate in *Sphaerathyris*). The new genus is distinguished from *Eobiernatella* by the absence of dental plates and by the different origin of the accessory lamellae. From *Biernatella*, the new genus differs by the presence of well-developed cardinal plate and by the origin of the accessory lamellae from the distal end of the jugal stem. In *Biernatella*, the inner hinge plates are weak and do not merge medially, and thus, the cardinal plate is not developed.

Occurrence. Early Emsian (Early Devonian), southern China.

Sinathyris crassa sp. nov.
Figures 2A–B, 4–7

LSID. urn:lsid:zoobank.org:act:147C01C5-6C47-4628-B0F2-F8469DB501B1

Derivation of name. Latin *crassus*, thick, referring to the thickened shell.

Holotype. Complete articulated shell PKUM02-649 (Fig. 4W–AA).

Paratypes. Complete articulated shells PKUM02-645–648 (Fig. 4A–E, G–K, M–Q), PKUM02-650–653 (Fig. 4AB–AF, F, L, AG–AI); serial sectioned shells PKUM02-653 (Figs 4AG–AJ, 6A), PKUM02-654–657 (Figs 6B, 7A–C); 850 mostly complete articulated shells (PKUM02-658–670, ZPAL Bp 74); all from the type locality.

Diagnosis. As for the genus.

Type horizon and locality. Road side south-west of Mode village, Nandan County, Guangxi Province, southern China (coordinates: 24°53′53″–24°53′55″N, 107°23′22.5″–107°23′23.5″E; Fig. 1); Lower Devonian, upper part of the Yilan Formation, early Emsian, lower part of the conodont *nothoperbonus* Zone.

Description. Shell small to medium-sized, up to about 14 mm in length, ventribiconvex; outline variable: rounded subpentagonal,

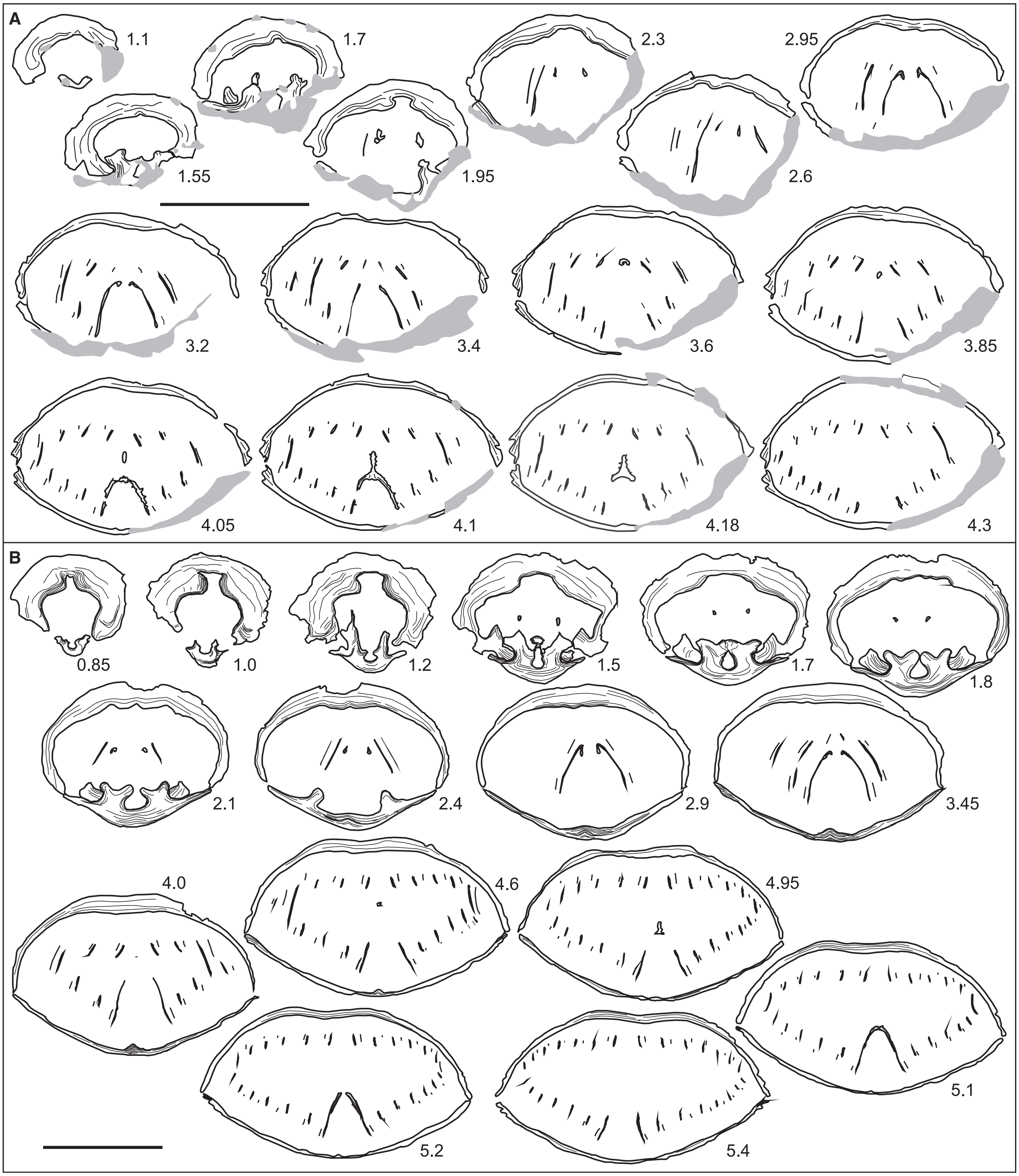

FIG. 6. Transverse serial sections through two shells of *Sinathyris crassa* gen. et sp. nov. from the upper part of the Yilan Formation, near Mode, Guangxi Province. A, PKUM02-653. B, PKUM02-654. Distances measured in millimetres from the tip of the ventral umbo. Scale bars represent 5 mm.

subtriangular, to circular, wider than long to elongated (Fig. 5); hinge margin angular, short, constitutes about half of the shell width; lateral margins rounded, anterior margin weakly rounded to truncated, rarely weakly emarginate; anterior commissure usually weakly uniplicate, rarely almost rectimarginate.

Ventral valve with inflated, strongly curved umbo; palintrope distinct, curved, but frequently obscured by strongly incurved

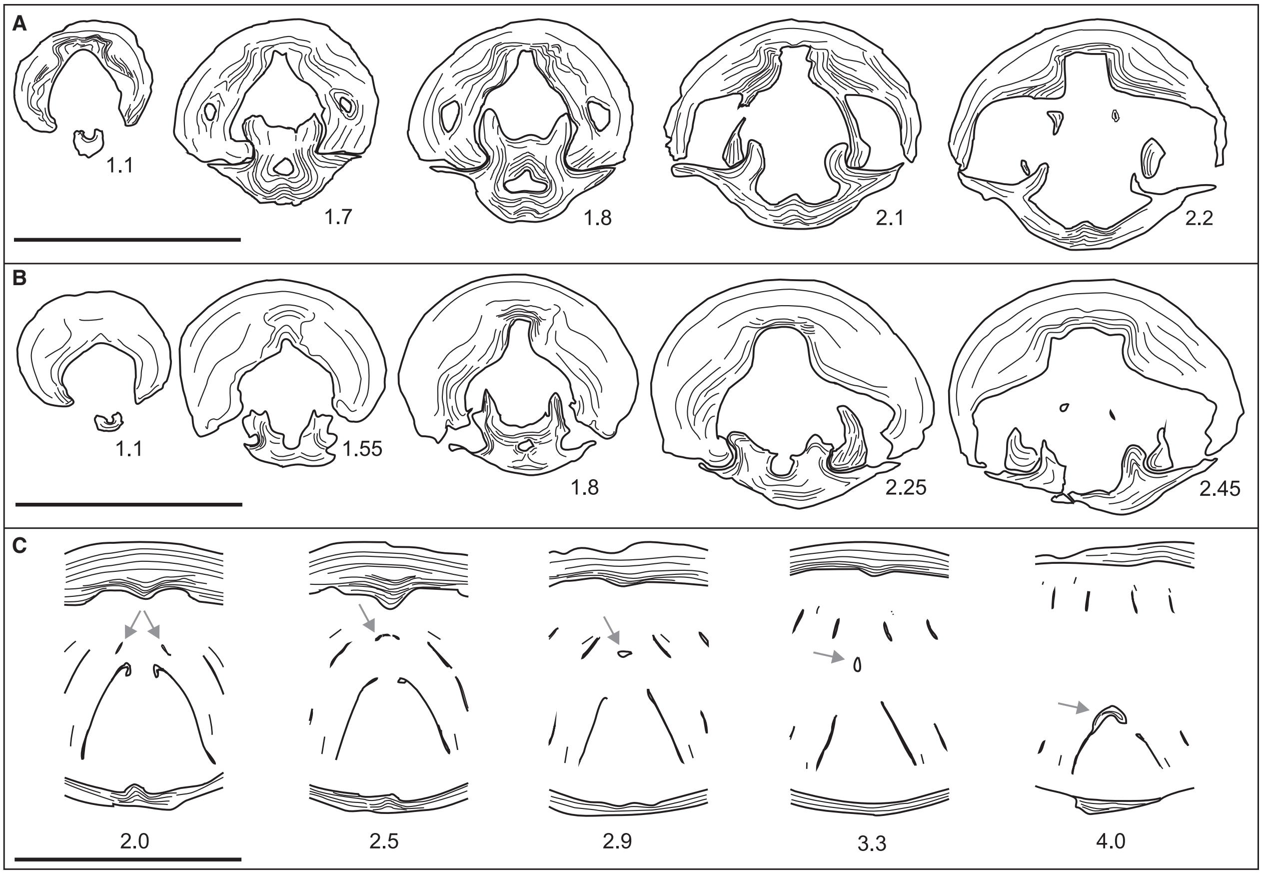

FIG. 7. Transverse serial sections through three shells of *Sinathyris crassa* gen. et sp. nov., from the upper part of the Yilan Formation, near Mode, Guangxi Province. A, PKUM02-655. B, PKUM02-656. C, PKUM02-657. Arrows indicate bifurcated distal end of the jugal stem and beginning of the accessory lamellae (section 2.0), distal part of the jugal stem prior to bifurcation (sections 2.5–3.3) and the jugal arch (section 4.0). Distances measured in millimetres from the tip of the ventral umbo. Scale bars represent 5 mm.

beak in mature shells (Fig. 4L); delthyrial cover not observed; sulcus poorly defined, shallow, rather narrow (sulcus width to shell width ranges 0.37–0.47), originating in posterior one-third of the valve length. Dorsal valve elliptical to subpentagonal in outline, with the greatest convexity slightly posterior to mid-length, umbonal region inflated; widely parabolic in anterior view; fold absent or very weak near anterior margin of large shells, occasionally shallow median groove or median flattening may be developed.

Interior of ventral valve generally without dental plates, exceptionally short supports expressed in the development of small dental cavities, buried by secondary shell thickening, may be present (Fig. 7A); teeth massive and strong; muscle attachments deeply impressed in umbonal region.

Dorsal cardinalia with short, slightly ventrally divergent hinge flanges; cardinal plate thick, apically perforated, anteriorly with median incision; dental sockets wide; median septum absent, but low and wide myophragm is developed; crura anteriorly directed, distally bend abruptly posterodorsally giving rise to umbonal blades of the primary spiral lamellae; jugal branches arise at about 4–5 mm from the tip of the ventral beak of adult shells (slightly posterior to mid-length), extend ventro-medially and unite forming rather massive, tuberculate or spinose (observed in the serial sections), U-shaped jugal arch; jugal stem projects postero-ventrally reaching a position close to the crural ends, distally bifurcating giving rise to a pair of arms of the jugum and then further extended as accessory lamellae intercoiled adjacent to the primary lamellae up to the tips of the spiral cones; accessory lamellae narrower and more delicate than the primary ones; spiral cones laterally directed, usually with 6–7 evolutions.

Shell much thickened, especially in posterior regions.

Shell surface smooth except for rare growth lamellae which in large specimens are usually more crowded near anterior margin.

Occurrence. As for the type species.

CONCLUSIONS

Numerous specimens of smooth athyridide brachiopods with brachidium with double spiralia from the upper part of the Yilan Formation (early Emsian) of Guangxi Province, southern China, were assigned to a new genus and species, *Sinathyris crassa*. This is the first record of an athyridid with double spiralia from China. The serial sections of *S. crassa* proved that the accessory lamellae of double spiralia arise by distal bifurcation of the jugal stem. This is in contrast to members of the subfamily Helenathyridinae, a group of Devonian athyridids with double spiralia, in which the accessory lamellae developed directly from the jugal branches. These differences suggest that the double spiralium in *S. crassa* might have evolved independently from the analogous structure in the helenathyridins. The phylogenetic analyses indicate that *Sinathyris* is a member of subfamily Didymothyridinae.

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DATA ARCHIVING STATEMENT

Data for this study are available in the Dryad Digital Repository at http://dx.doi.org/10.5061/dryad.7vm65

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